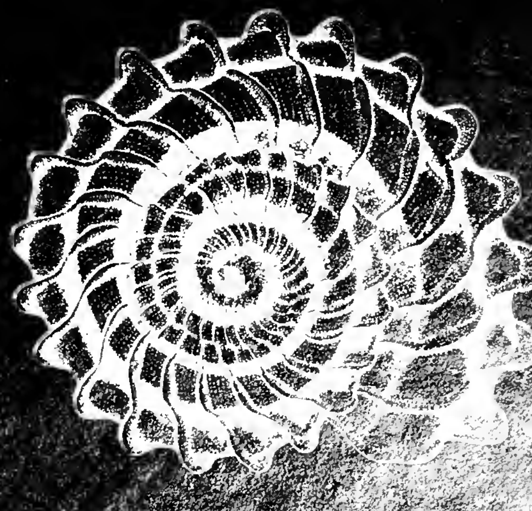
ENDODONTOID LAND SNAILS FROM PACIFIC ISLANDS

(Mollusca: Pulmonata: Sigmurethra)

Part I

Family Endodontidae

Alan Solem



Field Museum of Natural History
Chicago, Illinois

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Alan Solem

Curator of Invertebrates
Field Museum of Natural History

With the technical assistance of
Barbara K. Solem

Field Museum of Natural History
Chicago, Illinois

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INTRODUCTION

The small, radially ribbed, usually flammulated pulmonate land snails that dominate, in terms of species numbers, the faunas of southern temperate regions traditionally have been lumped into a single family unit, the Endodontidae. Several family units are involved and many genera cannot yet be assigned to a particular family. In discussing various genera and structures, I have found it convenient to use several terms in a restricted fashion. These are:

charopid – member of the family Charopidae
charopinine – structure agreeing with the typical Charopidae pattern
endodontid – member of the family Endodontidae
endodontinine – structure agreeing with the typical Endodontidae pattern
endodontoid – having the general aspect of several families
punctid – member of the family Punctidae
punctinine – structure agreeing with the typical Punctidae pattern

Other terms either conform to standard malacological usage or are defined in the text.

This is the first of two monographs on the endodontoid land snails of Polynesia, Micronesia, and Fiji. It reviews the larger and older of the family groups, the Endodontidae. A second contribution[1] will cover the specifically less diverse and more recent Punctidae and Charopidae, together with detailed zoogeographic and faunistic analyses. Together these papers are based on more than 26,000 specimens and review 285 species-level taxa in 45 genera. Most of these were previously unreported, with 84 per cent of the genera and 54 per cent of the species described as new (table I).

This survey, started in 1960, is incomplete, since about 290 unnamed Hawaiian species-level taxa are preserved in the collections of the Bernice P. Bishop Museum (table II). The latter represent a monophyletic radiation involving limited supraspecific, but extensive specific level differentiation. Analysis of the approximately 58,000 Hawaiian specimens would have required far more time than was available. Hence consideration of the Hawaiian fauna has been restricted to a brief synopsis of the 30 previously named taxa, one new description, and sufficient dissections to place these groups within the Endodontidae.

In addition, collecting efforts on the Pacific Islands are far from being comprehensive. A few hours in 1970 on Thithia and Tuvutha Islands in the Lau Archipelago of Fiji resulted in finding two new taxa, *Priceconcha tuvuthaensis* and *Thaumatodon spirrhymatum* (Solem, 1973d), that are only cross-referenced in this study. Many islands in Lau have not been collected on at all, the higher elevations of the Society and Marquesan Islands have been inadequately sampled, and relatively fragmentary collections have been made on some islands of the Palau Group. I suspect that these 573 species-level taxa of endodontoid snails may represent only 75 per cent of the fauna extant in 1900. Unfortunately, a high percentage is now extinct through habitat alterations by man, predation by accidentally introduced ants, and possibly because of competition from introduced snails.

These figures show that the endodontoid snails are the most diverse land snail group found in the Pacific, substantially surpassing in numbers the fabelled Hawaiian Amastridae (294 species and subspecies, Zimmerman, 1948, pp. 99-100) and mainly Hawaiian Achatinellidae (ca. 200 species, Cooke and Kondo, 1960).

One other family-level grouping has an equally wide distribution and shows high generic level diversity. The zonitoid families Helicarionidae and Zonitidae (H. B. Baker, 1938b, 1940, 1941) total 32 genera with 266 Pacific Island species (H. B. Baker, 1941, p. 347). Compared with the 45 genera and 573 species level endodontoid taxa, this is proportionately greater generic differentiation and lower specific differentiation. For the zonitoid taxa an average of 8.31 species/genus compares with an average of 13.2 species/genus in the endodontoid families. This undoubtedly reflects the fact that the zonitoids are much more recent colonizers of the Pacific and represent a greater number of colonizing stocks. There has been less time for local differentiation. Seemingly there has been a greater niche balance in terms of colonizing stocks and hence less opportunity for diversification.

Other families that are significant in terms of species numbers on Pacific Islands include the Succineidae, Pupillidae (*sensu lato*), Diplommatinidae, Helicinidae, and Assimineidae. Probably each has about 150 species on the Pacific Islands. Generally, each family shows only one or two major centers of specific diversity: the Succineidae in Tahiti and Hawaii,

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[1] Hereafter referred to as Part II.

TABLE I. - PACIFIC ISLAND ENDODONTOID TAXA

	Genera		Species		Subspecies	
	Known	New	Known	New	Known	New
Endodontidae	5	19	81	88	2	14
Punctidae & Charopidae	2	19	45	43[1]	-	7
Subtotals	7	38	126	131	2	21
TOTALS	45		257		23	

[1]. Three species listed as new but not described are omitted.

Pupillidae in Hawaii, Assimineidae in the Mariana and Caroline Islands, Diplommatinidae in Micronesia and Fiji.

The great diversity found in the endodontoid taxa has not been recognized previously because the group has been virtually ignored during this century. Some 76 per cent of the described species were named prior to 1890 (table III). Outside of a few radular sketches published in the 1870's to 1890's, and partial dissections of three *Endodonta* from Hawaii (Cooke, 1928), no anatomical information has been recorded in the literature. The reasons for this are simple. The species are very small (96.4 per cent are less than 7 mm. in maximum size), secretive inhabitants of litter or may be found on moss-covered tree trunks in dense and undisturbed forests. They are found only by the most skilled collectors. Endodontoid snails are of no known economic importance and are sparsely represented in even the largest museum collections of the world.

My own interest in these taxa was sparked by the recovery of Miocene to Pleistocene fossil endodontoid snails from the deep-core drillings on Bikini, Eniwetok, and Funafuti Atolls (Ladd, 1958, 1968). I had worked on endodontoid species from the New Hebrides (Solem, 1959a) and examined the limited Polynesian material in mainland American museums. Seeing the fossil species suggested that a revision of the living endodontoid taxa from Polynesia and Micronesia might provide insights into the historical zoogeography of that region, present a time dimension to the colonization of the islands, and permit some observations concerning the rate of evolution in these island populations. I was led to believe that perhaps 100 living species might be involved in such a survey. Exposure to the vast collection resources of the Bernice P. Bishop Museum soon wrought drastic revisions in this program. The fossils barely show species or species group differentiation from living taxa, add only one major modification to a current geographic range, and provide no significant data concerning possible evolutionary rates (pp. 116-118). The huge quantity of material, potentially 84,000 specimens of 573 species level taxa, soon led to quite a different focus than simple species sorting and classification formation.

Although the endodontoid snails do not show determinate growth upon reaching sexual maturity, there are distinct patterns of growth change (pp. 11-12) that enable separation of adult from juvenile examples. The many large sets and essentially synchronic samples in the Bishop Museum suggested that detailed meristic analysis of populational variation should replace the conchologically traditional, non-statistical means of studying variability and in delineating species. Most endodontoid snails have a highly complex surface sculpture, show moderate shape variation, and have a few to many complex barriers within the aperture of the shell. Thus a wealth of characters was available for study. Most of this basic species level analysis was done during the period in which phenetics enjoyed its youthful flush of enthusiasm.

Since the previous classification of the Pacific Island endodontoid snails dated from a checklist (Pilsbry, 1893a) that used such dichotomies as "teeth-no teeth" plus "rounded shell-angled shell" for generic placement, the temptation to experiment with phyletic clustering techniques could not be resisted. By this stage of the study (mid-1960's), dissections had indicated that at least two major groups were represented in the fauna. These groups differed strikingly in their anatomy, but showed equally striking similarities in shell appearance. Several shells

TABLE II. - HAWAIIAN ENDODONTOIDS

Genus	Previously described	In Bishop Museum Collection		
		Number of species	Number of subspecies	Number of catalogued sets
<u>Endodonta</u>	9	77-79	55	2,124
<u>Cookeconcha</u>	17	105	55	2,564
<u>Nesophila</u>	4	12	9	339
<u>Punctum</u>	1	5-9	-	170
TOTALS	31	199-205	119	5,197

from widely separated archipelagoes were virtually identical in overall appearance. Even microscopic shell features appeared the same under 32-96× magnification, but the animals had totally different anatomical structures. The computer programs available to me at that time did not allow use of characters for which information was lacking in regard to certain taxa. Hence only conchological variables and no anatomical data could be utilized. Beautiful clusters of conchological convergences from disparate areas (figs. 59-61) were produced by these phenetic attempts. While this numerical dabbling did not produce a usable classification and added few phyletic insights, it did serve the extremely important functions of greatly increasing the number of shell characters observed, requiring me to systematically record the variational state of each character for each species, to focus on the patterns of change for various characters, and to start systematically reviewing the effects of particular character variations on the standard measurable shell features.

A more important feedback came in correlating shell variations as analyzed and recorded during this phase of the study with anatomical variations discovered during the dissections. Initial focus in the dissecting was to sort out major groups, then to study patterns probably indicative of generic clusters, and finally to study the variations shown within a genus, particularly in regard to sympatric congeners. A second and much more critical phase of the anatomical survey involved detailed analysis of the variational

TABLE III. - DATES OF SPECIES DESCRIPTIONS

	Endodontidae		Charopidae
	Hawaiian	non-Hawaiian	
1820's	2		
1830's		1	
1840's	4	5	2
1850's	3	3	
1860's	5	8	2
1870's	1	16	14
1880's	3	18	6
1890's	3		6
1900's	8		5
1910's			
1920's			1
1930's	1		4
1940's			
1950's		2	3
1960's			2
TOTALS	30	53	45

patterns within organ complexes, and finally attempts to determine probable directions of character change in the various systematic units.

Perhaps a majority of the species was extinct before this project started, and only 100 of 283 taxa could be dissected. With the high degree of conchological convergence noted above, a major problem involved how to classify species whose anatomy could not be studied. Fortunately, the advent of scanning electron microscopy provided a tool that enabled finding highly obscure but stable shell features correlating with the major anatomical types (pp. 30-37, 63-65).

Considerable time has been spent in dissecting endodontoid taxa from Norfolk Island, Lord Howe Island, New Caledonia, New Zealand, South America, and South Africa in an attempt to determine: 1) the names that should be applied to the Pacific Island family units; 2) how closely the Charopidae are related to the Endodontidae and if any transitional species are still extant; and 3) what are the basic anatomical patterns of variation in the Charopidae. While the name problem is settled, at the present time the other two problems are still unresolved.

Phyletic interpretations are received today with greater enthusiasm when outgroup comparisons are made with more primitive and presumably ancestral taxa. The problems of circularity in reasoning are very great when work is limited to discussion of trends within the group or groups being reviewed. Attempts to pinpoint taxa that might be ancestral to the Endodontidae have met with a total lack of success to date. Dissections of Succineidae, which many authors recently have stated to be a primitive land snail, suggested instead (Solem, 1969b, In press B) that this is an advanced group belonging to the same suborder as the endodontoid taxa, while dissections of several orthurethran and mesurethran taxa demonstrated that these have nothing in common with the anatomical patterns of the endodontoid taxa and cannot be considered ancestral to them (Solem, *unpublished*). At present I can only state that the Endodontidae have the greatest number of primitive features found in any sigmurethran land snail. I cannot point to any land snail family as being a possible ancestor to the Endodontidae (pp. 102-104). Hence meaningful outgroup comparisons have not been possible.

What began as a zoogeographically oriented faunistic survey changed drastically in orientation. Analysis of the patterns in both conchological and anatomical variations, scanning electron microscope studies of shell and radular structure (Solem, 1972a, 1972c, 1973a, 1973b), revision of the family-level classification for endodontoid snails (pp. 105-107), and most of the new ideas concerning slug evolution plus a revised ordinal-level classification of the stylommatophoran pulmonates (Solem, In press B) have developed from these endodontoid revisions.

The above discussion outlines the goals and evolutionary chronology of this study. Obviously many aspects pursued involved use of many more characters than are needed to enable keying out species or characterizing genera. Several of these objectives are discussed in subsequent papers or in the second monograph. But documentation of these conclusions requires that the basic data be readily available. Computer programs are far more sophisticated than those used in the earlier stages of this study and, in particular, factor analysis could be expected to aid the interpretation of this data. Neither computer time nor personal computer competence is available for pursuing these aspects.

Equally important is the matter of species limits in island organisms. For those accustomed to working with continental faunas, the bewildering pattern of diversity and the, at times, minute conchological differences between species come as a surprise. Fewer than 15 per cent of the previously described species could be identified with one of the delineated population complexes without direct comparison with type or syntype specimens. Descriptions and illustrations that focused on differentiating only a few among many species were totally inadequate when the percentage of total taxa available for study increased. From many islands, such as Tahiti and Moorea, only partial and preliminary single, high altitude collecting transects have been made up to the present time. Sampling of additional populations can be expected to yield not only undescribed taxa, but populations that will cause revision in some of the species concepts outlined below, and add much additional data on microgeographic variation. Detailed descriptions and illustrations will greatly aid work on future collections.

Finally, a good proportion of the material reported was collected from reasonably restricted stations that are localized with as much precision as the lack of man-made markers and inadequate maps permitted. It will be possible, except where extinction has taken place, to sample the same populations on an allochronic basis. By recording the available data on variation in local populations, as well as summary data on species units, suggestions both as to the locations for new field collecting and the interpretation of the results from such field collections will be facilitated.

Hence the diagnoses, descriptions, and discussions of taxa include far more data than is necessary to separate related species at our current level of species recognition and understanding of species limits. Whenever a character or character complex was found to show systematically significant variation between any pair of species units, the state of this character was recorded for each species in the family. For obvious reasons, this has been limited to optically visible conchological characters and such anatomical data as was available for particular species. All data on which statements concerning variational trends and character correlations are made thus have been recorded in the systematic section and are readily available for others to use in further analyses.

Particular emphasis in this volume is laid in analyzing the variations in shell features and their correlations with size and shape variations. Equivalent patterns are found in the Charopidae, subject to alterations correlated with shifts in ecology. Discussion of the basic adaptive value of these variations is deferred until the second volume to permit inclusion of the full data.

Following a brief summary of previous reports, material studied, and methods of analysis, the patterns of morphological and ecological variation are reviewed. Discussions of family level classification, probable phylogeny and generic classification precede geographic keys and the main systematic review. A short, preliminary zoogeographic analysis concludes this report.

ACKNOWLEDGEMENTS

Success of this project has been possible only because of work done previously by the late C. Montague Cooke, Jr. and Yoshio Kondo. For 46 years (Kondo and Clench, 1952) Dr. Cooke assiduously amassed unparalleled reference collections of Pacific Island non-marine mollusks at the Bernice P. Bishop Museum, Honolulu. His own large collections from the Hawaiian Islands resulted from 10 personal expeditions. Much additional material resulted from the activities of colleagues and amateurs inspired by his example. During the 1930's, Cooke was responsible for three expeditions to Polynesia (Mangarevan Expedition, 1934), Micronesia (Micronesian Expedition, 1935-1936), and Fiji (Henry G. Lapham Expedition, 1938). These trips provided the bulk of the material upon which this report is based. The wealth of preserved soft parts and shells resulting from these efforts stands as a permanent monument.

Cooke never rushed into print with fragmentary discoveries. His list of publications is comparatively short. From 1939 to 1941 he spent considerable time sorting the endodontid material into species, making a few preliminary notes, and overseeing preparation of illustrations by Yoshio Kondo. For a limited number of species, he drew up preliminary descriptions of shell features. Cooke preferred to let a project sit for several years and thus benefit from more mature reflection. He also was more interested in the Tornatellinidae. These factors combined to shelve the endodontid work in 1941. The magnificent revision of the Achatinellidae and the Tornatellinidae published by Cooke and Kondo (1960) resulted from Cooke's endeavors between 1941 and his death in 1948.

Without Cooke's efforts, this material would not have been collected. Without his years of museum work, it would not have been available for study. Without his preliminary sorting and notes, my task would have required at least two additional years.

Cooke's preliminary work had been restricted to shell features. Descriptions had been written only for Henderson Island, Mangareva, and the Tuamotu species. In reviewing material from these areas, I agreed with Cooke's species limits in most cases, made minor changes in others, and completely altered some species. While I take full responsibility for errors, I wish to recognize Cooke's great contributions not only through the taxa named after him, but by having the species he wrote up in a preliminary fashion cited subsequently as described by "Cooke and Solem," or "Solem and Cooke" in cases where I altered species limits. All published diagnoses and descriptions were prepared by myself, but where so indicated, species authorship should be cited as a joint responsibility.

Yoshio Kondo began collecting for Dr. Cooke during the Mangarevan Expedition while he was a crew member on the *Islander*. After the voyage he served as assistant, then as collaborator and finally became successor to Dr. Cooke. Kondo prepared illustrations for most of the Mangareva, Marquesas, Society, and Rapa Island species from 1939-1941. It was at his urging and encouragement that this monograph was started. During our work in Honolulu from August through December 1961, Dr. Kondo provided every facility and aid possible. Through his cooperation it was possible to borrow both soft parts and shell material for more detailed analysis and to publish his prepared illustrations. Figures prepared by Yoshio Kondo are indicated in the figure explanations by "YK." I am deeply grateful for his help and encouragement during all stages of this project.

The aid of the Bernice P. Bishop Museum in providing working space, allowing study of materials, and permitting publication of the many shell drawings has been crucial. I am greatly in their debt.

Establishing the identity of previously described species and reviewing the characteristics of extralimital species referred to Pacific Island taxa occupied an inordinate amount of time and effort. For assistance in locating material and/or loan of specimens, I am indebted to the following curators and institutions, which are listed in chronological order of visits and/or borrowings: Dr. A. W. B. Powell, Auckland Institute and Museum, Auckland; Dr. R. K. Dell, National Museum of Natural History, Wellington; Dr. Charles Fleming, New Zealand Geological Survey, Lower Hutt; Dr. D. F. McMichael, formerly of the Australian Museum, Sydney; Mrs. Hope Black and Dr. Brian Smith, National Museum of Victoria, Melbourne; the late Charles Gabriel, Melbourne; the late Bernard C. Cotton, South Australian Museum, Adelaide; Dr. A. Zilch, Natur-Museum Senckenberg, Frankfurt-a.-M.; Dr. E. Fischer-Piette, Muséum National d'Histoire Naturelle, Paris; Dr. A. Magne, Muséum d'Histoire Naturelle, Bordeaux; Dona Emilia García San Nicolás, Museo Nacional de Ciencias Naturales, Madrid; Dr. E. Tortonese, Museo Civico di Storia Naturale, Genoa; Dr. Eugene Binder, Musée de la Ville, Geneva; Dr. Lothar Forcart, Naturhistorisches Museum, Basel; Dr. H. Burla and Dr. H. Jungen, Zoologisches Museum der Universität, Zurich; Dr. J. Knudsen, Universitetets Zoologiske Museum, Copenhagen; Dr. Bengt Hubendick, Naturhistoriska Museet, Göteborg; Dr. Charlotte Holmquist, Naturhistoriska Riksmuseet, Stockholm; Mrs. W. S. S. van Benthem Jutting van der Feen, Dr. S. van der Spoel, Dr. H. Coomans, Zoologisch Museum, Amsterdam; Dr. C. O. van Regteren Altena, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. W. Adam, Institut Royal des Sciences Naturelles de Belgique, Brussels; Mr. Norman Tebble, Mr. John Peake, and Mr. S. Peter Dance, British Museum (Natural History), London; Dr. William J. Clench, Museum of Comparative Zoology, Harvard; Dr. W. K. Emerson, American Museum of Natural History, New York; Dr. R. Tucker Abbott and Dr. Robert Robertson, Academy of Natural Sciences, Philadelphia; Dr. Harald A. Rehder and Dr. Joseph Rosewater, National Museum of Natural History, Washington; Dr. Juan Jose Parodiz, Carnegie Museum, Pittsburgh; Dr. Vincent Conde, Redpath Museum, Montreal; Mr. Allyn Smith, California Academy of Sciences, San Francisco; Dr. A. Rodger Waterston, Royal Scottish Museum, Edinburgh; Mr. Colin Matheson, National Museum of Wales, Cardiff; and Dr. A. Myra Keen, Stanford University. While many of the institutions cited above do not have material listed in this particular report, their collections and materials have been indispensible to its completion.

For assistance during field work in Tahiti, Samoa, Fiji, New Caledonia, New Zealand, and Australia, I am indebted in particular to Mr. Laurie Price of Kaitaia, New Zealand, who collected on Rarotonga, Samoa, Lord Howe Island, Norfolk Island, Lau Archipelago, Viti Levu, New Caledonia, New Hebrides, and Tonga in connection with this work; Dr. Pierre Cassiau, Papeete; Mr. L. Devambez, formerly of New Caledonia and Fiji; Mr. Michael Watt, Apia; Dr. A. W. B. Powell; and Dr. D. F. McMichael.

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PREVIOUS STUDIES

The only summary studies of Pacific Island endodontoid land snails are the check list and descriptions of Pease (1871a), the collection of illustrations and brief diagnoses assembled by Tryon (1887), and the critical checklist and revised classification presented by Pilsbry (1893-1895). Tryon's classification was highly artificial and conservative. Pilsbry's effort was peripheral to his focus on the morphology of helicoid taxa and phyletic revision of the higher land snails. His treatment of the endodontoid taxa obviously was hastily done, but contained several significant advances in classification. It has served as the basis from which the generic lists presented by Thiele (1931) and Zilch (1959-1960) were derived.

After 1900, only the descriptions of Pilsbry and Vanatta (1905, 1906), the nomenclatural catalog of *Libera* by Ponsonby (1910), an extremely significant anatomical survey of some Hawaiian species by Cooke (1928), and the reports on fossil endodontoid taxa by Ladd (1958, 1968), and Ladd et al. (1970) require special mention. Other reports are simple compilations of names in faunistic catalogues (Gude, 1913; Caum, 1928; Germain, 1932), scattered descriptions of one or two species in faunal reports (Clapp, 1923; Cockerell, 1933; I. Rensch, 1937; Dell, 1955; Solem, 1960), or reports on faunistic collections without descriptions (Cooke, 1934; Aubert de la Rue and Soyer, 1958).

The available knowledge is essentially pre-1900, with all the deficiencies for modern systematic research that this implies. Fortunately, two of the workers, Andrew Garrett and Albert Mousson, were far ahead of their time in terms of systematic concepts and recognizing the need for precise geographic documentation. Garrett was an American missionary stationed on a number of different South Pacific Islands from the 1860's until his death in 1887. At first he sent specimens to W. Harper Pease, a merchant in Hawaii, who described a total of 17 species (Pease, 1861, 1864, 1866, 1867, 1868, 1870, 1871a), unfortunately, often with scant regard for locality data (Garrett, 1881, p. 390). Later Garrett started to do his own describing, first in a pair of strictly descriptive papers (Garrett, 1872, 1874), then in faunistic surveys of Rurutu, Austral Islands (Garrett, 1879), the Cook Islands (Garrett, 1881), Society Islands (Garrett, 1884), Samoan Islands (Garrett, 1887b), Fiji (Garrett, 1887a), and the Marquesan Islands (Garrett, 1887c). Including eight species collected by Garrett but described by W. Harper Pease, Andrew Garrett was responsible for 40 of the 128 previously known taxa. Not only were his descriptions detailed and accurate to the limits of optical viewing, but his extensive field experience was reflected in his precise localization of species and many observations concerning the degree of sympatry or allopatry on the same island. Most zoologists ignored such data until well into this century. Garrett's data has been summarized below, but consultation of his papers remains mandatory for anybody attempting field work in the South Pacific. Garrett's views of speciation were quite modern and few of his conclusions based on field work have been modified by subsequent studies. He was located far from the museum centers of Europe and North America, so that inevitable errors in synonymy occured, but these do not lessen the substance of his contributions. The only major limitation that can be placed on his work concerns the apparent restriction of his collecting efforts to reasonably low elevations. High-altitude collections in the Marquesas by the members of the Bishop Museum "Pacific Entomological Survey" (Adamson, 1935, 1936), in the Society Islands by members of the Mangarevan Expedition from the B. P. Bishop Museum (Cooke, 1935, p. 51), and on Rarotonga by a Field Museum Expedition (Solem, 1972b) have discovered many large and conspicuous species unknown to Garrett and failed to find a high percentage of his species. This suggests quite strongly that his efforts were restricted to the lower forested areas, whose fauna is now extinct, and that he did not attempt to reach higher elevations in his collecting.

Albert Mousson never visited the South Seas. His material was obtained from the Hamburg trading firm Godeffroy, mostly as a result of the efforts by Eduard Graeffe. The eight species described by Mousson (1865, 1869, 1870, 1871, 1873) are carefully delineated, well illustrated and accompanied by detailed locality data. His faunal accounts of species from Fiji, the Ellice Island, Tonga, and Samoa are inferior to Garrett's only because field observations are lacking.

The faunal report on the Caroline Islands by Otto von Möllendorff (1900) and the paper on Guam species by J. Quadras and Möllendorff (1894) are quite competent, as are the many Philippine studies that included the description of one endodontid (Möllendorff, 1888). The 11 species named in these studies are almost equaled by the 10 described by C. F. Ancey (1889a, b, c, 1899, 1904). Most of these are from Hawaii, and are briefly mentioned below. The two

Libera from the Society Islands and the single species from Mangareva were recognizable from his descriptions. The summary of Hawaiian land snails by Ancey (1889d) formed the basis for the more familiar compilations of Baldwin (1893), Sykes (1900), and Caum (1928), although it is infrequently cited today. From a wide variety of sources and localities, L. Pfeiffer (1845, 1846a, b, 1850a, 1853a, 1856, 1858, 1859a, 1862) named nine species. Otherwise there are the scattered descriptions of Ferussac (1824, 1840), Anton (1839), Hombron and Jacquinot (1841), Gould (1844, 1846a), Mighels (1845), Reeve (1851-1854), Cox (1870), Semper (1874), Liardet (1876), Tapparone-Canefri (1883), Tryon (1887), Beddome (1889), Sykes (1896), E. A. Smith (1897), Pilsbry and Vanatta (1905, 1906), Clapp (1923), Cockerell (1933), Dell (1955), and Solem (1959b, 1960).

To summarize the above data, Table III indicates the dates of description for the species recognized as valid in this study. It is obvious that the major contribution occurred between 1860 and 1890, when 57 per cent of the species were named. This is the primary period of activity for Pease, Garrett, Mousson, and Ancey, who account for 52 per cent of the previously named species. Since 1910, only 10 per cent (13 species) have been named, and all of these are fossil or extralimital to the main area of study. As indicated above, essentially no faunistic collecting was done except by the Bishop Museum program from the time of Möllendorff to the start of this study.

Not only little faunal data accumulated, but there was practically no data recorded concerning the anatomy of endodontoid taxa from the Pacific Islands. Semper (1874, pp. 135-136, pl. 16, fig. 18) figured the central radular tooth of a Tahitian specimen identified as *Libera bursatella* and briefly discussed the cusp structure. W. G. Binney (1875, p. 248, pl. 21, fig. 6) illustrated several teeth and recorded the radular formula of the Rarotongan *Libera tumuloides* (Garrett) as 10-7-1-7-10. Subsequently, W. G. Binney (1885, pp. 88-89, pl. 2, figs. L-N) figured and briefly discussed the radulae of *Libera tumuloides* (Garrett), *Nesodiscus huaheinensis* (Pfeiffer) (formula 12-6-1-6-12), and *Mautodontha parvidens* (Pease) (formula 7-4-1-4-7) as "*Endodonta incerta* Mousson," a *nude name* under which this species has been widely distributed in older collections. Pilsbry (1893-1895, p. 23, pl. 9, fig. 34) illustrated the radular teeth of *Libera recedens* Garrett. No information concerning other anatomical features were recorded until the work of Cooke (1928) on three species of *Endodonta* from Oahu, Hawaiian Islands. Unfortunately, this excellent paper has been overlooked or misinterpreted by subsequent authors.

Considerable information has accumulated concerning the external anatomy and radular structure of Australian and New Zealand taxa, primarily through the efforts of Charles Hedley (1891, 1893a) and Henry Suter (1890, 1891a, b, 1892a, b, c, 1893a, b, c, d, 1894a, b, c, d, 1901, 1903, 1913). Recently Frank Climo (1969a, b, 1970, 1971a, b) has published several revisions of New Zealand taxa utilizing genital anatomy in addition to shell and radular features. His work presents a large quantity of useful data and important observations, but as outlined below (pp. 106-108), we have very different interpretations of character weighting and phylogeny.

Prior to this study a high percentage of the species was unknown, and virtually no anatomical investigations, no study of interpopulational variation, and only limited ecological information were available. As documented on pp. 118-119, classification was still based on convenient "either-or" pigeon holes. Hence not only has it been necessary to do much work that is already accomplished for better-known groups, but the hunt for criteria to use in species recognition and clustering has been quite time consuming. The lack of previous work also necessitates considerable preliminary discussions concerning the characters used and their validity as "key" criteria.

MATERIAL STUDIED

As summarized in Table IV, some 26,000 specimens were studied in detail. Perhaps an additional 6,000 specimens, mainly involving sets with mixed species and localities that originated from the W. Harper Pease collection, were examined quickly, but neither measured nor listed. Pease himself was careless in handling his collection, noting in a letter to a correspondent that his small daughter delighted in playing with shells in the cabinets (Alison Kay, pers. comm.). In addition, many years later during shipment of Pease's collection from England to Harvard University, apparently there was extensive mixing of sets when cabinets were tilted and handled. In subsequent years, these shells have been traded widely to other museums and amateur collectors. Virtually all traded Pease material that I examined contained more than one species, often living on different islands.

While for the non-Hawaiian Endodontidae, the material examined per species-level taxon averaged 120.3, for the Charopidae it was only 75.9 specimens/species-level taxon. It is difficult to decide exactly how much of this is caused by artifacts of collecting and how much results from a true difference in relative abundance. The charopid taxa include a number of species from Melanesia and Indonesia, areas in which there has been far less intensive land snail collecting activity. Charopids also include more species from islands such as Niue, Rotuma, and various of the Ellice Islands where collections were made by non-malacologists and hence lower quantities of materials obtained. These factors probably reduced the average number of specimens by about 10. On the other hand, in the outer Polynesian Islands the Endodontidae were perhaps the dominant ground stratum snail. Where still extant, they can be collected in quantity from limited areas. In contrast, the charopids from the big islands of Fiji and Samoa, for example, are far less abundant than many helicarionids and rarely have been collected in any quantity. On some of the Micronesian Islands apparently the charopids locally are as abundant as many of the Polynesian Endodontidae. Probably in the Melanesian-Fiji area the charopids are not abundant under any circumstances. Certainly the charopids with apertural barriers of Fiji, Tonga, Samoa, and neighboring islands could only be classified as rare. Punctids are a marginal group in the area of study.

TABLE IV. - SUMMARY OF MATERIAL STUDIED

Endodontidae	Species Level Taxa	Specimens Examined
Hawaiian	31	238
non-Hawaiian	154	18,530
Punctidae	2	7
Charopidae	96	7,288
TOTAL	283	26,063

Hence the differing material per species numbers reflect both differential abundance and bias in collecting. Table V summarizes the abundance data on a slightly more refined basis. The rarity aspect of some charopid taxa shows very clearly in the increased number of species known from 1-3 specimens and decreased 4-8 specimen grouping. Otherwise the percentage distributions are quite comparable. Data concerning species abundance on particular islands will be presented in the zoogeographic analysis accompanying Part II of this monograph.

With the exception of pre-1900 species that have not been collected subsequently, the listing of specimens examined is confined to adequately localized and measured materials. Throughout the text the following abbreviations indicate the repository of the specimens:

AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
BPBM	Bernice P. Bishop Museum, Honolulu
Brussels	Institut Royal des Sciences Naturelles de Belgique, Brussels
Cardiff	National Museum of Wales, Cardiff
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Harvard University
Paris	Muséum National d'Histoire Naturelle, Paris
RSM	Royal Scottish Museum, Edinburgh
SMF	Natur-Museum Senckenberg, Frankfurt
USNM	National Museum of Natural History, Washington
Zurich	Zoologisches Institut der Universität, Zurich

Most of the material studied was in the Bernice P. Bishop Museum. In addition to samples of Garrett's and Ancey's materials from the last century, Cooke had assiduously accumulated materials from various Pacific Islands. E. H. Bryan and Y. Kondo collected extensively on Guam, P. H. Buck from some of the Cook Islands, Cooke and Wray Harris in American Samoa, and Harry Ladd brought back highly significant collections from some of the Lau Archipelago in Fiji. But it was the three expeditions sponsored by Bishop Museum in the 1930's that were most

TABLE V. - FREQUENCY DISTRIBUTION OF SPECIMENS EXAMINED PER SPECIES LEVEL TAXON

	Number and Percent of Species		
	Endodontidae		Punctidae & Charopidae
Number of Specimens	Hawaiian	non-Hawaiian	
0	6	-	-
1-3	6	22(14.3%)	22(22.4%)
4-8	10	29(18.8%)	7(7.1%)
9-19	7	24(15.6%)	13(13.3%)
21-60	2	33(21.4%)	26(26.5%)
61-100	-	13(8.4%)	8(8.1%)
101-260	-	19(12.3%)	17(17.3%)
300-882	-	9(5.8%)	4(4.1%)
1,000-1,900	-	5(3.2%)	1(1.0%)
TOTALS	31	154	98

productive. The Mangarevan Expedition from April 15 through October 28 in 1934 (Cooke, 1935), the Micronesian Expedition from December 8, 1935 to June 10, 1936 (Gregory, 1936, p. 40), and the Henry G. Lapham Expedition to Fiji from June 27 through September 28, 1938 (Buck, 1939, pp. 29-30) provided 70 per cent of the material on which this monograph is based.

The intensity of collecting can be indicated by the statement of Cooke *in* Gregory (1936, p. 15) that 37,593 land snails were collected on Rapa and 30,695 on Mangareva during the Mangarevan Expedition. Much of the field work on Rapa was accomplished under abominable weather conditions (Zimmerman, 1938, pp. 3-4), and on only a portion of the 31-day stay was "full day" effort possible. The magnitude of these collections is awesome. The focus of malacological collecting was "On the trail of the Tornatellinidae" (Kondo and Clench, 1952, p. 17). The endodontoid snails were a very secondary consideration. Despite this the 4,078 Rapan endodontids are 10.8 per cent of the material collected, while the 2,274 endodontids from Mangareva are 7.4 per cent of the total shells.

Most of the material was collected within a four-year period. The same people, C. M. Cooke, Y. Kondo, and E. Zimmerman, gathered the bulk of these collections. The collectors, collecting techniques, and field procedures were the same, so that comparisons of abundance and local distribution between archipelagoes are possible.

Curatorial methods at the Bishop Museum differ from those used elsewhere and require some explanation. As is customary, new field collections from single stations are sorted into species. Whereas most museums would assign a different catalogue number to each set, i.e., all material of one species collected at one locality at one time, each lot of the Bishop Museum mollusks is sorted in several growth stages — adult, paraneanic, metaneanic, ananeanic, and embryo (see Pilsbry and Cooke, 1914-1916, pp. x, xi for stage definitions). Each stage is given a separate, but usually consecutive, catalogue number. Sometimes gerontic individuals, unusual color or shape variations are segregated under yet other numbers. Thus what would be given a single number in most other museums, may have as many as 10 different numbers in the Bishop Museum collection.

Soft parts are extracted from each shell by means of a water jet (Kondo and Clench, 1952, pp. 27-28) and material from one set is stored in tiny homeopathic vials. The latter are grouped into pint jars and shelved in numerical sequence. The dried shells are housed in small pill boxes, generally 1¼ inch in diameter, with up to 48 such pill boxes placed in a covered cardboard tray. The latter are stored in open stacks. Only the catalogue number and a very abbreviated locality are with the specimens. Continual reference to the catalogue and field note books is necessary to retrieve full locality and ecological information.

This is a highly efficient and effective system of housing and storing quantities of minute material, keeping dry and alcohol storage separate, and enabling age-class recognition of anatomical material. With species under the size of perhaps 5 mm. this system causes little difficulty. With larger shells, the limitations of space within individual pill boxes tend to produce bias in sorting. Invariably the gerontic and larger adult individuals are clustered separately from the adults that are closer to average in size. "Large" and "average" adults have separate catalogue numbers. Measurements of such species as *Nesodiscus fictus,* many *Endodonta, Libera bursatella bursatella,* and the larger *Gambiodonta* had to take this sorting bias into account.

In total some 80 per cent of the specimens cited are from the Bishop Museum collections. Perhaps half of the remaining is either from the Field Museum collections or was obtained by myself and Mr. Laurie Price of Kaitaia, New Zealand for this project. My own collecting has been limited to Tahiti, Viti Levu, Upolu, New Caledonia, New Zealand, and Australia, while Mr. Price, over a series of years, has made collections from Lord Howe Island, Norfolk Island, Rarotonga, Upolu, Savaii, several islands of Tonga, New Hebrides, Viti Levu, Lau Archipelago, New Caledonia, and several parts of Australia. These collections are housed in Field Museum. The Lau collections were received too late to be other than cross-referenced in this study. The non-Polynesian collections have provided extensive comparative material on which most of the higher classification decisions have been based. The rest of the material studied consists of type specimens, remnants of the Garrett, Mousson, and Ancey collections, plus an occasional previously unstudied field collection and the subfossil to fossil species recorded by Ladd (1958, 1968) and Aubert de la Rue and Soyer (1958).

METHODS OF ANALYSIS

Island taxa bring both advantages and disadvantages to evolutionary studies. Particularly wherever the rate of immigration and species turnover is low and the opportunity for *in situ* speciation is thus enhanced, the possibilities of detecting convergences in structure between taxa on different islands or island groups are relatively good. Continental areas have been subject to the repetitive ebb and flow of faunal migrations, particularly in regions subject to the effects of the Pleistocene glaciation. Faunas of these areas usually are composed of multiple introductions, while the more isolated islands may have virtually monophyletic adaptive radiations. As is discussed elsewhere (Solem, 1973e), the Pacific Island land snails give evidence of low migration and high local speciation rates.

Several situations were encountered where species from widely separated archipelagoes appeared virtually identical in many shell features. Deeper analysis of the structures and how they are formed enabled recognizing that these similarities were convergent, although phenetic clustering techniques grouped them together.

In several ways this study departs from the normal systematic criteria and methodology as currently applied to mollusks. Far more statistical analysis of variation is utilized; an attempt is made to specify the philosophy used in recognizing species; and discussion of variational trends within generic units focuses on departures from an "ideal generalized morphotype" of that unit. Explanation of these procedures is a necessary prelude.

VARIATION IN ADULT SHELLS

Few people have attempted to undertake statistical analysis of variation in shells of molluscan species that do not show determinate growth, such as usually is indicated by a reflected lip and/or denticles. It has been assumed that growth would continue throughout life and hence age factors would seriously bias or obscure any pattern to size or shape variation. In the zonitoids "...growth is usually persistent; that is, most species become sexually mature when comparatively small but continue to add whorls almost indefinitely" (H. B. Baker, 1938b, pp. 5-6). Thus Baker picked certain standard whorl counts and listed the size reached at these marker points to indicate size differences between species.

Early in this study it became evident that postembryonic shell growth in the endodontids consists of two phases. For the first few whorls there is continuous growth, but then an alteration in pattern occurs that affects several features. In most taxa these changes are highly correlated, begin abruptly, and could be easily identified even by new assistants after an hour or so of instruction. These changes involve the pattern of rib deposition, umbilical decoiling, lip callus formation, and body whorl descension. The ribs become more crowded and/or irregular in spacing, often are reduced to a point at which they cannot be counted, and the microsculpture essentially disappears. The umbilicus becomes noticeably wider for a period of growth, then the umbilical lip suddenly may reflect slightly in toward the center of the umbilicus. At the same time, the inner lip margin, particularly on the columellar wall, becomes greatly thickened, frequently with a thick callus, whereas in juvenile shells it is thin and sharp edged. The edge of the parietal callus may thicken and the apertural barriers become slightly wider at their anterior end. Finally, starting with the change in rib deposition, there is a tendency for the body whorl to descend more rapidly. These changes are obvious in most species. A notable exception involves those species whose growth pattern results in a small umbilicus, reduced sculpture, and thick apertural callus at all stages. In these species the juvenile growth is virtually the same as adult growth. Not every species shows all of the changes cited above and some alterations may occur before others. Nevertheless, in only 1-2 per cent of the specimens is a judgment decision needed concerning whether a specimen is showing juvenile or adult growth. The adult growth may occupy as much as one-quarter of a whorl, very rarely three-eighths of a whorl. There are considerable differences as to when it starts. Some individuals may start "adult" growth more than three-quarters of a whorl earlier than others.

Such a change in growth pattern generally is correlated in animals with the onset of reproductive activity. Until that point, energy is channeled into increasing the size of the individual. Afterwards it is channeled into producing the next generation. Because the Bishop Museum mollusk collection is stored with the animals removed from the shell, it was not possible to study the timing link between reproductive maturity and these growth changes by dissecting individuals whose shell characters had been recorded. The only shell-associated endodontids available to me in quantity were *Thaumatodon hystricelloides* from

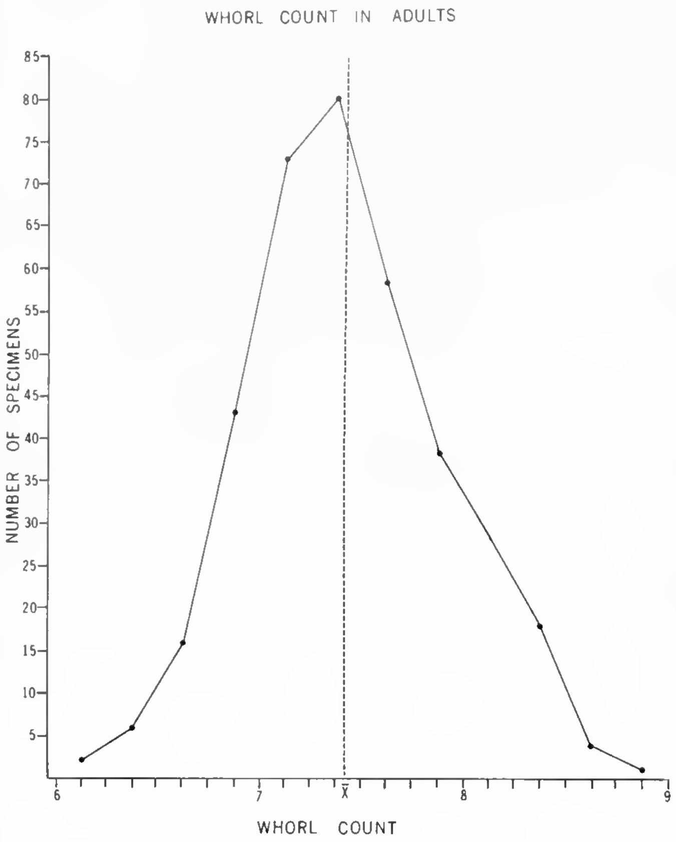


FIG. 1. Frequency distribution of whorl counts in adult *Libera fratercula* from quantitative samples.

Western Samoa, a species that shows very few adult changes, and *Libera fratercula* from Rarotonga, in which the formation of a brood chamber in the shell after reaching reproductive maturity is yet another modification.

Shells showing a "juvenile" pattern of growth can be segregated from those that have a presumed "adult" growth pattern. The significant question in terms of analysis is what distribution of meristic features is shown by the "adult" specimens. Data from a quantitative sampling of live *Libera fratercula* from Rarotonga have been summarized by Solem (1969a). In the present paper data are given on grouped variation in all live adults. Of some 623 living snails, 219 juveniles and 391 adults could be measured. The others showed repaired breaks in the shell or were otherwise unsuitable for analysis. Figures 1-4 graph the variation in whorl count, height, H/D ratio, and shell diameter, respectively. Except for the diameter, these agree with Quetelet's principle in distribution of the size classes. The diameter is affected by the fact that after the start of reproductive activity in this species, the snail grows and gradually narrows the umbilical opening to form a brood chamber. During this growth the shell diameter often remains stable. Hence the skewed nature of the diameter curve. The whorl count is symmetrical, but the height curve is skewed positively, reflecting the continued growth during adulthood to narrow the umbilical opening.

Smaller samples of other species show the same pattern, that of a normal distribution with at most a slight positive skewing, particularly in regard to rib counts (p. 42). I thus assume that measurements of adult shells will show either a "normal" distribution or slight positive skewing and hence can be compared through standard statistical analysis. The absence of determinate growth does not seem to have affected the basic normal distribution of adult variation in measurable and continuously variable shell characters, thus interpretation of variation is based heavily on statistical data concerning adult variation.

Nature of quantitative data presented

Basic quantitative data are presented in two formats. First, there is a summary of variation in size, shape, and apertural dentition for each species of that cluster. These tables are headed "Range of variation in ————." The second format records adult size and shape variation within either specific local populations (where such refinement of collecting data is available) or particular museum sets (either single sets or material originating from the same collection) in the case of specimens dating from the late 1800's. These tables are captioned "Local variation in ————." Unless stated otherwise in the discussion of a particular

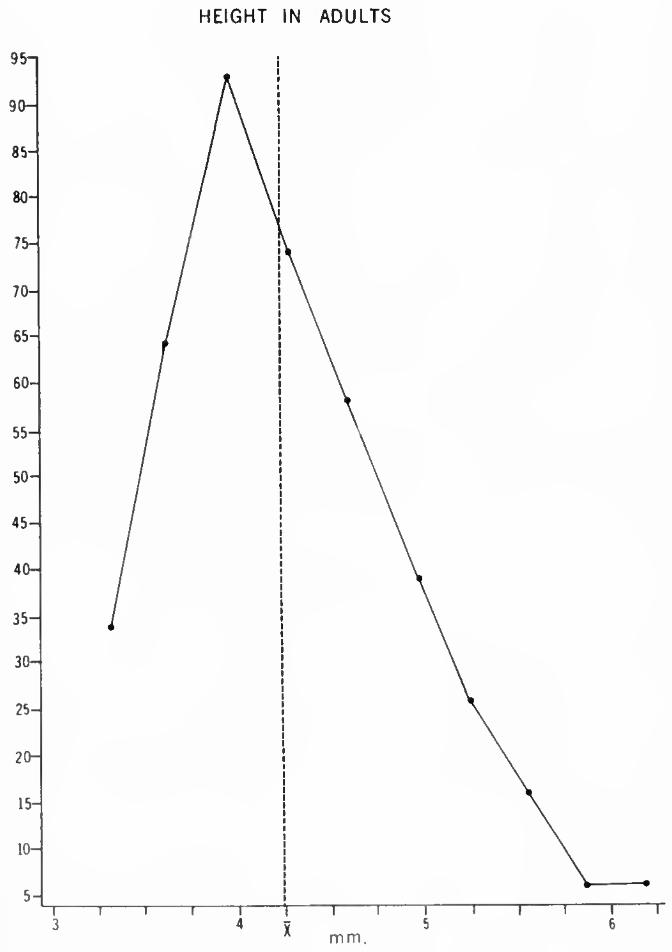


FIG. 2. Frequency distribution of shell height in adult *Libera fratercula* from quantitative samples.

species or set, all measurements were made only on adult and gerontic individuals.

In the tables summarizing range of variation, certain items require explanation. The number of specimens examined does not refer to the number of measured adults, but rather to the total number of specimens, both adult and juvenile, available for this study. For the ribs, height, diameter, Height/Diameter ratio (hereafter H/D ratio), and Diameter/Umbilicus ratio (hereafter D/U ratio), the first figure is the simple arithmetic mean of all measured adults. This is followed in parenthesis by the range. For the whorl counts, the cited range omits + and – signs. Where species have been collected again in recent years, these measurements summarize data from many snail generations apart. Under these circumstances, calculation of variance would serve no useful purpose.

Definitions of the apertural barriers are given elsewhere (p. 53). In the summary tables, Pr means parietal, C columellar, and P palatal. In each case, the numbers before the + sign refer to major barriers, the numbers following to minor traces. Where size reduction is involved, recognition of this difference involves considerable subjectivity. Where such arbitrary divisions were made, they are discussed in the text. Variation in barrier numbers is indicated in two ways. Two numbers connected by a dash (i.e., 3-4) indicate that at least one-third of the individuals have the less frequent state. If one of the numbers is underlined (i.e., 3-4), this means that the underlined number is found in less than one-third of the individuals examined. Usually it means a rare to infrequent character state. Occasionally, a number such as 2-3-4 + 4-6 may be seen. This is translated as usually 3 major barriers, rarely 2 or 4; normally with six accessory traces, rarely only four.

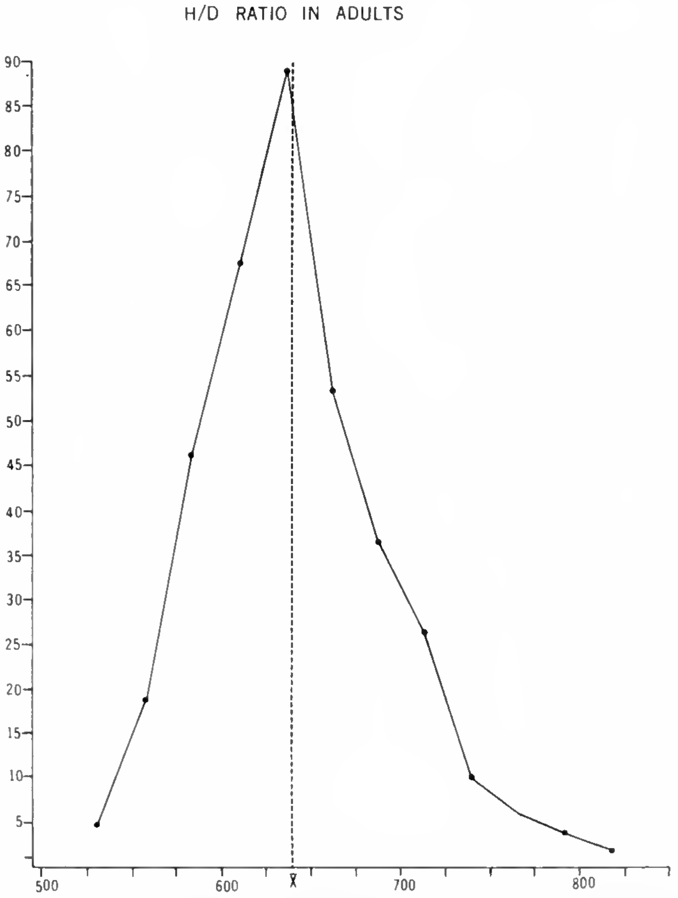


FIG. 3. Frequency distribution of Height/Diameter ratio in adult *Libera fratercula* from quantitative samples.

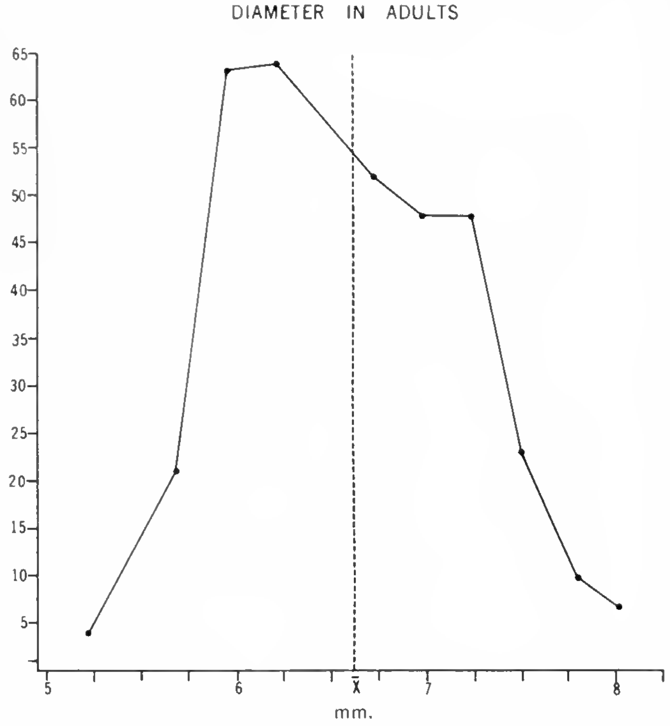


FIG. 4. Frequency distribution of shell diameter in adult *Libera fratercula* from quantitative samples.

In the tables documenting variation within local populations or single museum sets, the number of specimens refers to those actually measured. For the whorl counts, only the mean and range is given, since the measuring error is relatively large (p. 15). For the other parameters, mean, standard error of the mean, and range are given in that sequence, for example – 4.32 ± 0.036 (3.97-4.46).

Sample bias

The material in the Bishop Museum collected by Cooke and Kondo, plus the specimens in Field Museum of Natural History collected by Solem and Price, provide samples undistorted by subsequent museum activities. In the case of specimens from the Garrett and Mousson collections, we are dealing with small remnants of initially large sets. Specimens were traded in driblets of two or three to other collectors in exchange for species new to the trader. Those samples remaining in the Mousson and Garrett material are size biased. I have shown elsewhere (Solem, 1966b, p. 16) that such trading often will result in elimination of smaller shells from the sample, thus increasing the mean size significantly. This was especially noticeable in several species of *Libera* during this study, but even in the case of the 3-5 mm. endodontids, trading seems to have resulted in size bias. Hence only very cautious conclusions have been drawn from comparison of samples collected during the 1800's with material collected during the 1930's.

A seldom appreciated collecting phenomenon involves unconscious field bias towards selecting larger or "adult" specimens and neglecting the smaller, possibly juvenile individuals. This has been documented by H. B. Baker (1962b, p. 22) for North American *Allogona* and Puerto Rican pomatiasids. I have experienced this personally in relation to Panamanian *Mexcyclotus* and Samoan *Ostodes*. It is seen in this study with sets of *Libera bursatella orofenensis*. This difficulty is greater in those forms that do not have a cessation of growth that is marked by reflected lip formation at "adulthood." A strong bias towards gerontic and adult shells with a distinct neglect of subadult and juvenile specimens is quite possible, particularly when secondary interest is attached to the group, as in collection of snails by botanists or herpetologists.

Although they were not collected on a randomized or quantitative basis, material accumulated during the several Bishop Museum expeditions seems to have avoided such a bias. Most sets contain a broad mixture of age groups. I could detect very little evidence of selection for adults in the collecting process, and then only in species taken by non-malacologists. The collections were not quantitative samples, however, and only a few sets were large enough to infer data on population structure. The reason for the probable lack of sample bias stems from the purpose of the trips. The collectors were primarily concerned with obtaining members of another family, the Tornatellinidae (Kondo and Clench, 1952, p. 17). Even in this group, they were attempting to gather *all* specimens seen, rather than to take a "good sample" of the populations. Since 1) the small endodontids previously were essentially unknown; 2) they are very difficult to distinguish without use of a microscope; and 3) no particular emphasis was placed on the family by the collectors, I am convinced that there is minimal bias in the material.

Measurement reliability

All measurements of the shells were made by me under a Leitz stereoscopic dissecting microscope, using an 8× ocular, 1×, 2× or 4× objectives and an ocular micrometer. The micrometer was calibrated with a stage micrometer at several different times during this study. No significant differences in the calibration readings were noted. Measurements were taken to the nearest 0.5 micrometer unit. For the different objectives, one micrometer unit equals: 0.131 mm. with the 1× objective; 0.0658 mm. with the 2× objective; and 0.0329 mm. with the 4× objective. Most specimens were measured using the 2× objective. Sets with most or all specimens under 2.75 mm. in diameter were measured with the 4× objective and sets with most specimens over 5.00 mm. in diameter were measured with the 1× objective.

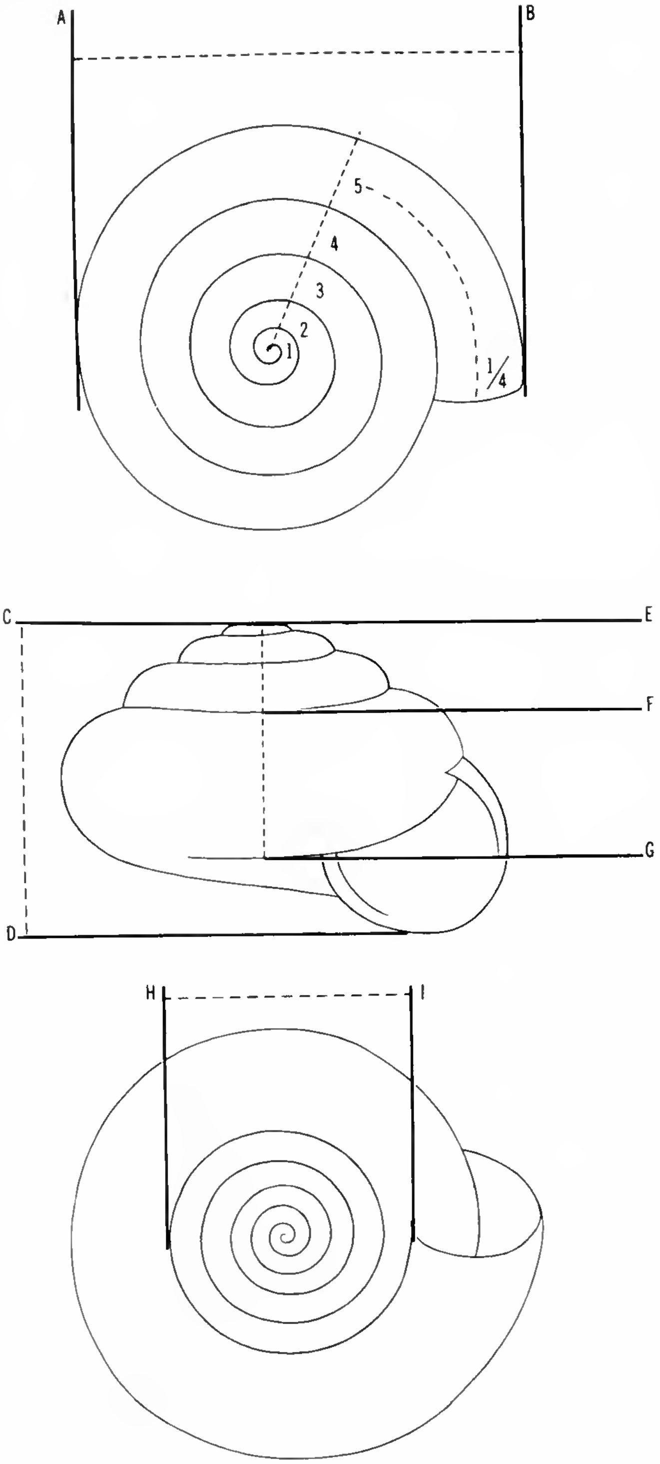


Fig. 5. Method of measuring specimens. **A-B**, shell diameter; **C-D**, shell height; **E-F**, spire protrusion; **F-G**, body whorl width; **H-I**, umbilical width.

Accuracy of measurement was tested by remeasuring individuals in several small sets five times over a four-year period. No reference was made to previous measurements before or during each trial. It was possible to compare specimen with specimen rather than having to depend on means, since there was a wide size range within these sets. Reproducibility of the measurements varied with the parameter. Basically standard measurements were used and taken as indicated in Figure 5. Greatest accuracy was obtained in measuring the diameter, least in making the whorl count. The diameter rarely (less than 5 per cent) varied more than 0.5 units in a measurement of 40-50 units or 1 unit in 80-90, an accuracy of 1.0-1.25 per cent. The more subjective height measurement showed a greater range of from 1 unit in 35-50 to 1.5 units in 65-70–an accuracy of 2-2.9 per cent with the heights measured in fewer units being less accurately recorded than those in larger numbers. Determination of umbilical width varied inversely with the size of the umbilicus–the wider the umbilicus, the more accurate the measurement. For very narrow umbilici, those whose D/U ratio was more than 7, but less than 10, error was in the range of 8-12 per cent. For those with tiny umbilici, D/U ratio 10-30, errors of 25-50 per cent were present, since often only one or two units were measured with an error of 0.5 units. The wider umbilici, D/U ratios 2-4, could be measured to within a 2-5 per cent error. Rib counts (fig. 32) were accurate usually to within one rib in 50, two in 100 and up to six for over 200 ribs–generally a 2 per cent error except where the ribs were very fine and numerous, which often resulted in a 3 per cent error. Most of these errors resulted from judgment decisions concerning rib status at repaired breaks or on gerontic growth sections. Whorl counts normally showed a ⅛ error, with estimated readings made to the nearest one-eighth. For this reason, no statistical treatment of whorl counts was attempted. Usually species differences in this category were either quite pronounced or not noticeable.

The margin of possible error in the basic measurements naturally affects the accuracy of calculated ratios. Particularly in regard to the higher D/U ratios, the actual numbers become virtually meaningless. These figures only serve to indicate the small nature of the umbilicus and are worthless for statistical comparisons. Use of the lower D/U ratios is possible with a higher degree of confidence. Calculation of D/U ratios, using the margins of error cited above and arbitrarily selected figures, produced a range of possible error from 6.5-6.8 per cent in the 2-4 D/U ratios and from 7.6-14.3 per cent in the 7-10 D/U ratios. Calculation of sample H/D ratios produced a possible range of error between 3.3 per cent and 3.8 per cent. It must be stressed, however, that these margins of error represent the calculated extremes. It was not thought worthwhile to determine the mean margin of error in measuring individual specimens, but for three samples that had been measured several times, I computed the means for H, D, H/D, and D/U. With 7 to 11 specimens involved, the sample means varied by:

H - 0.4-0.7%;
D - 0.1-0.3%;
H/D - 0.5-1.0%; and
D/U - 1-2% for ratios less than 8.

In making comparisons between samples, the above figures have been given considerable weight in deciding whether calculated differences are significant, or represent random variation.

CRITERIA FOR SPECIES RECOGNITION

Recognition of species on the same island presents a different problem from dealing with allopatric populations on different islands. Closely related sympatric species must have "species recognition" features to maintain genetic integrity. These differ with the group of organisms. Where congeneric species of endodontid snails are sympatric to the extent of living under the same log, character displacement in terminal genital structures has occurred (tables LII-LIV). One repetitive type of such character displacement is for the normal pattern of two penial pilasters that are equal in size to become altered. One of the species will have the conservative pattern, while in the other, one pilaster will be greatly reduced. Examples of this are seen in *Libera micrasoma* (fig. 171h, two simple pilasters) and *L. cookeana* (fig. 172a, two unequal pilasters) from Station 865 on Tahiti and in most of the Rapan *Opanara* where there are extensive and complex sympatric-allopatric species groupings. An interesting variation is seen in the Marquesan *Taipidon,* where *T. fragila* (fig. 138f) and *T. varidentata* (fig. 138h) on Hivaoa and *T. centadentata* (fig. 139f) and *T. semimarsupialis* (fig. 139b) on Nukuhiva are sympatric or the handful of known specimens have been collected on the same ridge in different years within 90 ft. recorded elevation. In each case the first species has the pilasters broken up into a series of longitudinally arranged tubercles, while the second species retains the "typical" pattern for that genus. In the Nukuhiva *Planudonta intermedia* (fig. 147b) the 4.6 mm. long penis has two pilasters that are almost circular in cross-section, while the probably sympatric *P. concava* (fig. 147d) has one pilaster of the 6 mm. long penis altered into a high folded ridge.

Where more than one genus from a monophyletic assemblage and several species are sympatric, as on Rapa Island, there are changes in size of penis, number of pilasters, shape of pilasters, and the length of the penial pilasters. Data on these alterations are given in the generic discussions and in Tables LII-LIV. They are not repeated here. What is basic is the concept that endodontid land snails use penial surface features in species recognition. When sympatric populations show dimorphic penial surfaces, I conclude that they are distinct species. In all such cases discovered so far, the differences in penial structure correlate with conchological differences. The differences may be large and obvious, as between *Taipidon centadentata* (fig. 144) and *T. semimarsupialis* (fig. 143e-f) or *Planudonta concava* (fig. 149a-b) and *P. intermedia* (fig. 149c-d); or the differences in shell features can be relatively small, as in *Taipidon fragila* and *T.*

varidentata (fig. 145). Although the size of the morphologic gap in shell features varies, these differences correlate with the penial gap and make it possible to sort the station material into two species. The penial differences indicate recognition of genetic incompatibility by the snails. The conchological differences are expressions of underlying genetic shifts that led up to the point of genetic incompatibility.

Anatomical study of sympatric material thus made it possible to recognize which snails consider each other different species. Analysis of shell variation provided greater to lesser correlated shell changes by which the species could be identified.

When populations are allopatric because of a distinct water gap between islands or from living at opposite ends of a large island, there will have been no selective pressure for "species recognition" characters to evolve. If these isolated taxa have not been sympatric with congeners or closely related genera, then selection probably would be toward a stabilized penial surface. Any deviation from a "normal" pattern would be at a selective disadvantage, and would tend to have less reproductive success. In all probability the extremely conservative pattern of penial structure in the family relates to just this situation.

At the same time, the populations will have been subject to varying selective pressures in their different habitats. Genetic change in other systems having adaptive value to local conditions will be selected. In keeping with the general pleiotropic nature of mutations, such changes can be expected to be expressed in shell feature shifts, even if the particular selective advantage of the change does not involve the shell directly. If these allotropic populations with different genetic systems but virtually identical penial surfaces became sympatric, either the genotypes would mix (if genetic compatibility existed) or rapid selection for species recognition characters would occur (if cross-population matings produced reproductively sterile or no offspring). It is obviously impossible to test the breeding potential of the many allopatric populations with similar penial types. In judging their reproductive potential it is necessary to make predictions on the basis of observations concerning sympatric populations.

The extent of conchological variation within populations can be measured and the minimum degree of conchological difference between sympatric species determined. In the vast majority of cases the degree of difference will exceed such minimums. There is no reason to assume that the currently observed minimum represents the actual minimum necessary for genetic incompatibility to exist. Nevertheless, this is the best available starting point for evaluating the significance of observed differences between populations. It is based on the premise that genetic divergence will be reflected by phenotypic alterations in the shell. When the genetic systems have diverged to the point of reproductively significant incompatibility, then, if sympatry occurs, selection for species recognition characters on the functioning surfaces of the penis will take place.

After the minimum conchological difference for a sympatric pair of species in the family is determined, the relationship of allopatric populations is judged against this standard. If the degree of difference is less than the standard, either clinal variation or subspecific differentiation is proposed. If the degree of difference is equal to or exceeds the standard, then the populations are assigned to different species regardless of the similarity in "species recognition characters."

A precise definition of "minimum conchological difference" is difficult because shells can vary in many ways and different taxa show different sets of variations. Probably *Taipidon fragila* and *T. varidentata* show the least substantial changes of any absolutely or near sympatric species pair where it was possible to dissect both species. The former (fig. 145) has a flatter spire, narrower umbilicus, finer ribbing with fewer microradials between, and a greatly reduced number of apertural barriers. These are uncorrelated characters in this situation, since flattening the spire normally will widen the umbilicus, while finer and more widely spaced ribbing will have more microradials between each pair of major ribs. Taken singly, each of these characters can be shown to vary within a species unit as widely as they do between the two *Taipidon*. *Ruatara oparica* from Rapa has the nominate race (fig. 113c-d) with prominent apertural barriers, a subspecies *R. o. reductidenta* (fig. 114e) with greatly reduced barriers, and a third geographic race, *R. o. normalis* (fig. 114a, c, d), with an intermediate condition. Races of *Opanara areaensis* from Rapa (fig. 104) differ in spire protrusion or ribbing and umbilical size, but retain anatomical features in common. It is the combination of uncorrelated shell and penial differences between the two *Taipidon* that is significant. I am reluctant to establish a minimum number of uncorrelated differences to be used as a fixed criterion for species separation. Instead I have given conscious weight to the apparent "key character usefulness" of a character within the context of that section of the family in making particular decisions.

Again using Rapan taxa as examples, it is instructive to examine two other situations where judgment had to be made concerning the status of allopatric populations. Two pairs of taxa in *Opanara* that consist of essentially single relict populations (fig. 100) show virtually equivalent shell differences. Table VI summarizes morphometric data. The differences between the races of *Opanara megomphala* (Fig. 106a-d) stem primarily from a single change in spire elevation that affected the H/D ratio and D/U ratio, but had little effect on the diameter and ribbing. Because there was no noticeable difference in the

TABLE VI. - SIZE AND SHAPE VARIATION IN RELICT, ALLOPATRIC RAPAN OPANARA

	O. m. megomphala	O. m. tepiahuensis	O. caliculata	O. altiapica
Diameter	3.21(2.83-3.52)	3.36(2.98-3.77)	3.27(3.09-3.39)	2.82(2.63-3.03)
H/D ratio	0.511(0.486-0.564)	0.434(0.353-0.481)	0.617(0.595-0.660)	0.719(0.664-0.761)
Whorls	5 1/4-6 1/8	5 1/2-6 1/8	4 5/8-5 1/4	4 7/8-5 5/8
D/U ratio	2.22(2.15-2.35)	1.95(1.72-2.08)	4.74(4.09-5.22)	4.69(3.91-5.53)
Ribs on body whorl	73.7(71-76)	64.6(54-81)	120.3(117-125)	80.0(64-91)

genitalia and the statistically significant differences were the result of a single alteration, the populations are called subspecies. *Opanara altiapica* and *O. caliculata* differ in rib spacing (fig. 105a, c), coiling of the last whorls, size, and penis structure. They are called different species because there were several uncorrelated shell characters in addition to the penis "key," although the degree of statistical difference in respect to measured variables is no greater than between the races of *O. megomphala*.

While each marginal case has to be decided on its own merits, where three or more substantial, non-correlated conchological differences exist between allopatric populations, and these changes are not known to differ significantly within populations in that section of the family or genus, then allopatric populations have been ranked as distinct species. If fewer than three such changes are present and there is no indication of "species recognition" differences in the terminal genitalia, then normally less than specific level differentiation is proposed.

Subspecies have been recognized in two situations: where there are one or two uncorrelated characters that shift with at most slight overlap between populations on different islands or where there are dramatic "step cline" patterns of change involving adjacent areas of the same island. The few subspecies delineated in this study are true "incipient species." Further work might demonstrate that they have reached the level of being distinct. Except for the populations of *Orangia cookei, Opanara areaensis,* and *Ruatara oparica* on Rapa, natural test of sympatric or near sympatric populations occurrence does not exist. The decision on species level *versus* subspecies level designation has been, of necessity, subjective. For the Rapan taxa, the populations are nearly sympatric and the absence of "character recognition" features has led to the subspecies-level designation. As indicated in Table VI, the degree of measurable difference may be just as large between some of the subspecies as it is between certain sets of species. For this reason, species and subspecies have been given equal status in analyzing patterns of species level variation.

Nature of Comparative Remarks

If comparisons are being made between the species living on a single island or at a single station, where either there are character displacement phenomena in respect to closely related species, or the species come from a variety of phyletic lines, then both quantitative and qualitative distinctions usually are obvious. Most users of this monograph will be attempting to identify species from a particular island, and hence for ease both in construction and user convenience, most keys are based on geographic units. A meaningful and usable comprehensive key to generic units would require extensive use of anatomical features observable only by dissection, since conchological variation is sufficiently large to require multiple entries and a highly artificial arrangement. Within genera, keys are based on the known species and represent artificial identification aids, not an attempt to depict phylogeny. Again, to be of maximum usefulness to the reader, they are based on conchological data.

When comparing generic-level taxa, it has been possible, in most situations, to use easily observable and sharply distinct features. To some extent such remarks are based on departures from idealized basic morphotype for the family. The various genera are viewed as progressive departures from a basic pattern represented among extant taxa by *Minidonta* and *Cookeconcha*. Such patterns of change have been somewhat repetitive, as recognized by the *Mautodontha, Nesodiscus,* and *Libera* levels of specialization. Hence generic comparisons are a combination of direct character differences and patterns of departure from the more primitive conditions seen in less specialized, potentially ancestral genera.

Within genera, the non-sympatric species may differ by combinations of characters that are hard to define precisely and that are not reflected by averages of the relatively crude shell measurements. Hence it was decided, before writing the definitive descriptions, diagnoses, and comparative remarks, to determine the average pattern within that genus, or in the case of genera with one to three species, to use the presumed ancestral group average as the standard of comparison. As species depart from the average pattern, these differences are commented on in the diagnoses and remarks. This view of a genus as a monophyletic unit, where a homeostatic genetic system has been bent in several directions under diverse environmental pressures, is implicit in most systematic literature, but frequently has not been articulated or rigorously applied in analysis. This procedure tends to magnify the size of differences between species, but is a necessary facet of communication.

PATTERNS OF MORPHOLOGICAL VARIATION

Initial investigations were carried out using gross methods to study shell and details of anatomic features observable at 100× magnification or less with a dissecting microscope. Slide mounts of unstained radulae and jaws were examined using a Leitz Ortholux compound microscope under bright-field, dark-field, and phase-contrast illuminations. At a later period it was possible to make some scanning electron microscope observations of shell structure and sculpture (pp. 30-41), apertural barriers (Solem, 1973b), and radular denticles (Solem, 1972a, 1973a). Histological and cytological investigations of anatomical structures were not attempted. The Bishop Museum anatomical material had been preserved according to the method of Cooke (Cooke and Kondo, 1960, p. 4). This involved drowning the snails for 12 hr, followed by storage in 50 per cent alcohol until they could be sorted in the laboratory — perhaps weeks or months later. After sorting the material into species and age classes, the soft parts were extracted by a water jet or tweezers (see Kondo and Clench, 1952, pp. 27-28 for a description of the process). The soft parts often broke and only terminal portions of the genitalia were available for study in many species. After a short immersion in 95 per cent alcohol, permanent preservation of the soft parts was in 75 per cent ethyl alcohol. While this procedure often yields material that is quite satisfactory for dissection and gross study, specimens preserved in this way are not suitable for histological investigations. Sometimes there was distinct tissue degeneration in the post-pallial systems, so that apical genitalia could not be studied.

The following discussion surveys the extent and frequency of occurrence for patterns of variation found in various shell and anatomical features as observed under the limitations outlined above. Where necessary to understand the significance of certain features, contrasts are made with the same structures found in the Charopidae, but a detailed family-level comparison of shell structure is withheld until Part II. Some data on family level differences have been presented previously (Solem, 1973b). Statements concerning the direction of character change are presented below without direct justification. The rationale for determining primitive and derived in relation to the Endodontidae is covered in the section on phylogeny and classification (pp. 102-116). Classification has been based on anatomical rather than conchological criteria, but the shell is the most usable guide to species identification. In view of the virtual extinction of the family, the shell is the only system that will be available for future study. Hence patterns of conchological variation are reviewed first, and phylogenetic trends are discussed later.

SIZE AND SHAPE VARIATIONS

The following statistical calculations and most charts omit data concerning the Lau Archipelago species, *Priceconcha tuvuthaensis* and *Thaumatodon spirrhymatum,* described by Solem (1973d). Their inclusion would not have materially altered the results, but would have required repeating a great deal of work and revising figures for little purpose.

For each species and formally delineated subspecies, means and ranges of the basic measured parameters were calculated and then, together with other variational data, coded and key punched onto IBM cards for analysis. While these data indicate a few general patterns of change and permit some statements concerning the effect that various structural alterations have on gross measurements, these averaged data must be used with caution. The extent of variation within members of a population in regard to shell shape and form is far greater than would be suggested by the computer-simulated shells of Raup (1962) or the studies on *Poecilozonites* and *Cerion* by Stephen J. Gould (1969, 1971). Particularly in regard to variations in ratios reflecting umbilical size and shell form, individual specimens of endodontoid species show little close linkage of variables. The endodontids have a messy, highly varied, and frequently individualistic "generating curve" that frequently changes drastically and perversely during ontogeny. A prime example of this is the formation of a "brood chamber" or "brood pouch" from the shell umbilicus by secondary inward growth of the umbilical lip over a short segment of a whorl to more than a full whorl of shell growth (pp. 27-30). In *Anceyodonta* (figs. 81c, 82f) there are the rapidly changing umbilical contours. Major spire protrusion alterations can be seen within populations of one species, *Nesodiscus taneae* (fig. 152), and between subspecies of *Opanara areanensis* (fig. 104a, c, e). Zonitoids, in contrast, are far more regular in growth form.

While minimum, mean, and maximum adult dimensions were recorded for each taxon, graphing of the minimums, selection of which involved judgment

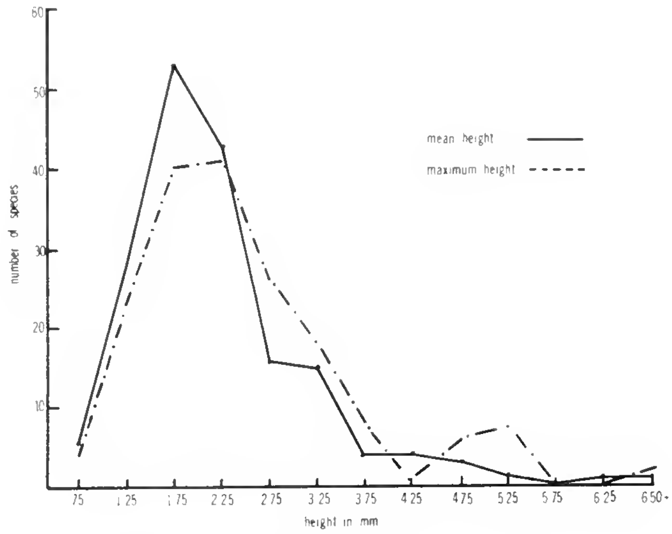


FIG. 6. Frequency distributions of mean and maximum shell height in the Endodontidae.

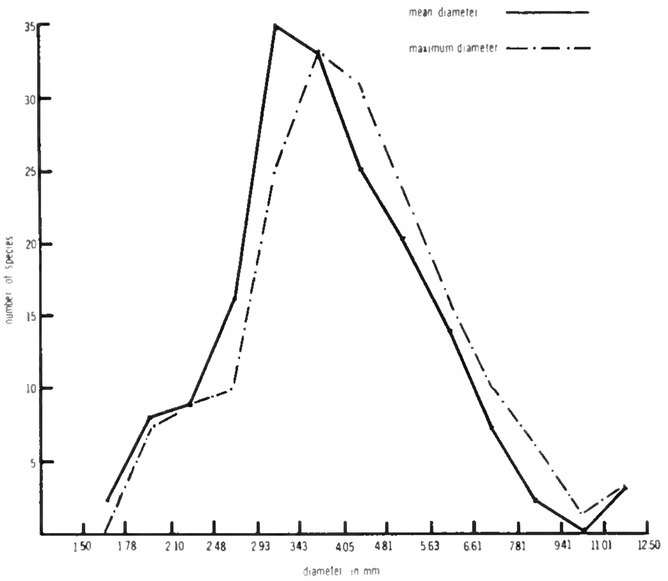


FIG. 7. Frequency distributions of mean and maximum shell diameter in the Endodontidae. Diameter intervals are arithmetically equal segments from a logarithmic scale.

decisions, is not presented for basic parameters although it is for most ratios. The pattern of shell height (fig. 6) is positively skewed in distribution, resulting from the evolution of species with a secondary brood chamber. As the shell continues to grow and narrow the chamber opening, height increases at a far greater rate than do other parameters. The growth vector alters to increase the height, whereas the diameter of these species is but little affected or even remains stationary. The diameter plot (fig. 7) is on a log basis and is symmetrical. As would be expected, the Height/Diameter ratio is slightly skewed, (fig. 8) reflecting the height asymmetry. Whorl count (fig. 9) correlates well with the height pattern (fig. 6), again reflecting the number of species with a "brood chamber," since the increased height results from a greater whorl count. Most endodontids lay their eggs in the shell umbilicus, but on Rapa and Mangareva Islands there was a tendency for closure of the umbilicus. Figure 10 charts, on a log scale, the mean Diameter/Umbilicus ratio for all taxa. Figure 11 separates the Mangarevan and Rapan taxa for comparison with the overall pattern. Except for the two subspecies of the Palau Island *Aaadonta fuscozonata* (Beddome) (fig. 206), barely perforate or closed umbilici are limited to species from Rapa and Mangareva. For those species in which the number of ribs on the body whorl can be counted, the frequency distribution of rib counts is relatively symmetrical (fig. 12), although the pattern of rib spacing is more strongly skewed (fig. 13).

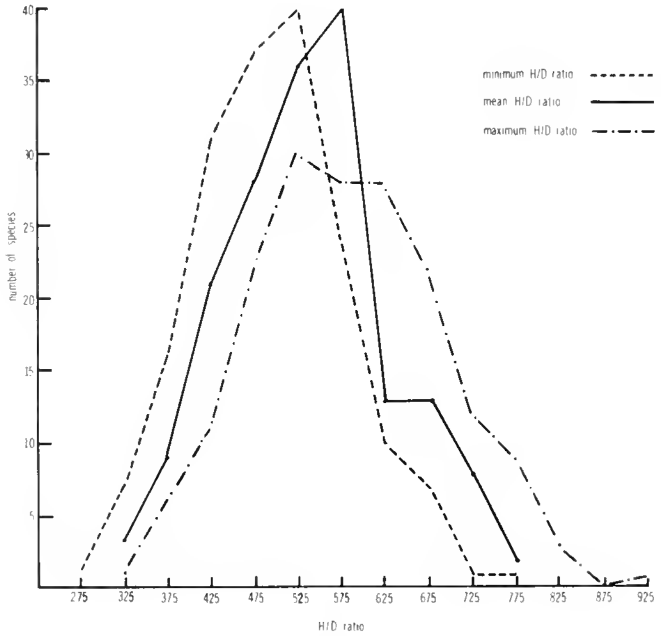


FIG. 8. Frequency distributions of minimum, mean, and maximum H/D ratios in the Endodontidae.

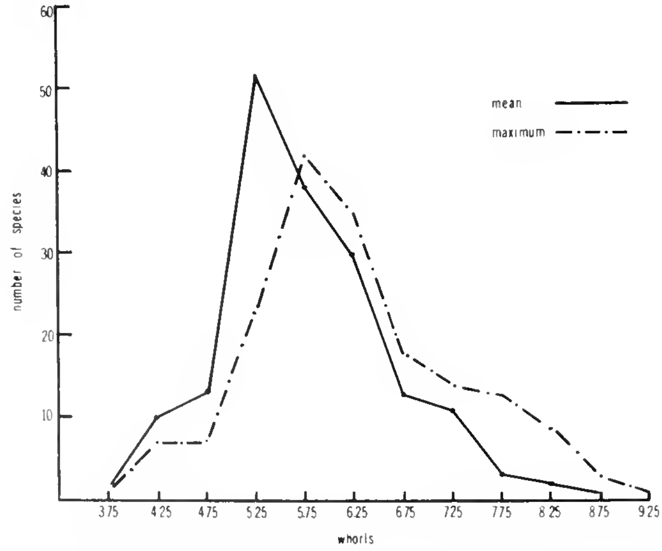


FIG. 9. Frequency distributions of mean and maximum whorl counts in the Endodontidae.

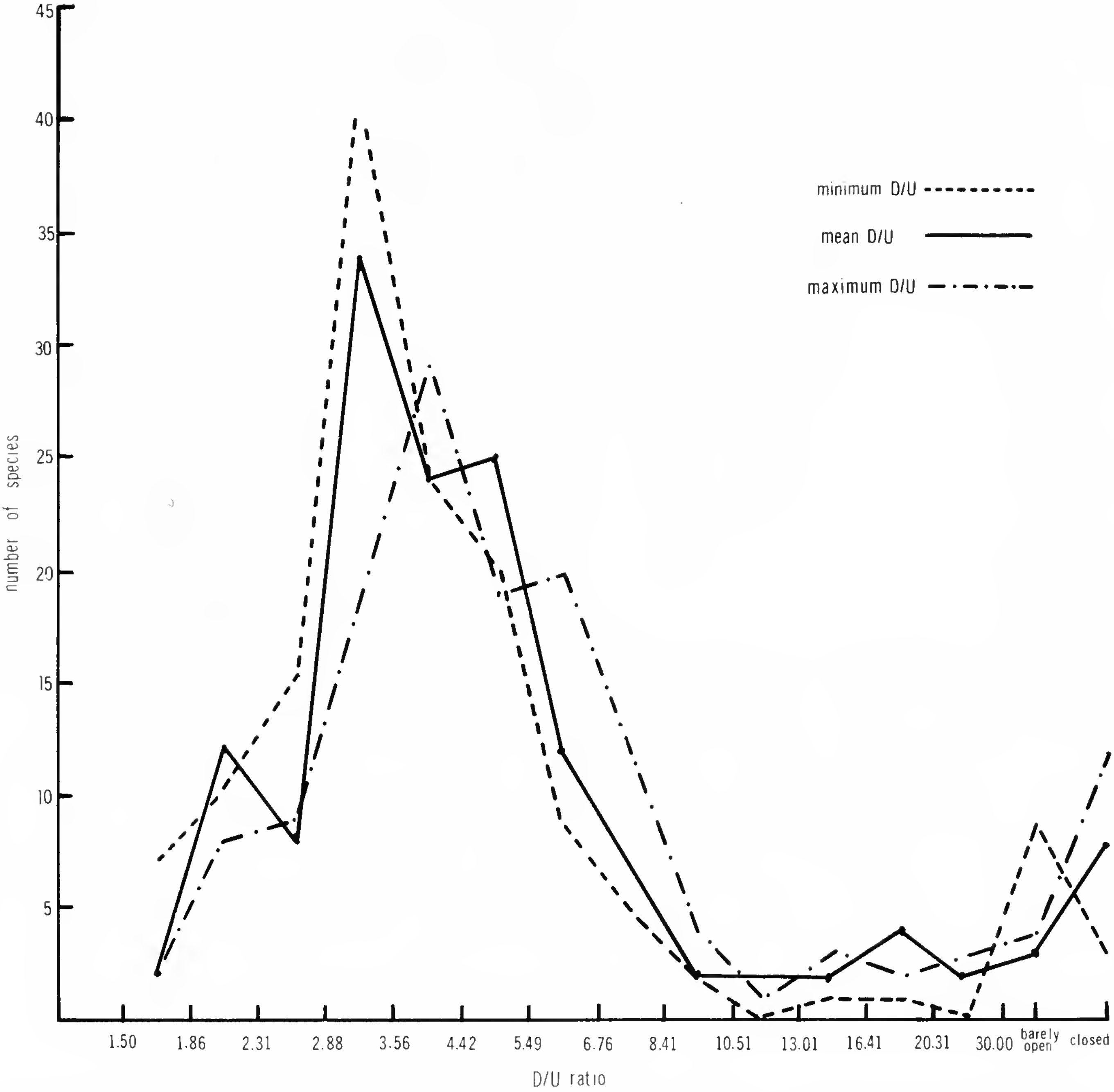


FIG. 10. Frequency distributions of minimum, mean and maximum D/U ratios in the Endodontidae. D/U ratio intervals are arithmetically equal segments of a logarithmic scale.

Each of the above basic measurements results from the interaction of several variables. Factor analysis would permit assigning weight to individual elements, but this would require far more elaborate and accurate measurements prepared from shell cross-sections than seemed worthwhile for this systematic review, plus computer competence and access that were not available to me. As examples of the changes, discussion is presented here concerning the effects of two more obvious changes, body whorl contour and spire protrusion, in relation to the basic measurements. Then a brief review on the pattern of change in umbilical contours precedes consideration of brood chamber formation and its effects on shell size and shape. A short concluding section on whorl count correlated variation provides background data for subsequent phylogenetic analysis.

Body whorl contour

While no quantitative measurement of body whorl contour was possible, visual coding into five categories was relatively unambiguous. The actual coding of the states was done from specimens, the written diagnoses, and illustrations, with difficult judgment decisions necessary in only a few cases. The approximate contour states are indicated in Figure 14A-E. These are termed: A) laterally compressed; B) evenly rounded; C) flattened slightly above and below a

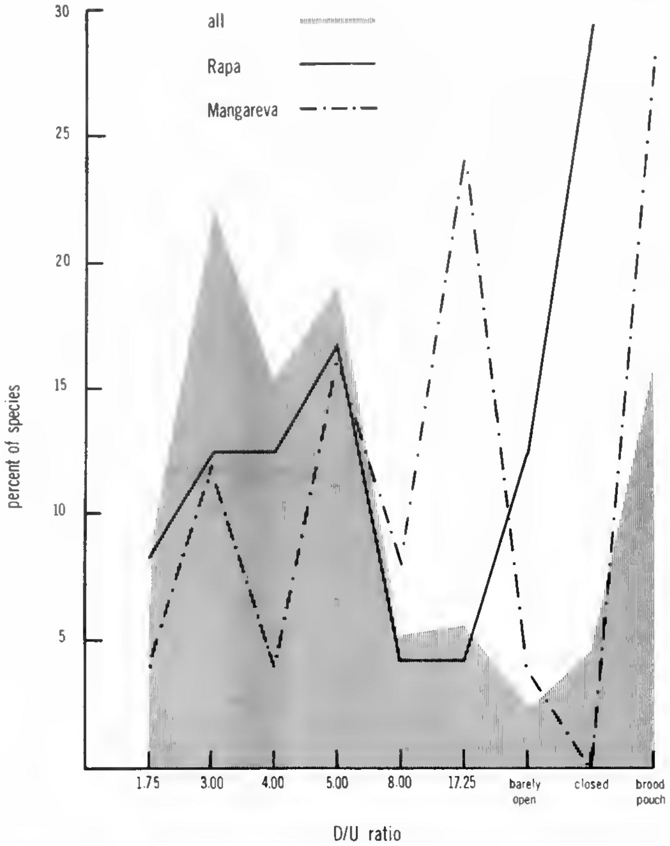


FIG. 11. Pattern of umbilical size in Rapa and Mangareva Island Endodontidae compared with the frequency distribution for the entire family.

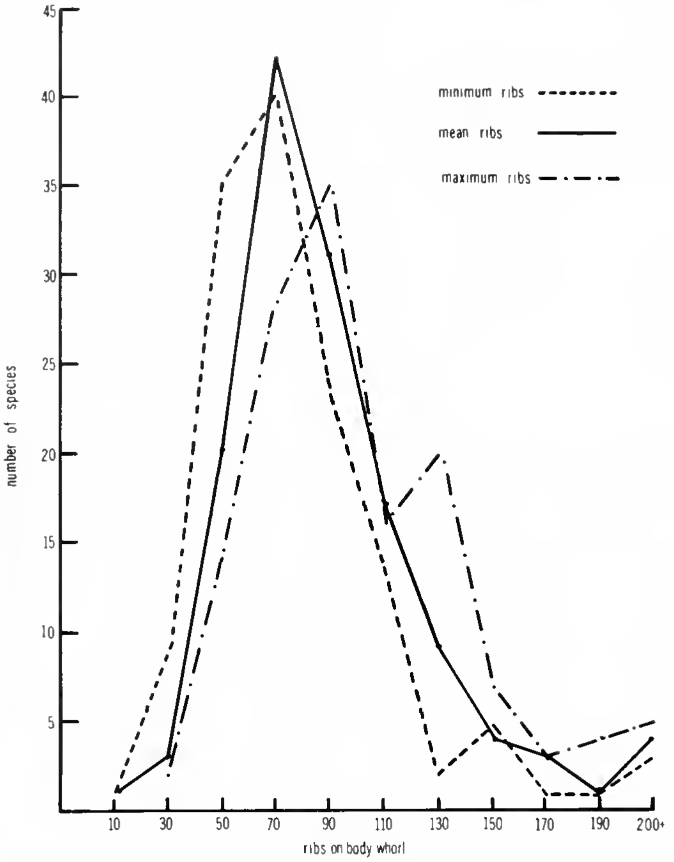


FIG. 12. Frequency distributions of minimum, mean, and maximum rib counts on the body whorl in the Endodontidae. Species with reduced or irregular ribbing omitted.

rounded periphery; D) flattened above and below an angled periphery; and E) distinctly keeled. A sixth category, F, contains all species in which a brood chamber has been developed. The latter change overrides the alterations in whorl contour. Treatment of these taxa separately is essential.

In the four charts, the x axis digits refer to the number of taxa in that grouping, while the y axis figures give the measurement range for the particular parameter. There is no correlation between D/U ratio (lower right of fig. 14) and body whorl contour variation, and virtually no change in shell height (upper left) until a protruded keel is developed. The development of a peripheral keel reduces the options for attachment of succeeding whorls. To fasten the parietal-palatal margin above such a keel leaves the parietal wall with a strong projection into the very area of the apertural cross-section where the comparatively bulky heart and kidney lie and through which (at the apertural opening) the head with its bulbous buccal mass must be withdrawn. Such a procedure would be highly inefficient. I know of no snail in which the attachment lies well above a protruded keel. The peripheral keel itself, or even slightly below it, marks the attachment point for subsequent shell growth. The slight height increase shown by keeled species probably reflects a negative feature, in that once the keel is started, reduction in shell height becomes mechanically far more difficult to accomplish. Brood chamber species (state F) are included to emphasize their increased shell height.

Shell diameter (upper right of fig. 14) increases steadily with the change in whorl contour, except for going from state C to D. Since the only alteration in this transition involves the upper and lower lateral margins of the body whorl, the periphery-to-periphery distance would remain unchanged. In state E the

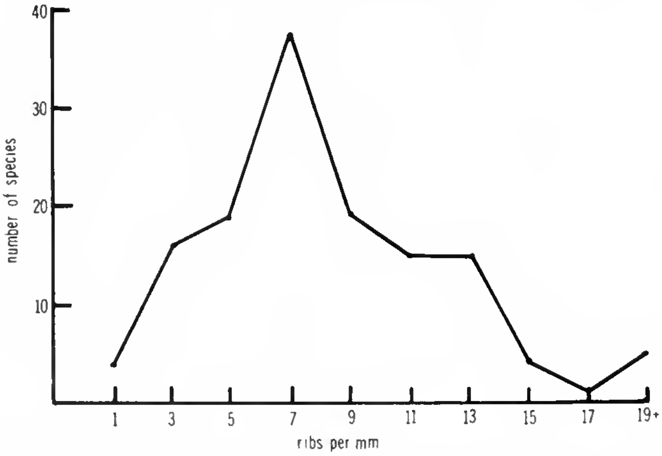


FIG. 13. Pattern of rib spacing on the body whorl in terms of ribs/mm. of peripheral circumference. Species with partly reduced or irregular ribbing omitted.

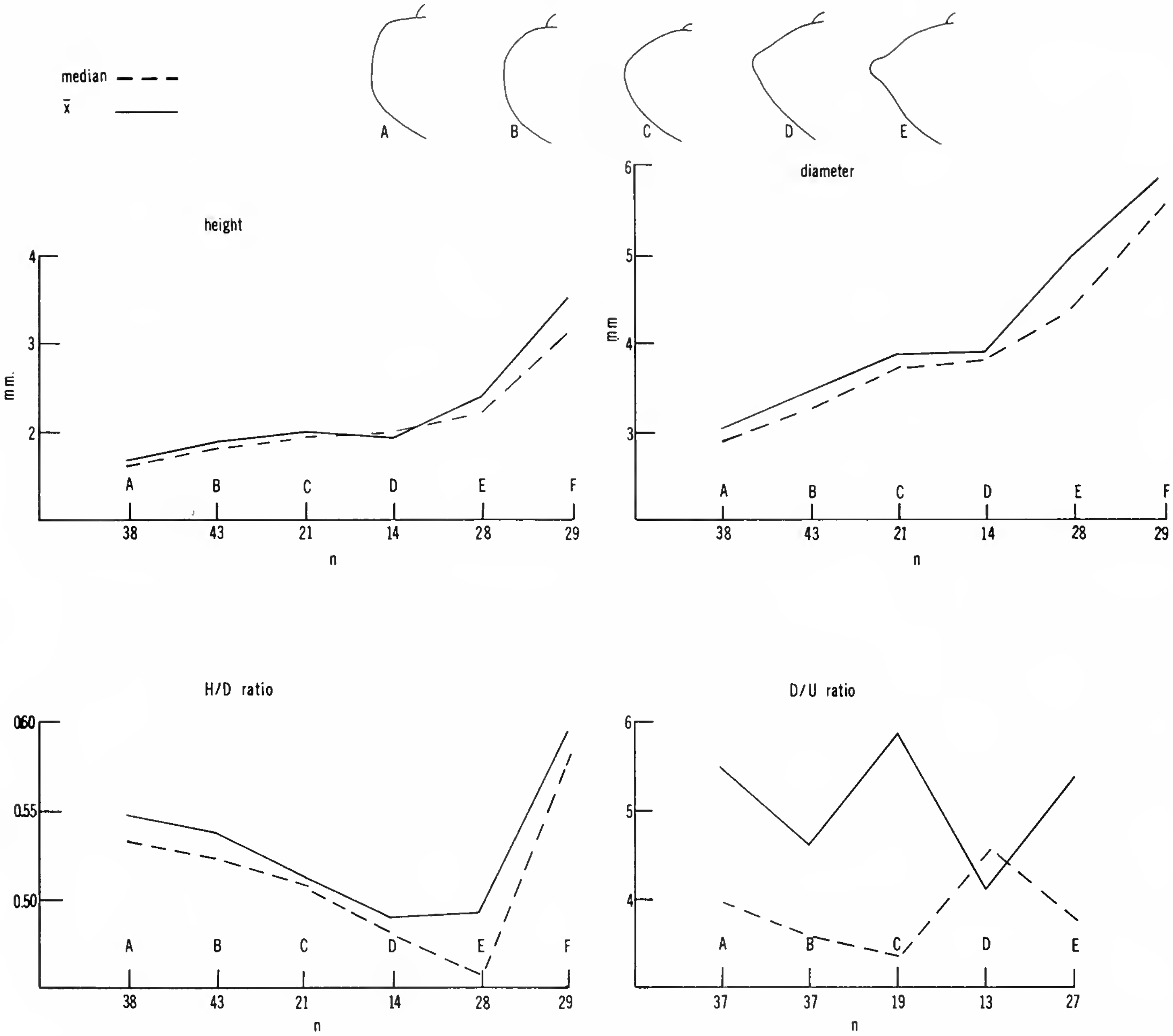


FIG. 14. Effects of changes in peripheral whorl contour on some basic measurements in the Endodontidae. See text for explanation of character states A-F, "n" refers to the number of species level taxa having each state. The D/U ratio graph omits species with closed or barely perforate umbilici.

actual lateral protrusion of the periphery on each side would, and does, drastically increase the diameter. The proportionate increase in diameter from states E to F is less than the change in height (upper left). Again this reflects the mechanics of brood-chamber formation.

Correlated with the increase in shell diameter, which results from further lateral expansions of the body whorl, is a gradual decrease in the H/D ratio (lower left). The slight mean levelling in the H/D ratio of state E and rise in height for group E results from the Palau Island *Aaadonta* being mostly in this group. This genus has by far the most elevated spire and greatest number of species with keeled peripheries for any genus in the family.

Data on whorl count correlations are presented in Table VII. The difference from state C to D is not significant ("*t*" = 1.3373 with 33 df), but the change from C to E is significant ("*t*" = 2.6954 with 47 df), It may be that the increase in shell diameter combined with keeling is a mechanism that serves to decrease shell-height increment as the whorl count is raised. A retardation of the increase in shell height would keep open narrower niches for the snail to retreat into. The keel protrusion would adjust cross-sectional whorl area to compensate for the lessened height increment.

In summary, changes in the whorl contour directly affect the shell diameter and H/D ratio, but have no correlation with D/U ratio and only slight direct effects on shell height. Whorl-count increase correlates slightly with keel formation, but otherwise there are no major identifiable results from whorl contour changes.

TABLE VII. - WHORL CONTOUR AND WHORL COUNT CORRELATIONS

Character state	$\bar{X}$ and SEM whorl count	Number of taxa
A	5.44±0.11	38
B	5.35±0.11	42
C	5.35±0.12	21
D	5.66±0.21	14
E	5.87±0.14	28
F	6.78±0.11	29

Spire protrusion

If the whorls of a typical shell could be unwound and then coiled in different fashions, certain changes would be obvious. If the rate of whorl descension was great, resulting in a protruded spire, and the whorl count remained the same, the shell height would be larger, the diameter less, the H/D ratio would approach nearer to unity (or even above), the umbilicus would be narrower, and the D/U ratio larger in number. If the spire was flattened or depressed resulting in little or no whorl descension, the height would be less, the diameter greater, the H/D ratio a lesser proportion of unity, the umbilicus wider and the D/U ratio lower in number.

Isolating spire protrusion for analysis is difficult, since the degree of body-whorl deflection during adult growth varies greatly between taxa. This parameter has great influence on shell height and some influence on shell diameter. To use the ratio of spire protrusion above the body whorl to total shell height would add the variable of body whorl descension. I have chosen to indicate the degree of body whorl protrusion through use of an index obtained by dividing the actual spire height above the body whorl (E-F in fig. 5) by the body whorl width (F-G in fig. 5) taken at a point directly below the spire. Adjustments in the latter measurement to allow for the changes resulting from keel protrusion would slightly refine the data, but were not feasible or thought necessary at this level of analysis. Measurements were made on type specimens only, with the exceptions noted below.

The resulting data were clumped into five states, which are characterized as: A) spire flat or depressed; B) index 0.01-0.250; C) index 0.251-0.500; D) index 0.501-0.750; and E) index 0.751 to the observed maximum of 1.33 in *Gambiodonta grandis*. About 10 per cent of the species were sufficiently near the group dividing points that several specimens were measured and the means used to decide group placement. Individual variation within large populations was far less than found in the Charopidae, although the total range frequently overlapped two states. The vast majority of taxa could be assigned to a group without question. A rough indication of the divergent appearance is given by the small diagrams at the top of Figure 15. Both mean and median parameters are given in the diagrams.

The major effect of spire elevation is on H/D (lower left) and D/U (lower right) ratios. As the spire is protruded, the H/D ratio increases and the umbilicus becomes narrower. Two minor shifts in the charts require explanation. The lack of H/D ratio change between C and D probably reflects the fact these ratios are the typical pattern for the family (fig.

TABLE VIII. - SPIRE PROTRUSION AND WHORL COUNT CORRELATION

Character state	Brood chamber absent		Brood chamber present	
	Whorl count $\bar{X}$ and SEM	Number of taxa	$\bar{X}$	Number of taxa
A	5.21±0.19	17	---	0
B	5.24±0.12	43	7.63	1
C	5.52±0.09	59	6.98	4
D	6.03±0.12	21	6.40	10
E	6.08±0.16	5	6.93	14

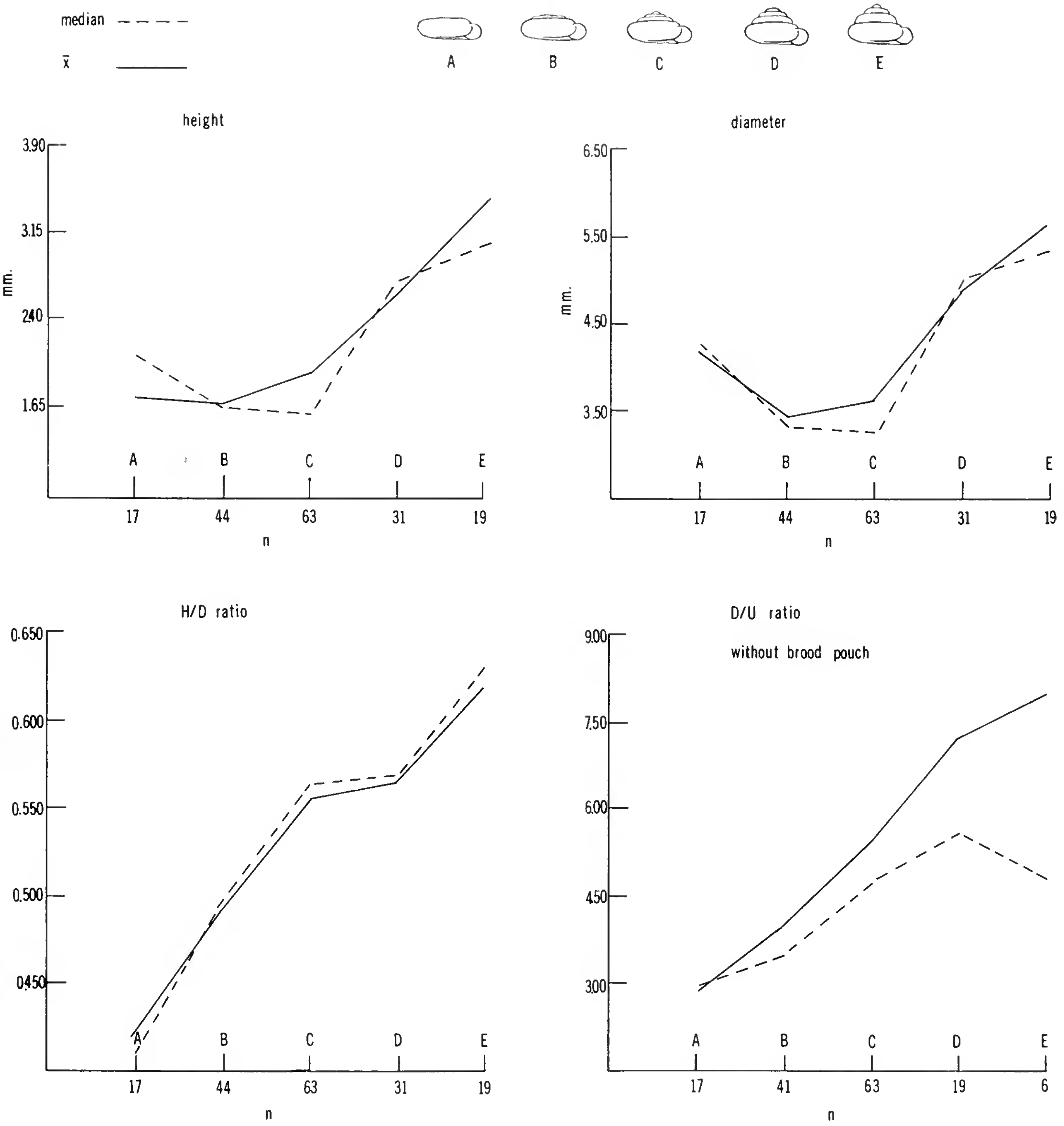


FIG. 15. Effects of changes in spire protrusion on basic measurements in the Endodontidae. See text for explanation of character states A-E, "n" refers to the number of species level taxa having each state.

8). Either a more or less protruded spire represents a departure from the norm and hence may drastically alter the H/D ratio. In the D/U ratio chart, the dip in the group E median results from inclusion of the very widely umbilicated *Nesodiscus* in this category.

Changes in shell height (upper left) follow the common sense evaluation of the data, as essentially do the changes in shell diameter (upper right). If the spire is pushed down and into the middle of the coiling plane, then in order to preserve the same total whorl volume, diameter would have to increase; thus the greater diameter for the group A taxa. Flat or depressed spires apparently are advanced characters in the Endodontidae, thus part of the diameter increase probably is phylogenetically determined. The greatly increased diameter in groups C, D, and E reflects two factors—an increasing percentage of taxa with brood chambers developed and an increase in whorl count. This is documented in Table VIII, which shows that the development of a brood chamber correlates with a moderately high spire, but there is no correlation among brood pouch species between spire protrusion and whorl count.

Umbilical contour

Umbilical openings are used by endodontids as an egg deposition site. The variations in umbilical contour and basic shape are far greater than in mollusks where this opening is a byproduct of growth and lacks other functional significance. In discussing the taxa, the umbilicus was described as showing one of 11 shapes and contours. These were subsequently coded as States:

1. V-shaped, regularly decoiling (40 taxa)
2. V-shaped, last whorl decoiling slightly more rapidly (3 taxa)
3. V-shaped, last whorl decoiling much more rapidly (2 taxa)
4. U-shaped, regularly decoiling (23 taxa)
5. U-shaped, last whorl decoiling more rapidly (22 taxa)
6. cup-shaped (18 taxa)
7. U-shaped, barely decoiling (17 taxa)
8. secondarily narrowed to form a "brood chamber" (29 taxa)
9. barely perforate (10 taxa)
10. closed by contraction (3 taxa)
11. closed by reflection of the columellar lip (7 taxa).

Rough cross-sectional views and an indication of the multiple directions in character change are shown in Figure 16. The difference between V and U shaping is a factor of early ontogeny. In those with a V-shaped umbilicus, the initial umbilical width is narrower. During subsequent growth the point of attachment for the columella on the basal margin of the preceding whorl remains the same. The shape of the opening is a simple V. A good example of this is seen in *Minidonta hendersoni* (fig. 63d). In those with a U-shaped umbilicus, the initial umbilical width is proportionately wider and the point of attachment for the columella on the preceding whorl is much nearer the basal-umbilical margin. The same point of attachment is maintained through subsequent growth. The basic shape thus becomes a U with only slight to moderate divergence of the sides as in *Endodonta ekahanuiensis* (fig. 166c). The difference in appearance is caused by both a different initial width of the umbilicus at the apex and changed attachment point for the succeeding whorls. There is no strict taxonomic linkage, since the two types of umbilici occur in equal numbers of *Thaumatodon* and *Mautodontha,* but *Cookeconcha, Taipidon,* and *Australdonta* have mostly V-shaped umbilici, while *Opanara* and *Endodonta* show mostly U-shaped variants.

Table IX summarizes the size and shape correlations with umbilical contour shifts. The difference in whorl count between States 1 and 4 is significant ("*t*" = 2.9974 with 61 df), but the other changes are not statistically meaningful. Taxa with U-shaped umbilici, States 4, 5, and 7, do show differences from each other. Those in which the umbilicus is regularly decoiling (State 4) have an obviously wider umbilicus and significantly lower H/D ratio ("*t*" = 2.0833 with 38 df) than those with a barely decoiling umbilical opening (State 7). Those in which the last whorl decoils more rapidly (State 5) average smaller in diameter than the others, but the range in size is so great that the difference is not significant ("*t*" = 0.7851 with 37 df). Unfortunately, there is virtually no data available concerning egg size in the Endodontidae, so that the significance of the essentially identical D/U ratio for States 5 and 7 is uncertain. It may be coincidental. Umbilici that are cup-shaped (State 6) occur primarily in taxa at the *Nesodiscus* level of specialization. These taxa have a statistically significantly higher whorl count than State 7 ("*t*" = 2.2095 with 32 df), an

TABLE IX. - SIZE AND SHAPE CORRELATIONS WITH UMBILICAL CONTOUR CHANGES

Umbilical shape	N	Mean and SEM Height	Diameter	H/D ratio	D/U ratio	Whorls
State 1	40	1.85±0.14	3.78±0.24	0.489±0.010	3.80±0.15	5.08±0.09
State 4	23	1.96±0.17	3.95±0.38	0.507±0.013	3.84±0.17	5.57±0.15
State 7	17	2.04±0.12	3.72±0.25	0.562±0.024	5.79±0.41	5.61±0.15
State 5	22	1.78±0.19	3.32±0.39	0.550±0.017	5.74±0.49	5.46±0.17
State 6	18	2.08±0.18	4.84±0.27	0.429±0.012	2.17±0.09	6.15±0.19

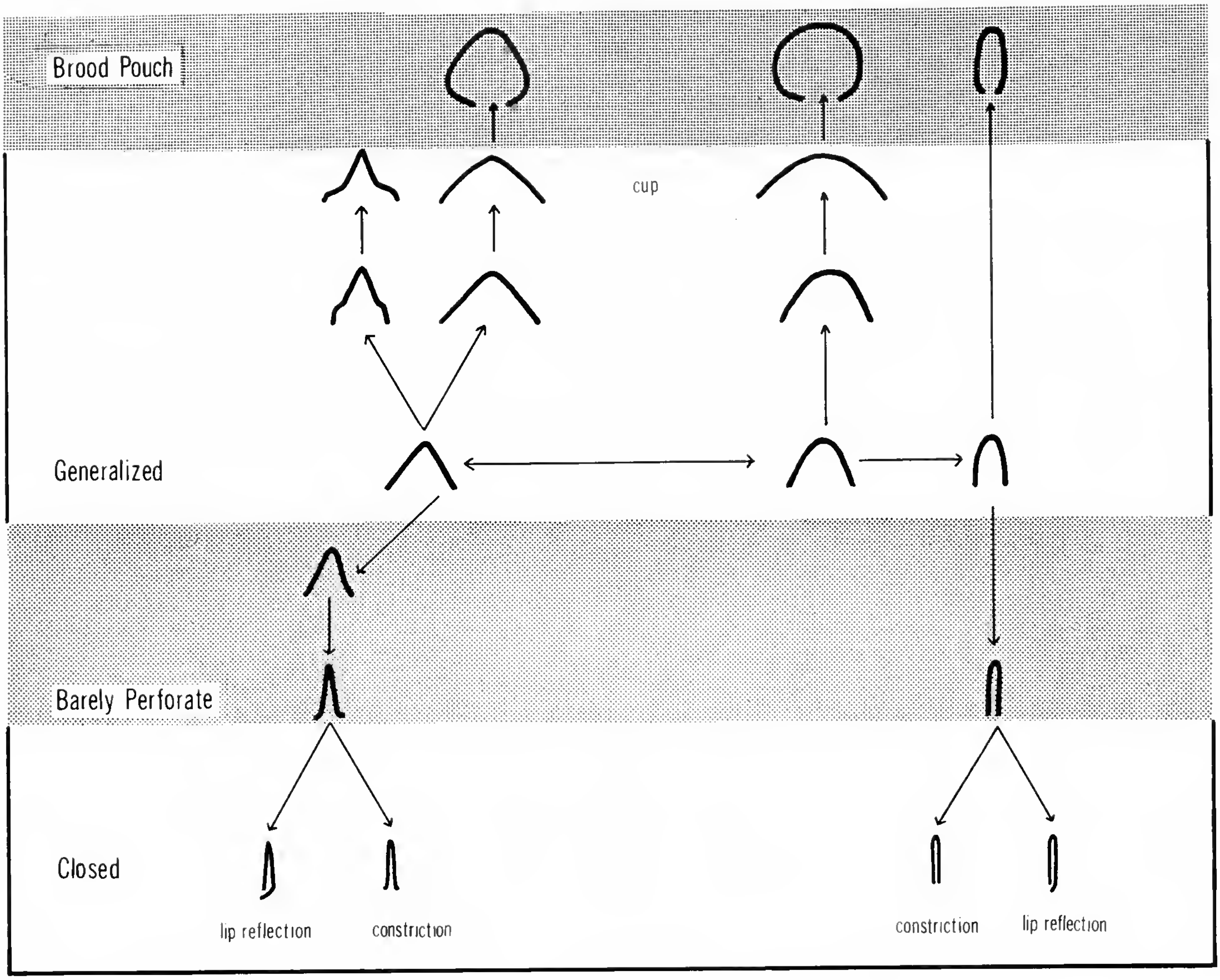


FIG. 16. Patterns of phyletic change in umbilical shape and size.

obviously wider umbilicus, lower H/D ratio, and are larger in size.

Table X shows the relative lack of strong correlations between degree of spire protrusion and umbilical contour, except for taxa with either a brood chamber (State 8) or barely perforate umbilici. Spire protrusion is symmetrically distributed in frequency (see Totals column of table X). There are some skewed correlations in contour. V-shaped umbilici are restricted to forms with relatively low spires. This corresponds to the doming effect mentioned by Gould (1969, p. 432). The shift in frequency shown by States 4 and 5 may be partly caused by the same phenomenon, as is the restriction of perforate umbilici (State 9) to those taxa with elevated spires. In contrast, closed umbilici, those barely decoiling, cup-shaped umbilici, and those with the last whorl decoiling more rapidly do not correlate with spire protrusion.

Inspection of Figure 16 shows that from the generalized conditions, specialized states can be achieved in several different ways. In the systematic discussions under particular genera, the patterns of such change are reviewed individually. Such data is based on gross examination. A more elegant analysis would have been possible by using cross-sectional profiles, but the time needed for such preparations was not available. One aspect that greatly influences umbilical volume is the interior wall contour. Frequently the sides of the umbilicus are flattened. No accurate measurement of this was practical and, although mentioned throughout the systematic section, no general analysis is presented.

The above sketchy data on umbilical shape and contour is necessary as an introduction to the major conchological change seen in the family, formation of a brood chamber. It also serves to suggest some of the complexities concerning the umbilicus in the Endodontidae, nearly all of which relate back to its functional use for egg deposition.

Brood-chamber formation

Shell growth that secondarily narrows a widely open umbilicus to form a brood chamber has occurred at least five different times in the Endodontidae. Three genera, *Pseudolibera*, *Libera*, and *Gambio-*

TABLE X. - UMBILICAL CONTOUR AND SPIRE PROTRUSION

		Umbilical States							
Spire Elevation	Totals	1-3	4	5	6	7	8	9	10-11
Depressed or flat	17	9			7	1			
0.01-0.250	44	16	13	7	3	2	1		2
0.251-0.500	63	20	6	13	3	8	4	4	5
0.501-0.750	33	1	2	3	3	5	10	5	2
over 0.751	19		1		2	1	14	1	

donta, contain nothing but species with brood chambers. In two other genera, single species (*Endodonta marsupialis* and *Taipidon semimarsupialis*) show the secondary narrowing. Other species of the same genera have a U-shaped umbilicus that would require only the secondary narrowing to form a brood chamber. An additional three species show slight umbilical narrowing during the last whorl of growth and hence form prototype brood chambers. *Kleokyphus callimus* (fig. 95c) from Makatea, Tuamotu Islands, *Kondoconcha othnius* (fig. 162c) from Rapa, and *Thaumatodon euaensis* (fig. 194c) from Eua, Tonga all are relatively narrowly umbilicated species that have last whorl constriction of the openings. Thus a total of eight lineages in the family produced species in which the umbilical openings have become secondarily narrowed to form an egg-holding cavity.

The three genera in which all species show striking umbilical alterations are very similar in size and shape. The method of chamber formation is different in the three genera and independent derivation of the chamber is certain. *Pseudolibera* from Makatea (fig. 168) has the narrowing process occur over 1½ whorls. After a period of stabilized umbilical width, there is gradual inward growth of the entire columellar wall that accelerates for one-half whorl, then finally stabilizes in the same position relative to the shell axis for the last one-quarter whorl of growth. In *Gambiodonta* (fig. 185) from Mangareva, the columellar-basal margin first becomes angulated, then keeled. Following this there is an abrupt one-quarter to one-third whorl growth toward the middle of the umbilicus, followed by three-quarters to two-thirds whorl growth with the columellar-basal margin retaining the same position relative to the geometric center of the umbilicus. Completing the one whorl of growth produces a brood chamber with sharply narrowed opening. In *Libera* from the Society and Cook Islands, closure is the result of gradual inward columellar growth over about two whorls of shell increment. The only exceptions to this pattern are seen in such depressed species as *Libera gregaria* and *L. recedens* (fig. 175) from Moorea and *L. streptaxon* (fig. 179) from Tahiti, where parietal wall detachment beginning at the last whorl of growth initiates and provides most of the impetus for umbilical narrowing. In these species this alteration seems to be a compensatory adaptation to preserve maximum volume inside the umbilical chamber. The depressed spires act to reduce the volume of the chamber, but the shorter closure period effectively adds to the volume.

Taipidon semimarsupialis (fig. 143e-f) from Nukuhiva, Marquesas has an inward curve of the entire columellar wall during the last 1¼ whorls of growth producing the brood chamber. In *Endodonta marsupialis* (fig. 167b) from Oahu, Hawaii there is an inward extension of the columellar-basal margin over the last two whorls of growth. Both of these species show many anatomical differences from the dissected *Libera.*

Despite being unable to dissect either *Pseudolibera* or *Gambiodonta,* the differences in brood-chamber formation combine with other conchological criteria to separate them generically.

Considering just the 29 specific-level taxa in *Pseudolibera, Libera,* and *Gambiodonta* plus *Endodonta marsupialis* and *Taipidon semimarsupialis,*

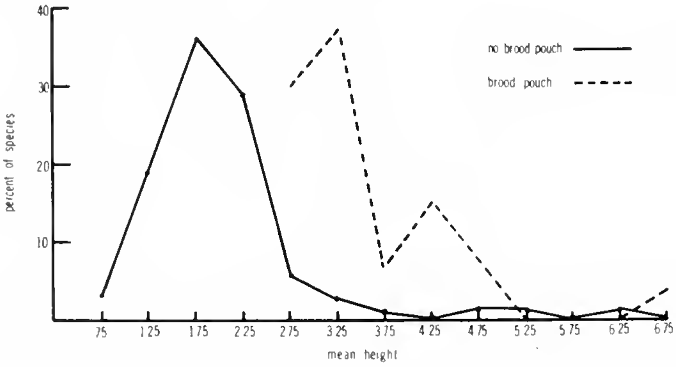


FIG. 17. Mean shell height in species with and without a brood chamber.

there are marked average differences from non-brood chamber species. Since the numbers of taxa involved are quite disparate, the data for Figures 17-20 have been converted into per cent of taxa for ease in direct comparison. Shell height (fig. 17) is obviously much greater in brood-chamber taxa, although a few of the normal taxa are as high. The nature of these exceptions involves gigantism (*Nesophila tiara*), a combination of large size and increased whorl count (*Nesodiscus magnificus, N. fabrefactus, Kleokyphus hypsus*), or high-spired, proto-brood chamber taxa (*Endodonta kamehameha, E. fricki*). Shell diameter (fig. 18) is less sharply demarcated in brood-chamber taxa, since the pattern of growth in forming the chamber involves height more than diameter. Selection for ability to retreat into narrow niches probably influenced the diameter and H/D ratio (fig. 19) to a marked extent. Finally, the increased whorl count (fig. 20) of brood-chamber taxa probably reflects the fact that brood-chamber formation is an improvement upon a functioning system. Endodontids obviously survive very well by laying eggs inside a "normal" umbilicus. Formation of the brood chamber permitted laying a larger number of eggs, increasing the per cent retained until hatching (particularly if the eggs are close to the chamber opening in diameter), and possibly reducing predation upon the eggs. Thus by continuing growth after reproductive maturity, the reproductive success rate would be increased. Hence the larger number of whorls involved in brood chamber formation might be compensated for by a reduction in energy directed toward egg production. Brood chamber narrowing occurs after there is already a sufficiently large umbilicus to hold eggs. Thus the average whorl count would be higher in brood-chamber taxa.

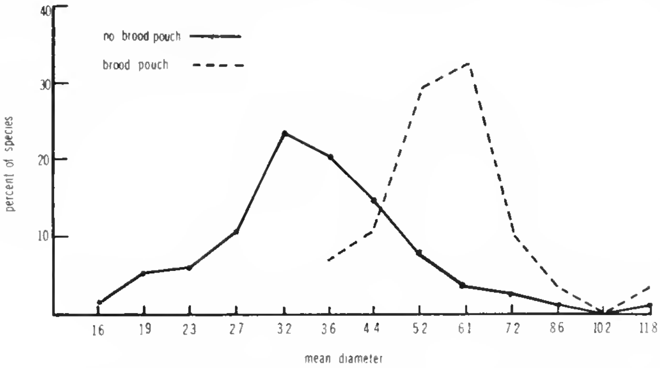


FIG. 18. Mean shell diameter in species with and without a brood chamber.

In at least some species the opening to the brood chamber becomes so constricted that the hatched young have difficulty exiting. In *Libera streptaxon* (fig. 180) specimens normally show eroded margins where the young apparently have gnawed their way to the external world. *Libera fratercula* from the Cook Islands carries this procedure to the ultimate possibility. During brood chamber narrowing the apical soft parts withdraw from the early whorls. Instead of leaving this area vacant or filled with mucus deposits, as is common in multi-whorled land snails, it is filled with calcium crystals, effectively turning the shell apex into a solid rock. The largest specimens will have soft parts in the last four whorls of growth with as many as 4¾ whorls "evacuated" and closed up with calcium. The young gnaw their way up through the shell apex in order to exit (Solem, 1969a, p. 11, fig. 3). Since this species lives in the shore-line coral rubble tossed up by severe storms, calcium is super-abundant. The extra calcium needed to fill in the apical whorls is readily available and retention of the young for a longer period keeps them in a humid niche for a longer time.

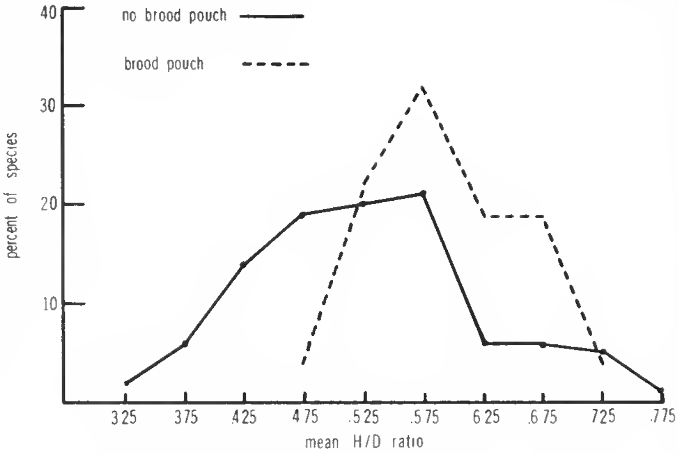


FIG. 19. Mean H/D ratio in species with and without a brood chamber.

No data is available concerning the exact size of the young at time of exit from the brood chamber.

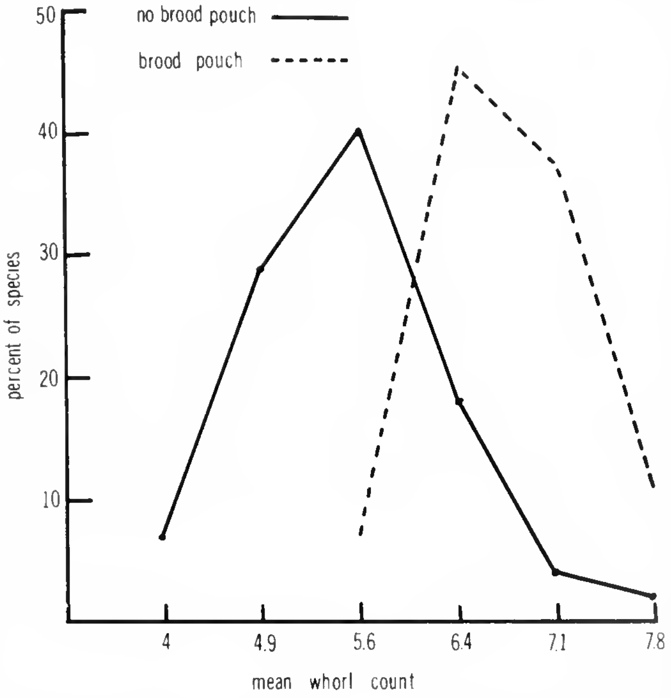


FIG. 20. Mean whorl count in species with and without a brood chamber.

TABLE XI. - WHORL COUNT CORRELATED SIZE INCREMENT

Whorl Count		Number of taxa	X̄ and (% of change from prior group)		
Range	Median		Height	Diameter	H/D ratio
3.6-4.95	4.55	27	1.46(-)	2.80(-)	0.497(-)
5.0-5.5	5.25	58	2.11(44.5%)	3.67(31.1%)	0.523(4.7%)
5.55-6.0	5.70	35	2.34(10.9%)	3.85(4.9%)	0.541(3.4%)
6.05-6.95	6.40	40	3.10(32.5%)	4.80(24.7%)	0.564(4.3%)
7.05-8.05	7.30	17	4.41(42.3%)	6.88(43.3%)	0.556(1.4%)

There is considerable variation in size of the young within the brood chamber, so that growth does occur after hatching and before exiting.

Effects of whorl increment

Although in the Charopidae there is considerable and obvious difference in the rate at which the whorl cross-sections increase in size, species in the Endodontidae have a relatively uniform pattern of change. Except for obvious cases of gigantism in which the size of the nuclear whorls is grossly enlarged, such as *Nesodiscus magnificus* and *Nesophila tiara*, size increase in the Endodontidae correlates with continued additive growth that results in a higher mean whorl count. Spire protrusion, body-whorl descension, keel development, and relative cross-sectional area influence and modify the results, but basically simple whorl count increase results in most of the observed size increment.

Data on this are summarized in Table XI. The whorl-count intervals are not equal in distance, since the clustering around the median whorl count of 5½+ was so great that a division into two parts seemed advisable. The relatively small size increment between the 5.25 and 5.70 medians is an artifact of shortened interval rather than a change in pattern. Both diameter and shell height increase regularly and dramatically as whorl count is increased. There is only minimal change in proportions correlated with whorl count, since the alteration in the H/D ratio is negligible, As has been demonstrated above (pp. 21-27), there are other factors that have much greater effects on shell proportions.

SHELL SCULPTURE

Since the 1850's almost any small helicoidal land snail with numerous radial ridges and/or a reddish-brown or flammulated color pattern was placed in the "endodontoid" complex. This was in contrast to the smooth, shiny-shelled "zonitoid" taxa. Dissections have split off various paryphantid, pyramidulid (pleurodiscid), strobilopsid, polygyrid, and camaenid taxa, but a core of sculptured litter dwelling taxa remain for consideration.

Recently I have been able to initiate scanning-electron-microscope studies not only of sculpture features on the shell surface, but also investigations of the mechanics used to bond together the periostracal and underlying calcareous layers. There appear to be major differences in bonding mechanisms, whereas similar external sculpture on the spire and body whorl has evolved in unrelated lineages. The data on bonding mechanisms are too fragmentary for presentation at this time. The Pacific Island endodontoid family taxa do show clear differences in their relative use of calcareous *versus* periostracal sculptural components, the formation of sculpture on the postnuclear whorls, and in the pattern of apical sculpture. Discussion of basic sculptural structure is restricted to these aspects pending completion of more detailed investigations on layer bonding and details of surface sculpture in Australian and New Zealand taxa.

Data is presented below on the nature of micro- and macrosculptural elements; family-level differences; additive sculptural features; patterns of variation in major rib numbers, size and spacing; the nature of changes correlated with rib spacing and rib reduction; and a brief hypothesis concerning the functional significance of shell sculpture in the endodontoid genera.

Types and growth patterns

Normal shell sculpture in the Endodontidae consists of major radial ribs plus a complex microsculpture that is barely visible at 80-100× magnification. The major ribs are visible either to the naked eye or at less than 30× magnification. The microsculpture can be analyzed with the scanning electron microscope (SEM) at 300-3,000× magnification. These two elements of sculpture are additive, with the microsculpture continuing onto and across the major swellings. This is quite clearly shown in, for example, *Rhysoconcha atanuiensis* (the lower half of fig. 21b). There are four to six microradial riblets in the "trough" between each pair of major ribs. After the initial abrupt "rise" of the major ribs, several crowded microradials are clustered on the upper and

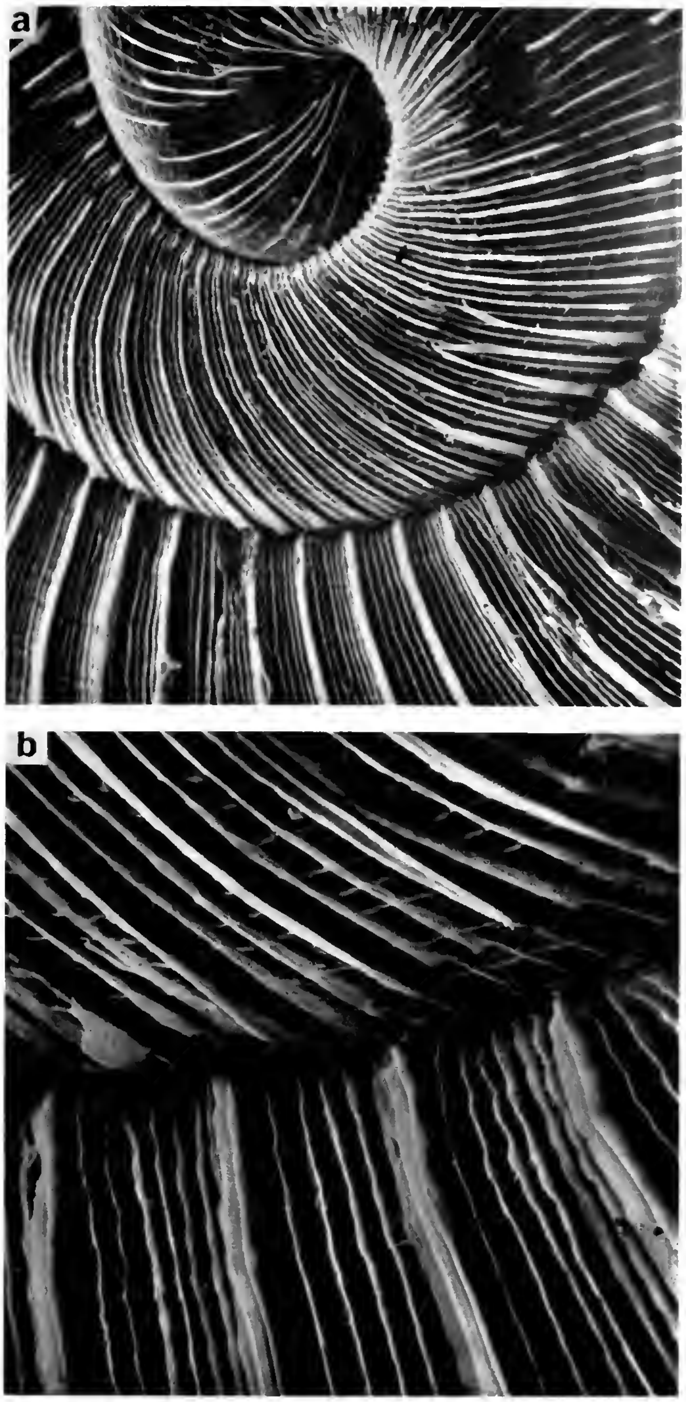


FIG. 21. Sculpture of *Rhysoconcha atanuiensis* and *Thaumatodon decemplicata* (Mousson): **a-b**, *Rhysoconcha atanuiensis*. Station 367, Atanui Bay, Rapa. BPBM 140161. *a*, apex and early postnuclear sculpture (ca. 300×); *b*, suture between apex and first postnuclear whorl, note absence of microspirals on postnuclear (ca. 1,000×); **c**, *Thaumatodon decemplicata*. Paratype. Nukufetau, Ellice Islands. FMNH 116990 ex Mousson coll.

anterior (descending) side of each major rib (left side in cited figure). The spacing between these microradials obviously is much narrower than between the riblets in the "trough" area. Inspection of other species shows similarity in results, but considerable variation. *Gambiodonta agakauitaiana* (fig. 22d-e) has riblet crowding on the posterior (ascending or right) side of the major ribs. *Australdonta raivavaeana* (fig. 23a-b), which has relatively low and inconspicuous major ribs, shows no consistent pattern of riblet crowding on one side or the other of the major ribs, although usually one side is more crowded. *Nesodiscus taneae* (Garrett) (fig. 31c-d), where major ribs are greatly reduced, shows no change in riblet spacing. Several Polynesian Charopidae (Solem, *unpublished data*) consistently had riblet crowding on the ascending rib side.

Such spacing variation can be investigated by growth studies. In the land prosobranch family Diplommatinidae, A. J. Berry (1962) has shown that *Opisthostoma retrovertens* Tomlin usually added one rib and an interspace during each 24-hr. period. Such growth could occur during both day and night periods, but usually happened overnight. Repair of shell breaks and drying of the habitat either interrupted growth or produced finer and more crowded ribs. When the snails were kept under conditions of high humidity and in total darkness, rib production increased to more than one per day.

Obviously, it is not possible to transfer this observational data to the totally unrelated Endodontidae. Available data does suggest the relative timing pattern involved in major rib formation, although not the length of the cycle. With the assumptions that the microradials are deposited at equal time intervals and that control of their deposition is partly independent of horizontal anterior growth, then the spacing pattern can be modelled quite simply. For example, in *Rhysoconcha* there would seem to be a sudden upward surge of both inter-riblet conchin template and calcium deposition that results in an underlying major rib protrusion accompanied by a widening of the area between adjacent microradials. Following this there is

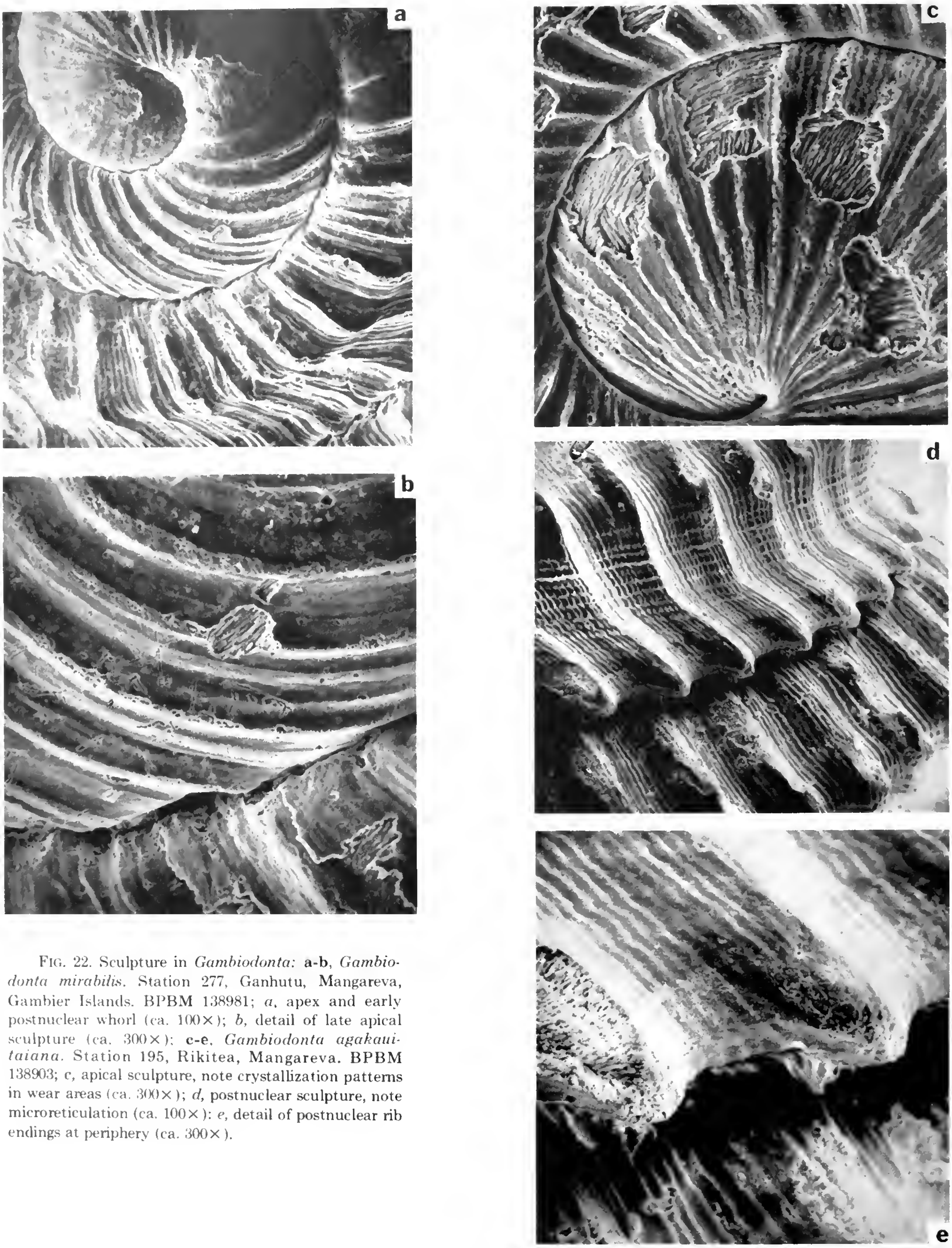


FIG. 22. Sculpture in *Gambiodonta:* **a-b**, *Gambiodonta mirabilis*. Station 277, Ganhutu, Mangareva, Gambier Islands. BPBM 138981; *a*, apex and early postnuclear whorl (ca. 100×); *b*, detail of late apical sculpture (ca. 300×); **c-e**, *Gambiodonta agakauitaiana*. Station 195, Rikitea, Mangareva. BPBM 138903; *c*, apical sculpture, note crystallization patterns in wear areas (ca. 300×); *d*, postnuclear sculpture, note microreticulation (ca. 100×); *e*, detail of postnuclear rib endings at periphery (ca. 300×).

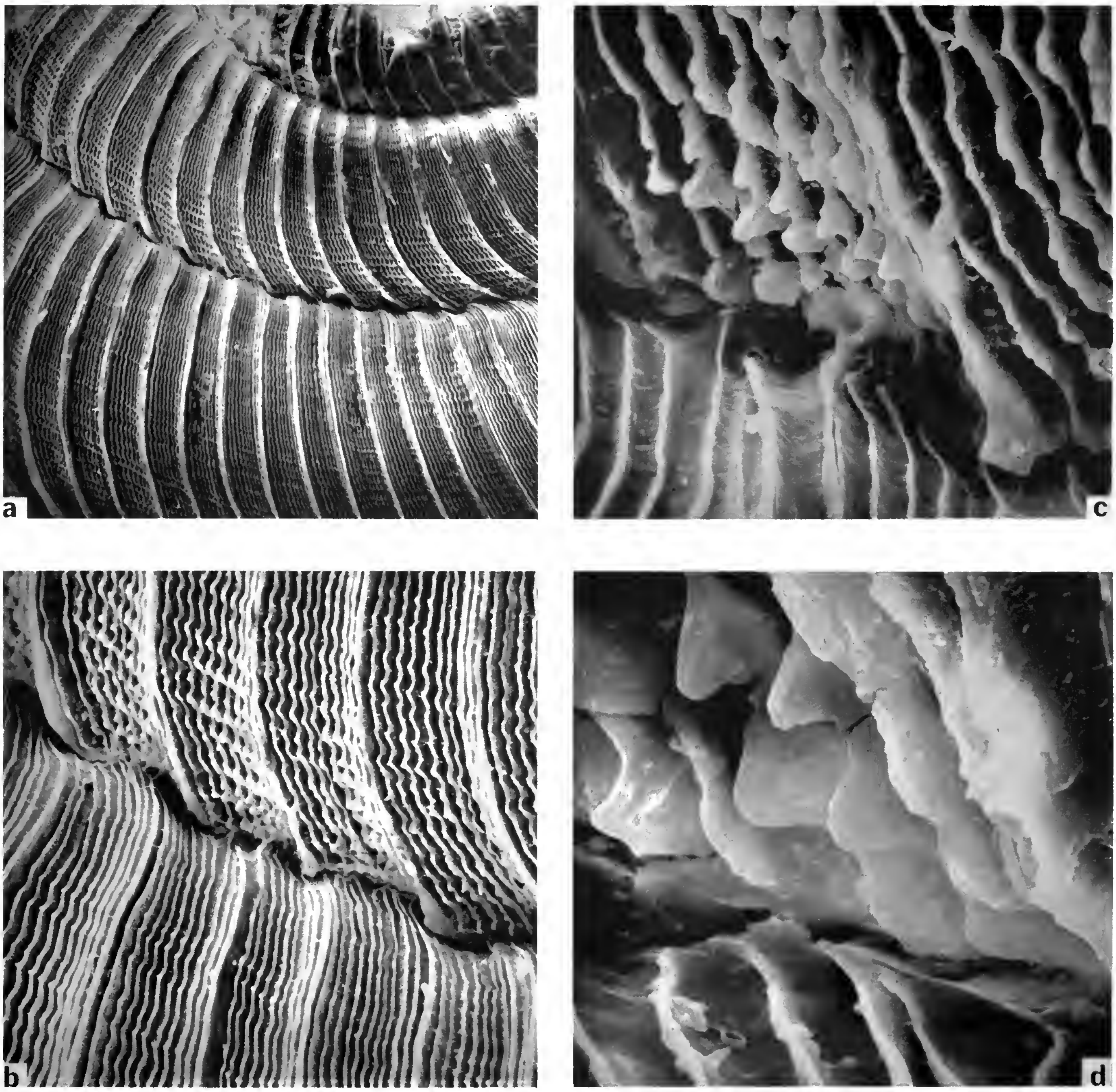


FIG. 23. Postnuclear sculpture of *Australdonta raivavaeana*. Station 674, Mt. Turivao, Raivavae, Austral Islands. BPBM 147529: **a**, portion of last two whorls, note grooved pattern in upper left (ca. 100×); **b**, suture between body and penultimate whorl (ca. 300×); **c**, detail of suture, note changed subsutural riblets (ca. 1,000×); **d**, suprasutural sculpture (ca. 3,000×).

a marked slowing in horizontal growth that results in several microradials being formed close together in the conchin template layer. Gradual return to a normal rate of horizontal increment and sudden lowering of the accretion plane to the whorl surface level starts a new rib interstice. Growth would continue at an even rate to the next surge point, starting the cycle over again. *Gambiodonta* and the Charopidae would appear to use the opposite tactic, with a slowdown in horizontal growth and resultant microradial crowding preceding the major rib peak. Acceleration of the horizontal growth rate would increase the distance between the microradials on the outer rib face before returning to the normal interval pattern. Forms with reduced ribs could have irregularity in surges producing the resultant variation in *Australdonta*. The lack of change in *Nesodiscus* probably is a result of low surface relief.

Figure 24 diagrams the pattern of these activities. The basic hypothesis that microradial construction occurs at regular time intervals, while horizontal growth is in irregular surges requires experimental testing. This theory does indicate a way in which the different riblet spacing observed could be achieved.

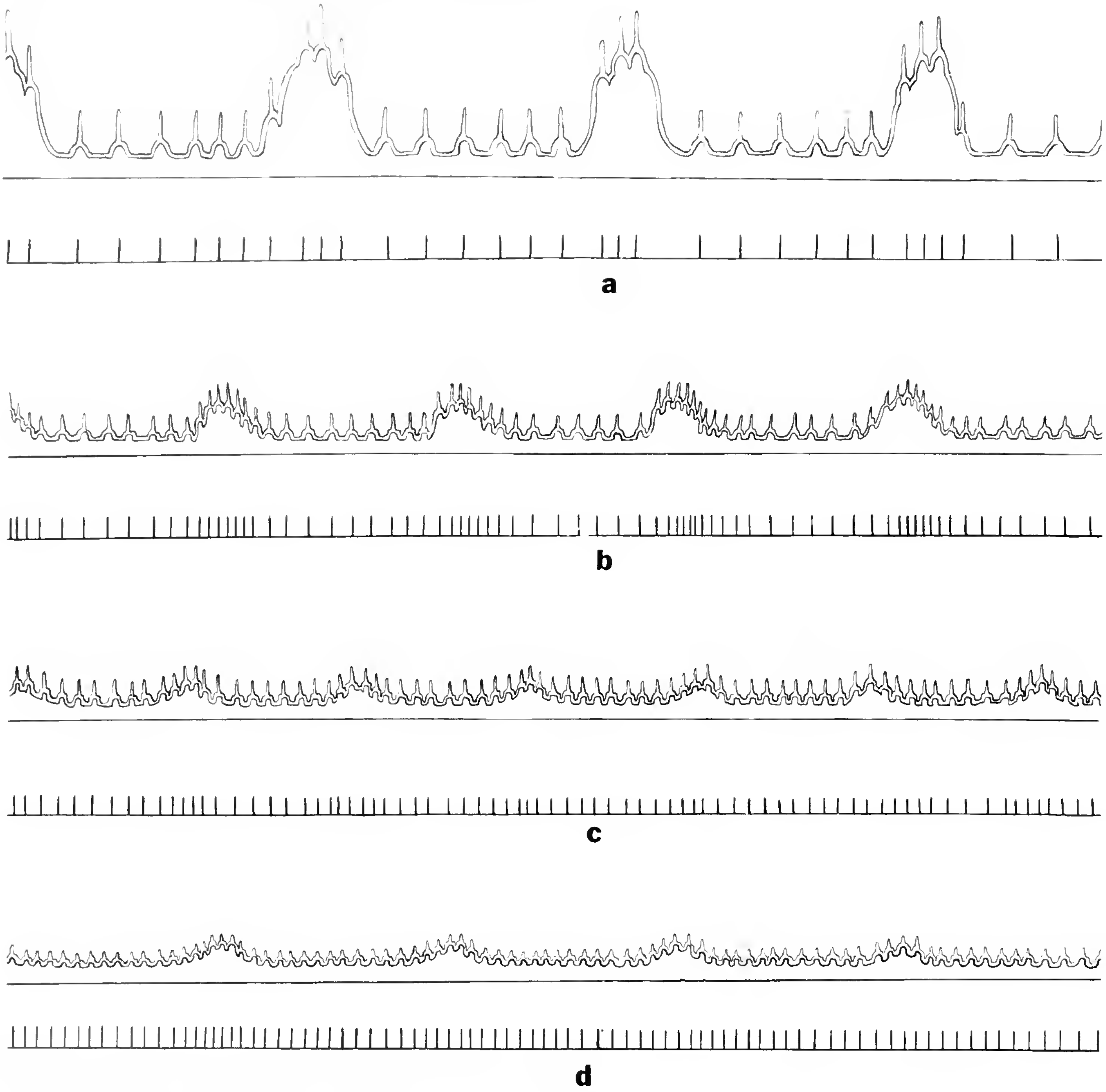


FIG. 24. Patterns of radial surface sculpture in selected Endodontidae: **a**, *Rhysoconcha atanuiensis*, based on Figure 21b; **b**, *Gambiodonta agakauitaiana*, based on Figure 22d-e, **c**, *Australdonta raivavaeana*, based on Figure 23a-b, **d**, *Nesodiscus taneae* (Garrett), based on Figure 31c-d. Upper diagram indicates cross-sectional view of shell differentiating conchin (outer) and intial calcium (inner) layers; lower diagram plots horizontal distance between radial riblets. All figures greatly enlarged, but not to same scale.

The outermost periostracal layer of conchin, a sclerotized protein layer, acts as template for the initial calcium layer. Whether this periostracum is present or splintered off in dried individuals, the apical microsculpture appears the same at 100× magnification. Even at 3,000× magnification (for example, *Minidonta hendersoni*, fig. 25d) bits of flaking periostracum are seen to conform exactly to the underlying calcium layer. This is not correct in regard to the postnuclear sculpture, where both riblets and ribs may have high, lamellate periostracal extensions. In a very few species, notably *Cookeconcha hystrix* (Pfeiffer) and *C. decussatulus* (Pease) (fig. 26a-c), the periostracum has elongated "hairs" or "setae" produced. In *Rhysoconcha atanuiensis* (fig. 21b) and *Australdonta raivavaeana* (fig. 23a) the partly lamellar extensions and underlying calcuim layers of particular ribs are obvious.

This means that while the major sculpture visible to the naked eye is composed mainly of calcium swellings, the microsculpture consists of a primary

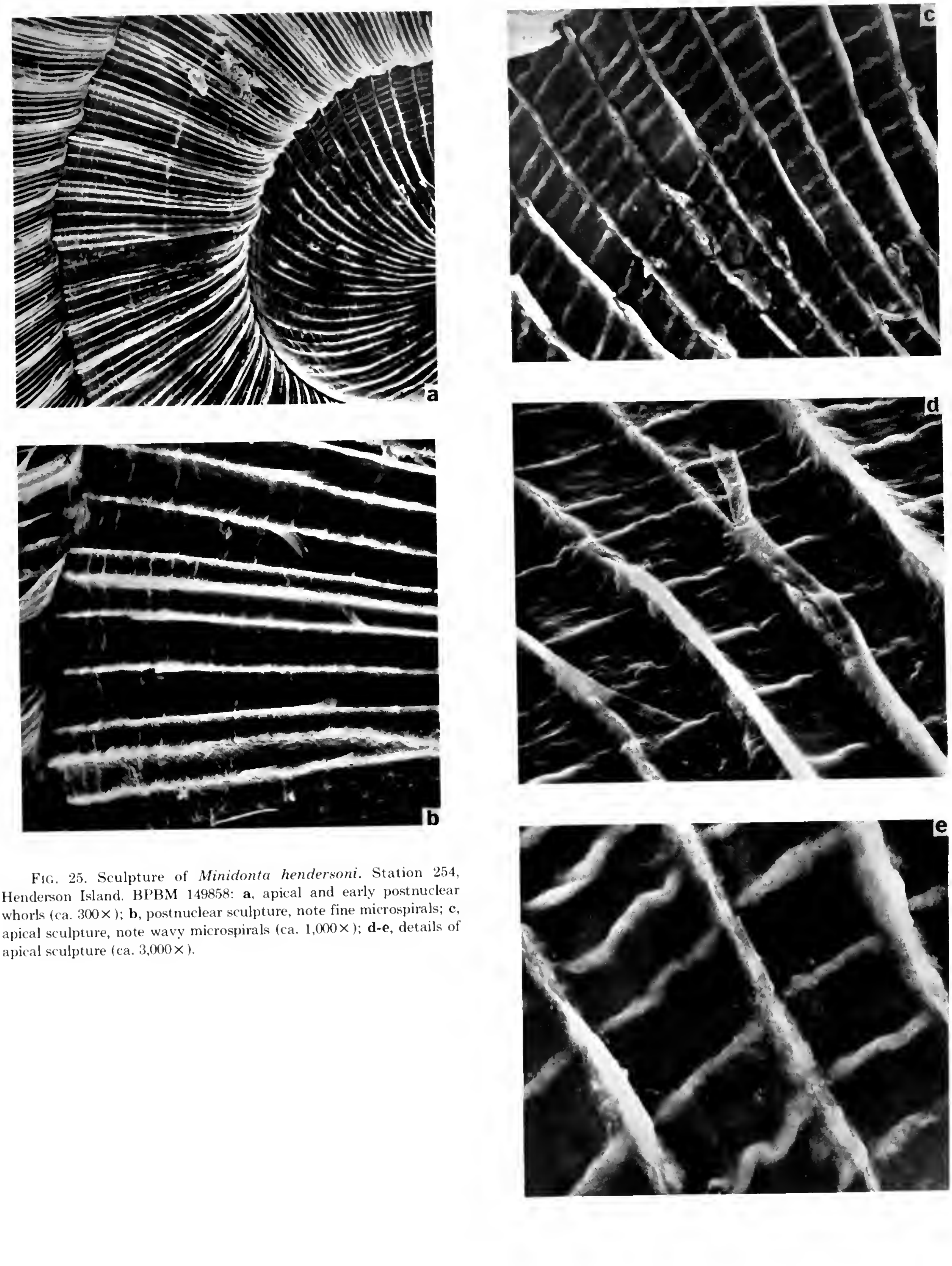
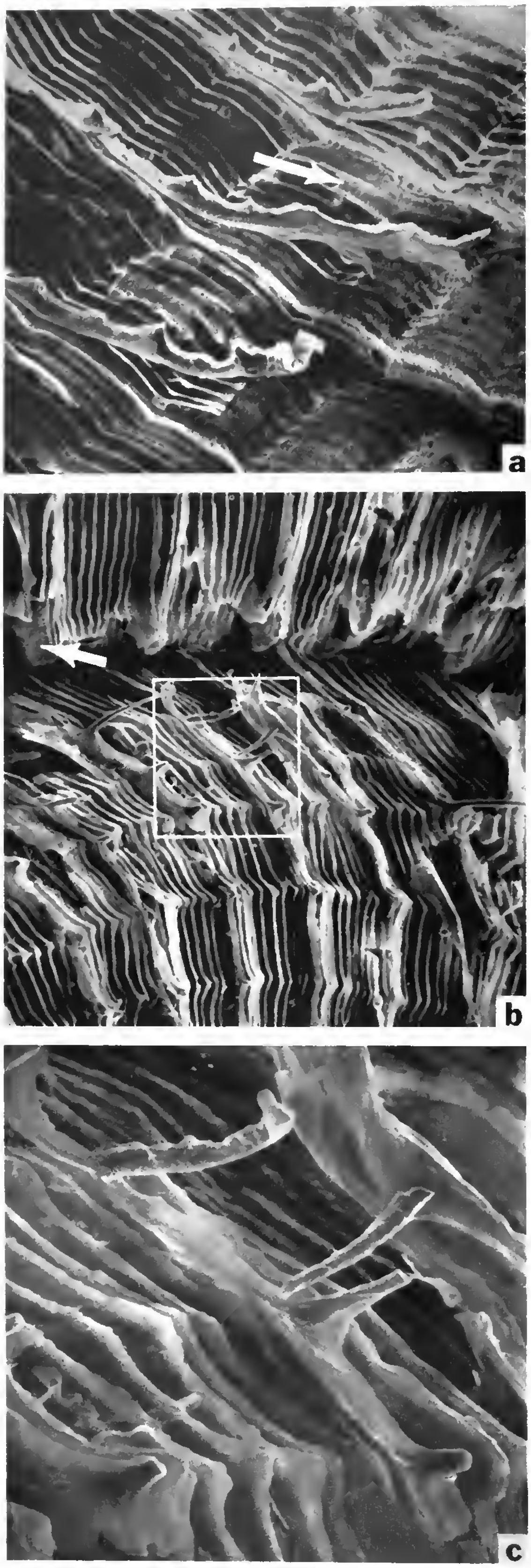


FIG. 25. Sculpture of *Minidonta hendersoni*. Station 254, Henderson Island. BPBM 149858: **a**, apical and early postnuclear whorls (ca. 300×); **b**, postnuclear sculpture, note fine microspirals; **c**, apical sculpture, note wavy microspirals (ca. 1,000×); **d-e**, details of apical sculpture (ca. 3,000×).



conchin layer underlaid, except for the periostracal fringes, by a duplicate layer of calcium. The fringes usually are extremely narrow. Probably the height of the underlying calcium riblet is a practical compromise between the need for a second line of surface irregularity in case of conchin layer loss and the desirability of keeping the vertical extensions narrow for as great a distance as possible, to retain a narrow edge when partial breakage occurs.

Family-level differences

Apical sculpture in the Endodontidae consists primitively of fine radial riblets and large single radial ridges combined with a very fine microspiral sculpture of "squiggly" cords. The latter look as if someone with a hangover had attempted, unsuccessfully, to squeeze a straight line of toothpaste from a tube. These microspirals are crowded, very narrow and seemingly independent of the radial sculpture. Typical in appearance is the apical sculpture of *Mautodontha aoraiensis* (fig. 27b). Even if the major radial elements are lost by mutation, as in *Aaadonta* (figs. 28, 29), the microspirals on the apex (fig. 29a) are diagnostic. In a few Hawaiian taxa belonging to *Cookeconcha* (fig. 30) both macro- and microsculpture are reduced on the apex, while complex postnuclear sculpture is retained. In the Lau Archipelago *Priceconcha* (Solem, 1973d) only remnants of microsculpture remain on the last two whorls. On early postnuclear whorls the microspiral sculpture usually is clearly visible, but on late postnuclear whorls secondary alterations in rib spacing or sculpture reduction frequently obscure this characteristic feature.

In contrast, the Pacific Island Charopidae have an apical sculpture primitively featuring broadly rounded spiral cords, usually 8 to 12 in number, without any radial elements. Frequently just before the termination of apical growth, one to three low radial undulations will appear in the shell surface. In a few species, the number of spiral cords has been increased to more than 20, and there are 10-20 radial undulations on the apical shell surface. Under optical examination, this mimics the appearance of the endodontid apex, but SEM examination shows that the spirals are simple cords and that the radials are surface undulations rather than ribs. Postnuclear sculpture in the Charopidae appears abruptly in a small fraction of a millimeter. Optically it resembles the Endodontidae very closely in having major and minor radials, plus secondary spiral microsculpture. The latter differ in that the microspirals are not

FIG. 26. Postapical sculpture of *Cookeconcha decussatulus* (Pease). West Maui, Hawaiian Islands. FMNH 46605: **a**, section of body whorl at 300× showing periostracum flaking from major ribs and difference in shape of periostracal extensions and underlying calcium ridge; **b**, early postnuclear sculpture at 300× showing secondary spiral cording, periostracal hairs and flaking periostracum; **c**, setal area in *b* at 1,000×, flaking periostracum at upper right twisted 90° to left and out of normal position. Arrows on *a* and *b* point to microspiral riblets in calcium layer of shell.

"squiggly," form buttresses to the microradials (for example, *Ptychodon microundulata*, see Solem, 1970b, pl. 59, figs. 9-11), and thus are much higher next to the riblets than in the trough middle.

On late postnuclear whorls the pattern of sculpture crowding and secondary modification complicates study of the microspiral elements. But no Pacific Island species has an apical sculpture that departs from the patterns outlined above. In extralimital areas, however, the pattern of apical sculpture is much more complex, with Charopidae from Australia and New Zealand, for example, showing a variety of types (Solem, 1970b, pl. 58, figs. 3-6, for example). Nevertheless, in regard to Pacific Island taxa, the nature of the apical spiral sculpture is completely correlated with the anatomically determined family units. It, together with the nature of the apertural barrier microarmature (pp. 63-65; Solem, 1973b), form the only absolute family-level differentiating conchological criteria.

Surface wear on the shell is the rule rather than the exception. Frequently the apical whorls will have sculpture remaining only in the sutures (fig. 21c). It is not unusual for specimens collected dead to have nearly all the microsculpture and much of the major sculpture missing. In such situations, cleaning of the umbilicus often will reveal perfectly preserved apical and early postnuclear sculpture. The sculpture is present in both lower and upper parts of the whorls. If transported by a stream of water, the umbilicus may hold an air bubble, while after silting of the opening, the umbilical shell surface is protected from abrasion and acid etching. Even fossils usually have unworn patches of sculpture somewhere on the shell surface or in the umbilicus.

Other sculptural elements

Additions to the basic sculpture appear macroscopically (100× magnification) as one of two types, either secondary spiral grooves as in *Mautodontha zimmermani* and all *Australdonta* taxa (except possibly *A. pharcata*), or secondary spiral cords in some 50 species. Macroscopic interpretation of the *Australdonta* sculpture (fig. 124) may be altered when additional SEM studies are made. Photographs of *Australdonta raivavaeana* (fig. 23) show a tendency towards formation of "spear-point" extensions on the microradials in the supra-sutural region and irregularly spaced undulations on the microradials as they traverse the lower whorl surfaces. Whether these are caused by undulations (= grooves) in the shell surface or by growth changes in the ribbing is unknown.

Unquestionably, a multitude of phenomena are gathered under the heading of secondary spiral cording. In species such as *Thaumatodon corrugata* (fig. 196e), *Libera garrettiana* (fig. 177c) and *Endodonta binaria* (Pfeiffer) the development of low spiral cords is obvious. In others, such as *Nesophila capillata* (Pease), *Libera umbilicata* (fig. 178c), *Libera bursatella bursatella* (Gould) (fig. 31a), and *Nesodiscus taneae* (Garrett) (fig. 31c, d), I cannot say whether the protrusions of the riblets result from the addition of very low spiral cords or represent upward protrusions of the riblets themselves. *Gambiodonta agakauitaiana* (fig. 22d-e) does seem to have low and very broad spiral cords producing the waved effect in the microradial riblets. *Aaadonta* (figs. 28c-e; 29b) seems to have small knobs on the microradial rib tops that appear as continuous cords under light microscope magnification. Throughout the text all of these phenomena are called "secondary spiral cording." While different structures are involved, reference of more than a few species to any particular type of secondary spiral sculpture is impossible without much additional use of the scanning electron microscope.

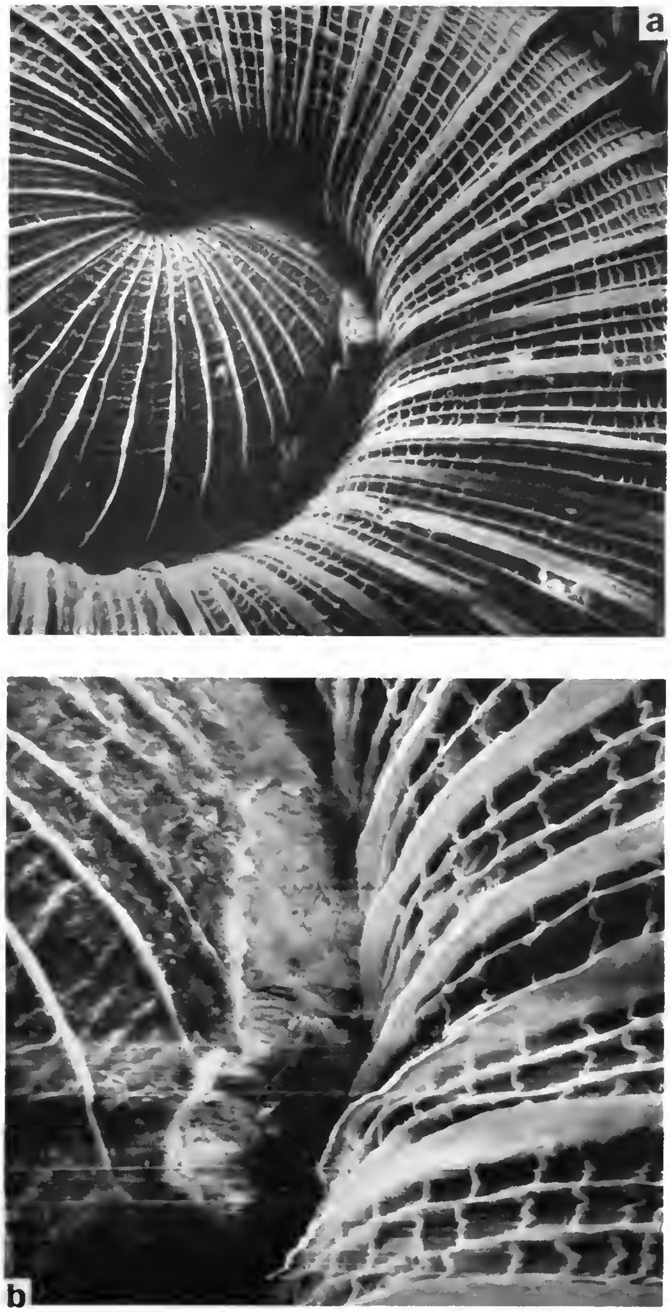


FIG. 27. Sculpture of *Mautodontha* (*M.*) aoraiensis. Station 863, Mt. Aorai, Tahiti. BPBM 145536 : **a**, apical sculpture (ca. 300×); **b**, early postnuclear sculpture, note wavy microspirals (ca. 1,000×).

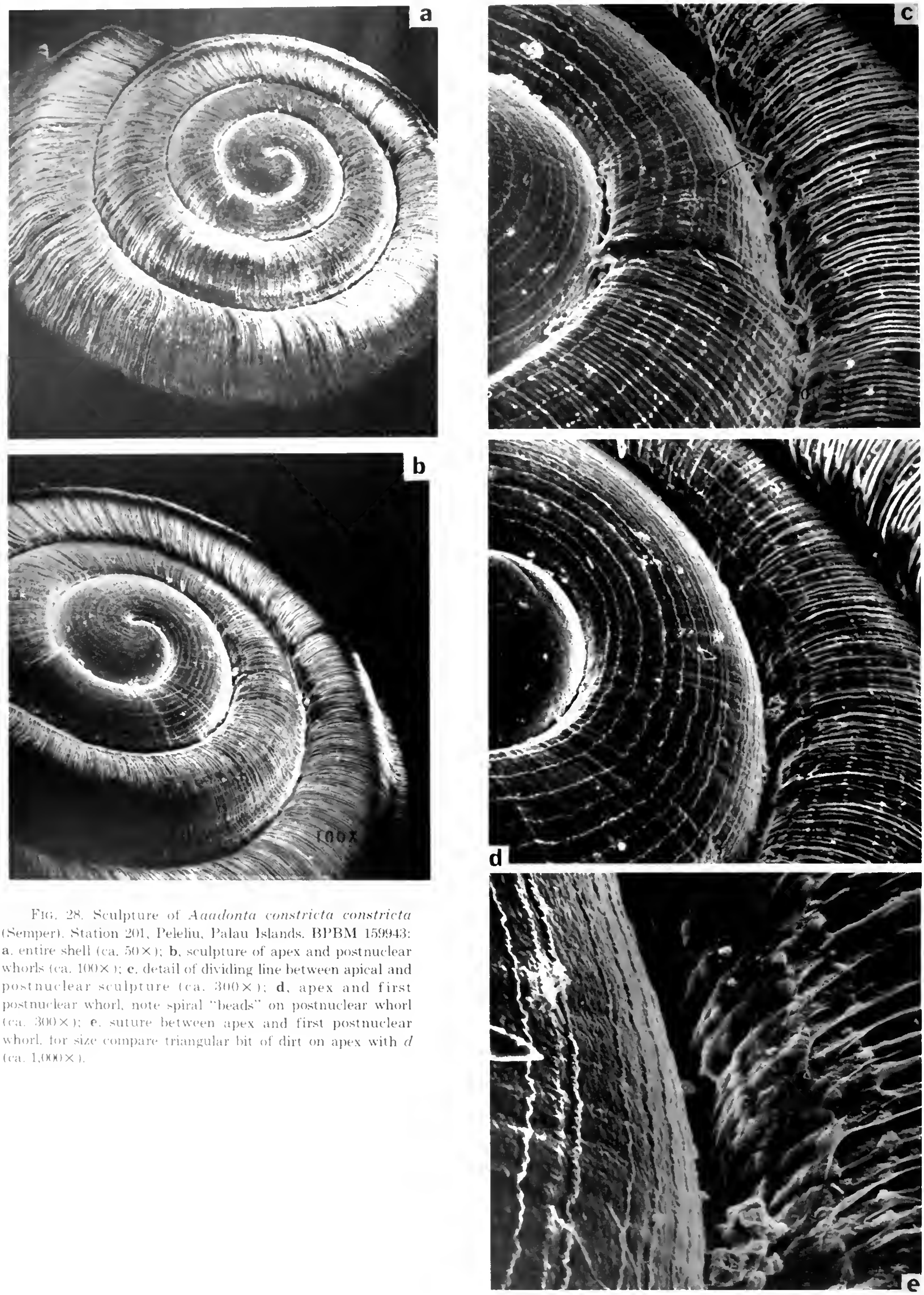


FIG. 28. Sculpture of *Aaadonta constricta constricta* (Semper). Station 201, Peleliu, Palau Islands. BPBM 159943: **a**, entire shell (ca. 50×); **b**, sculpture of apex and postnuclear whorls (ca. 100×); **c**, detail of dividing line between apical and postnuclear sculpture (ca. 300×); **d**, apex and first postnuclear whorl, note spiral "beads" on postnuclear whorl (ca. 300×); **e**, suture between apex and first postnuclear whorl, for size compare triangular bit of dirt on apex with *d* (ca. 1,000×).

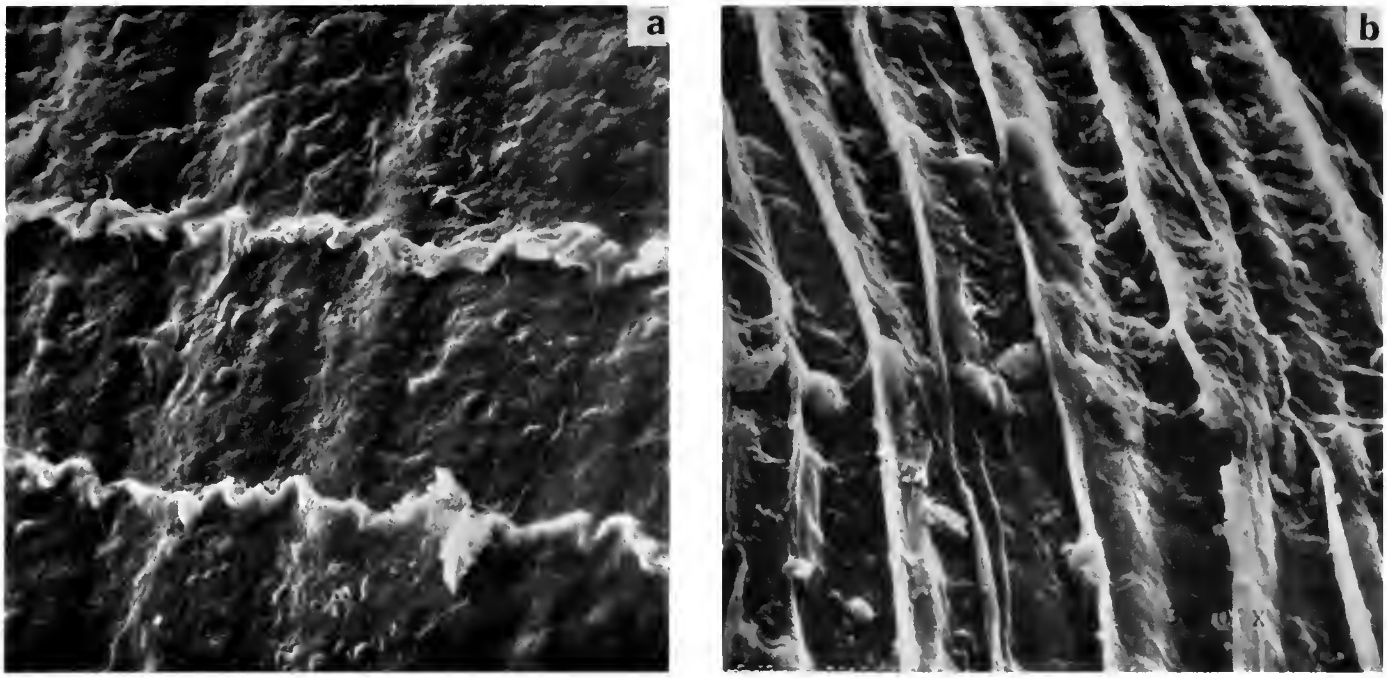


FIG. 29. Sculptural details on *Aaadonta constricta constricta*. Station 201, Peleliu, Palau Islands. BPBM 159943: a, spiral cords on apex, note irregular, wavy nature of light cords and broadly waved, lower radial growth wrinkles (ca. 3,000×); b, detail of postnuclear microradial riblets (ca. 3,000×).

Such secondary sculpture may be present on only part of the shell surface, all of the shell surface, or vary from specimen to specimen of a species. Appearance of secondary cording is not random, with only *Orangia maituatensis, O. sporadica*, and *Opanara fosbergi* of the 24 Rapan taxa having sculpture. Five of eight *Gambiodonta* and 8 of 12 *Anceyodonta* from Mangareva have cording. Eleven of 19 *Libera* and 5 of 11 *Taipidon* contrast with only 1 of 15 *Minidonta* and 2 of 17 *Mautodontha* having raised secondary spiral sculpture. Some species with secondary spiral sculpture are seen in *Cookeconcha, Endodonta, Nesophila, Thaumatodon, Pseudolibera*, and *Kleokyphus*.

Although 62 of 179 species-level taxa (34.6 per cent) have at least partial development of secondary spiral sculpture, I found no obvious correlations between development of such sculpture and other shell features. The mean adult size of taxa with such sculpture is 4.03 mm. compared with a mean of 4.18 mm. for those without secondary spiral sculpture. The latter category includes a higher percentage of those species lacking major ribbing (23.5 per cent as opposed to 15 per cent for those with secondary spiral cording). Since these are generally the larger species, I suspect the minor size difference is accounted for by this bias and does not signify any significant difference. Possibly strong secondary spiral cording in such species as *Thaumatodon corrugata* and *Libera garrettiana* is a substitute for lost major radial sculpture.

Patterns of variation

Variation in the major ribbing involves rib width, rib spacing, and reduction or loss of the sculpture. Most of the smaller species have the individual major ribs narrow, sharply defined and with almost vertical sides that flare outward just before the whorl surface. With increasing shell size, the degree of basal flare is accentuated. Finally, in several very large species such as *Gambiodonta grandis* and *G. agakauitaiana* (fig. 22) the major ribs become low swellings on the shell surface. They show scarcely any clear lateral demarcations. No meaningful measurements of rib width are possible in the latter situation, while the small size and relatively great surface relief of most species defeat any attempt at measuring individual rib widths when they are sharply defined. Considerable effort has been expended in indicating relative rib width in the illustrations prepared under my direction (MM, SH, SG, PR). The Bernice P. Bishop Museum drawings (YK) indicate only rib spacing and give no indication of rib width. Only general discussion of when widening of the ribs has occurred is presented in this report. Adequate quantification proved impossible. Usually this change is correlated with size increase, although the quite small *Thaumatodon hystricelloides* (Mousson) (fig. 197d-e), *T. euaensis* (fig. 194a-b), and *T. vavauensis* (fig. 196a-b) have broadened ribs.

Little agreement exists among malacologists concerning how to measure or the utility of rib counts. R. A. Cumber (1960, 1961, 1962, 1964) made considerable use of rib counts in analyzing geographic variation in New Zealand charopid land snails. Working primarily with species where there is a sharp break between nuclear and postnuclear sculpture, he has demonstrated least variability in counts obtained from the first or second postnuclear whorl. Successive whorls have noticeably larger standard deviations and standard errors. Most workers have counted ribs on

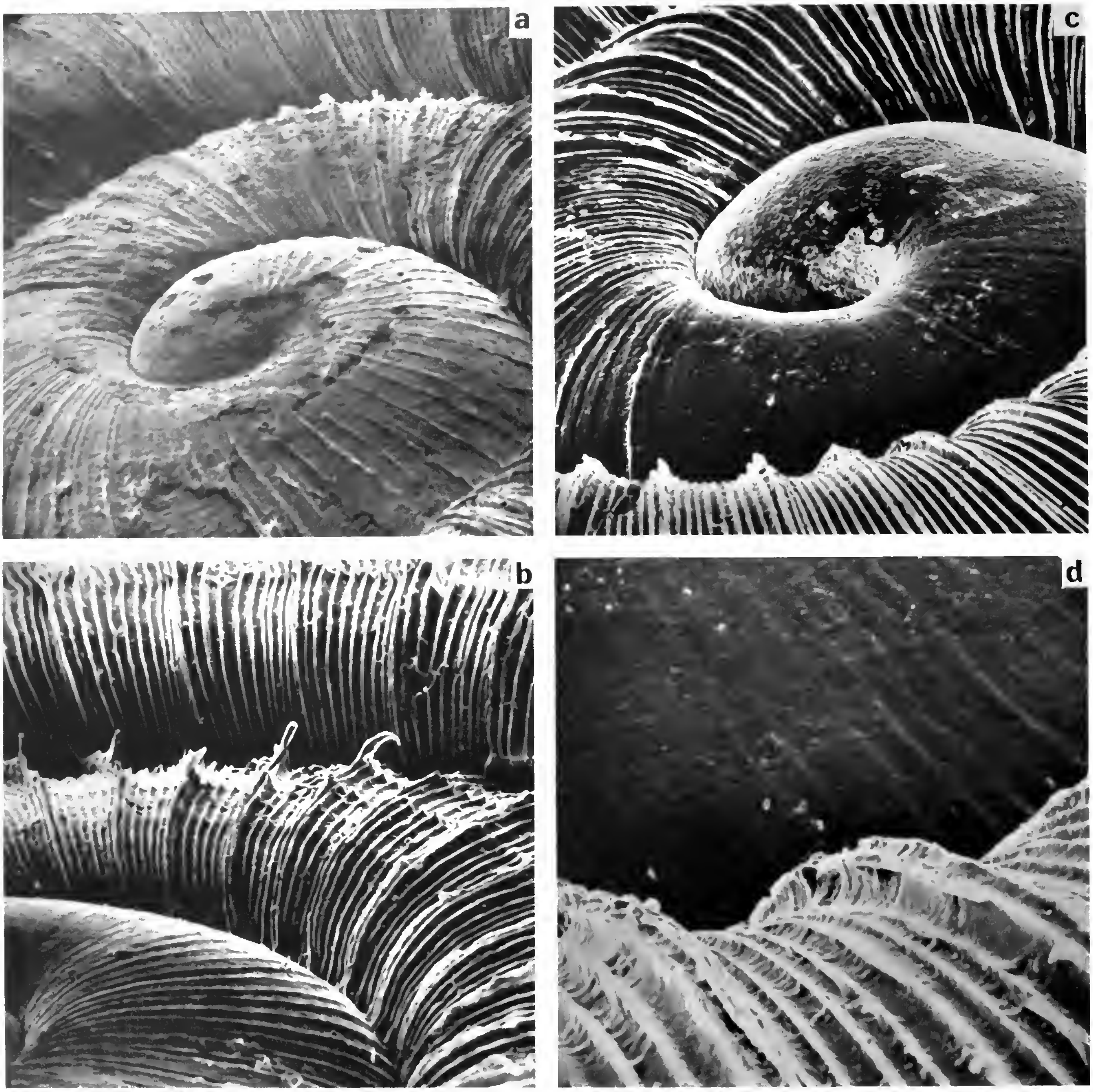


FIG. 30. Apical microsculpture of: **a**, *Cookeconcha nudus* (Ancey). Kawiki, Hawaiian Islands. FMNH 46422. 300×; **b**, *Cookeconcha decussatulus* (Pease). West Maui, Hawaiian Islands. FMNH 46605. 300×; **c-d**, *Cookeconcha hystrix* (Pfeiffer). Hawaiian Islands. FMNH 46444; *c*, apex at 300×; *d*, apex-postapical sutural area at 1,000×. Note periostracal setae on postnuclear sculpture in *b*.

the last complete whorl of growth. Cumber's method reduces intrapopulational variation, but makes a convenient index of rib spacing difficult to calculate. It also depends on having a clearly delineated nuclear-postnuclear boundary.

Species of Endodontidae have the apical sculpture continuing onto the postnuclear whorls, with at most a break in spacing that is very difficult to detect. Figures 21a, 27a, and 30a show typical examples where there is no change. Only in *Aaadonta* (fig. 28c) is a clear change visible. A practical problem of postnuclear whorl-limit recognition exists in the Endodontidae and would prevent use of Cumber's methods. The abundant material available for study was an even greater problem, since counting 60-200 ribs on each shell is quite time consuming. During post-reproductive and gerontic growth there is usually considerable crowding of the major ribbing. Frequently the last few ribs on the body whorl are highly irregular.

Rib-count measurements in this study were restricted to adult shells. In the majority of examples there was no clear nuclear-postnuclear whorl boundary, either because of growth continuity or surface

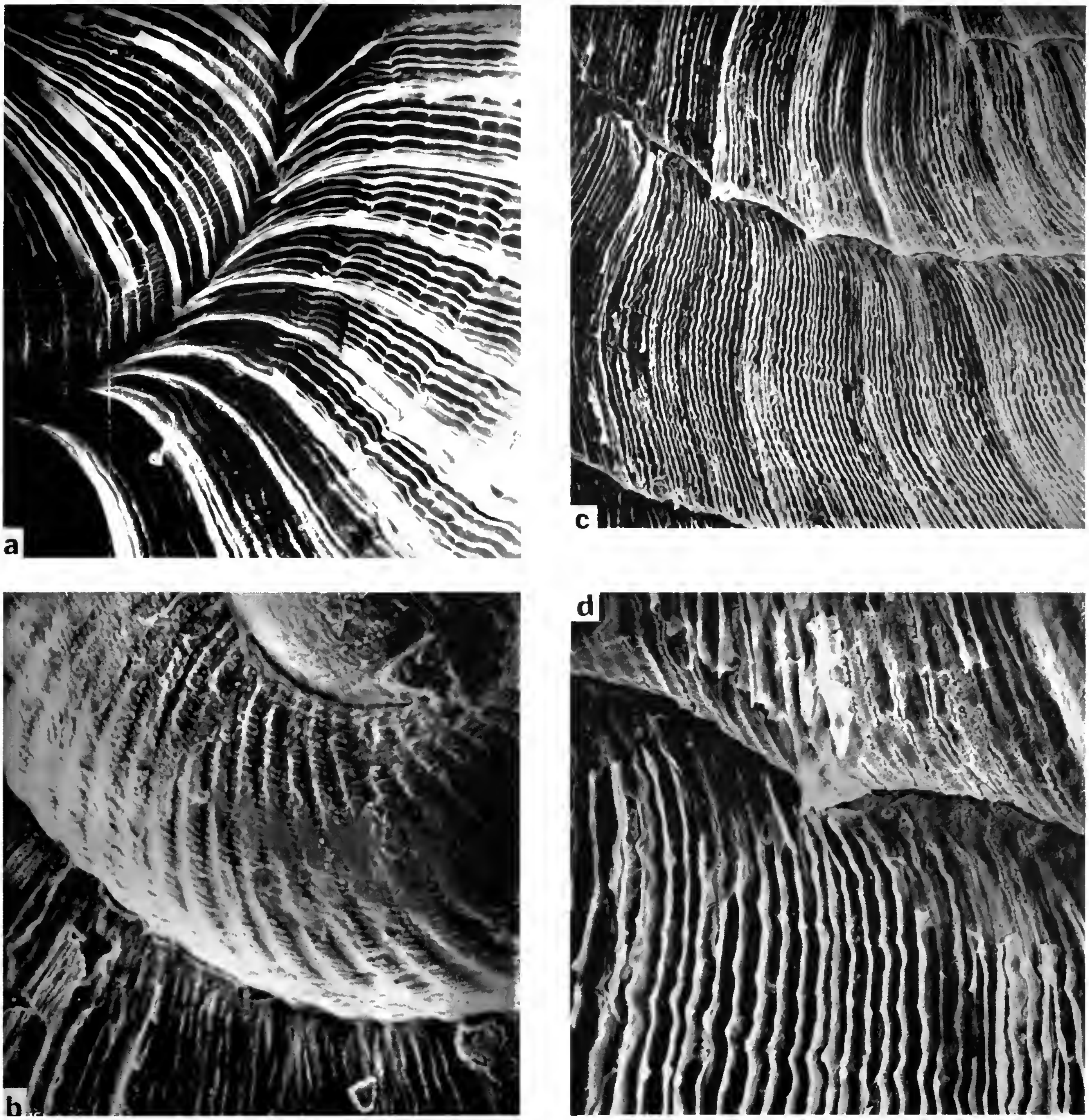


FIG. 31. Apical and postnuclear sculpture of *Libera bursatella bursatella* (Gould) and *Nesodiscus taneae* (Garrett): **a**, *Libera b. bursatella.* Station 863, Mt. Aorai, Tahiti. BPBM 142059, sutural area between apex and first postnuclear whorl, note very weak microspiral riblets (ca. 300×); **b-d**, *Nesodiscus taneae.* Borabora, Society Islands. FMNH 91853 ex Fred Button; *b*, shell apex, note broad radials and very fine and crowded spirals (ca. 300×); *c*, postnuclear sculpture with reduced major ribbing (ca. 100×); *d*, detail of postnuclear suture showing rib denticulation of lower whorl (ca. 300×).

erosion. Rib counts were made on the body whorl (fig. 32a) both to provide a convenient size dimension, shell diameter, for calculating rib spacing and because exact delineation of early postnuclear whorls was impossible.

Rib counts were made on about 40-50 per cent of the total adult specimens available. Since the complex apertural denticles found in virtually all Endodontidae provided criteria for species discrimination, detailed analysis of rib-count variation was restricted to a few large samples and the few situations involving subspecific taxa. These provide guidelines for interpreting variation in smaller samples. For every species where rib counts could be made, at least 25 per cent of the available adults were checked and species means calculated, provided less than 75 individuals were

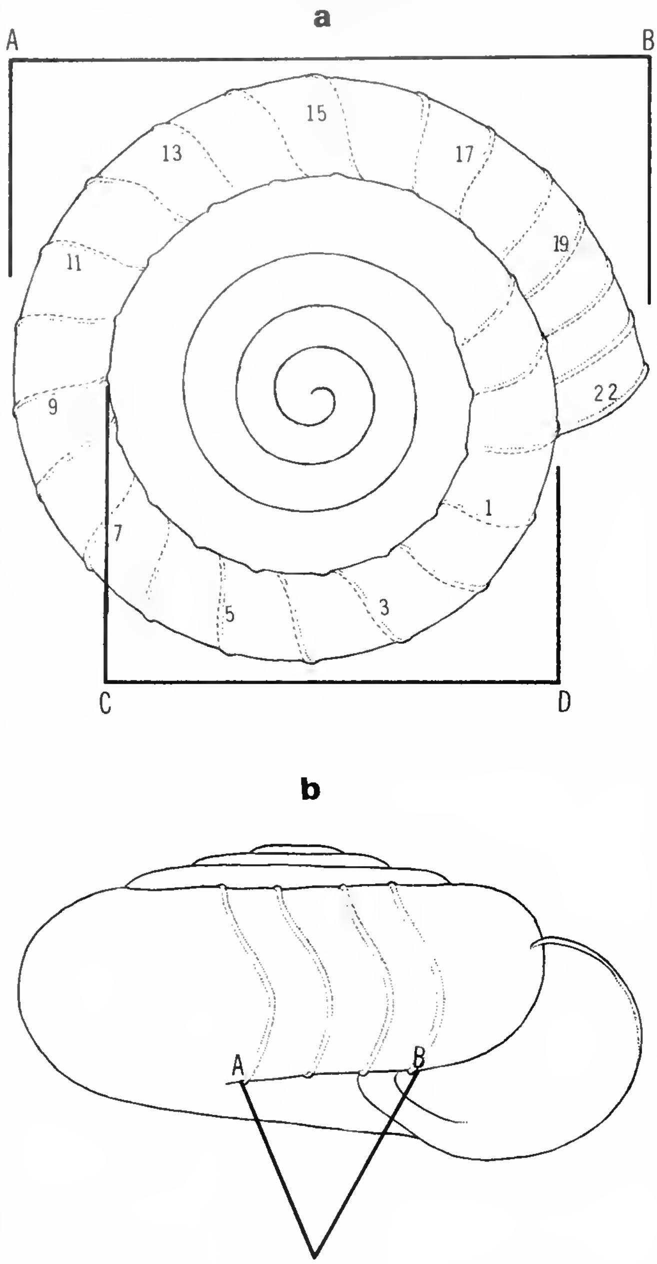


FIG. 32. Method of sculptural measurements in the Endodontidae: **a**, raw rib count with shell diameter (A-B) and body whorl sutural diameter (C-D) measurements indicated; **b**, area on body whorl (A-B) used in determining rib spacing and microriblet counts.

involved. If larger numbers were available, about 50 specimens were used. In the Charopidae, where most species lack the apertural denticles, far more attention was paid to shell sculpture variation.

Rib-count variation in local populations of *Orangia cookei cookei* (table LXXXVIII), *Rhysoconcha atanuiensis* and *R. variumbilicata* (table LXXXIV), plus *Opanara areaensis* (table LXXX) indicates only minor variation between populations of the same species or subspecies. The standard errors in these tables are consistently larger than those of Cumber (1960, p. 100) for early postnuclear whorl rib counts comprising the same order of magnitude. This reflects the variation added by grouping shells showing only a short section of gerontic rib crowding with those having up to one-quarter whorl of gerontic growth. While extending the upper range of the normal distribution curve and thus increasing the standard error, such grouping does not seem to have altered the usefulness of these counts. In a sample of 57 *Opanara areaensis,* for example, the frequency distribution of rib counts is moderately skewed (table XII). The skewness of any such frequency distribution will depend on the mix of barely adult and gerontic shells. Since even the large sample of *Libera fratercula rarotongensis* showed a slightly skewed normal distribution (figs. 1-4) quite comparable to that cited above, I have proceeded on the assumption that the samples of rib counts are approximately equally skewed unless a lack or surplus of gerontic individuals was noted during measuring. At the level of statistical analysis involved, the error introduced by this variable does not seem objectionable.

The major ribs are continuous from the parietal-palatal margin across the periphery, into the umbilicus and up to the columellar-parietal suture. The distance (= shell diameter) from lip edge periphery to the periphery on the opposite side of the shell (fig. 32a, A-B) obviously is greater than from the parietal-palatal suture on one side to the other side (fig. 32a, C-D), yet the rib number is identical. Thus any measure of rib spacing is going to be arbitrary. The ribs are more crowded at the sutures than they are on the periphery, yet they are identical in number and only slightly different in individual rib width at these two extremes. For ease in computation and expression of the zone of major environmental contact, I have chosen an index of rib frequency calculated from the raw rib count and the shell diameter. This is expressed as ribs/mm. on the body whorl. For each specimen this index was calculated by the following formula:

$$\text{Ribs/mm.} = \frac{\text{rib count on body whorl}}{\pi \times \text{shell diameter in mm.}}$$

There is an inaccuracy introduced by computing the circumference of a circle where the actual structure is

TABLE XII. - RIB COUNTS IN OPANARA AREAENSIS FROM STA. 383

Ribs	Frequency
45-49	1
50-54	15
55-59	23
60-64	9
65-69	8
70-74	1

one volution of a logarithmic spiral, but the same rib number would hold for both dimensions. Calculation of the growth curve for each specimen or species was impractical, so I have opted cheerfully for simplicity and slight inaccuracy. The bias is equally toward too great an outer whorl distance. An additional inaccuracy results from combining gerontic and pregerontic whorl sections with their quite different rib spacings. The frequency distribution for ribs/mm. (table XIII) in the same set of *O. areaensis* shows even more pronounced skewness, but is typical for measured material. The assumption is made that the same degree and direction of bias exist unless obvious departures were noted either during measurement or initial statistical analysis. Despite the inelegance of this index, it serves to differentiate closely related taxa and provides some data averaging out the number of ribs per unit distance on the shell periphery. The pattern of pregerontic rib spacing is fairly regular, but there are noticeable variations in distance between ribs. Some are caused by injuries, but most have no obvious explanation. As with the *Diplommatina* studied by Berry (1962), these probably reflect microenvironmental moisture or food fluctuations. For convenience, I have indicated these by stating the approximate width of the interstice compared with the breadth of individual ribs. These observations were taken from the body whorl periphery with the shell positioned for a side view. This area is approximately three-quarters of a whorl behind the aperture and well before the zone of gerontic rib growth (fig. 32b). A visual estimate of "one to two times," or "three to four times" their width was made to encompass variation observed over about one-eighth of the body whorl.

TABLE XIII. – PATTERN OF RIB SPACING IN OPANARA AREAENSIS FROM STA. 383

Ribs/mm.	Frequency
4.75-5.00	2
5.01-5.25	8
5.26-5.50	16
5.51-5.75	8
5.76-6.00	9
6.01-6.25	8
6.26-6.50	4
6.51-6.75	2

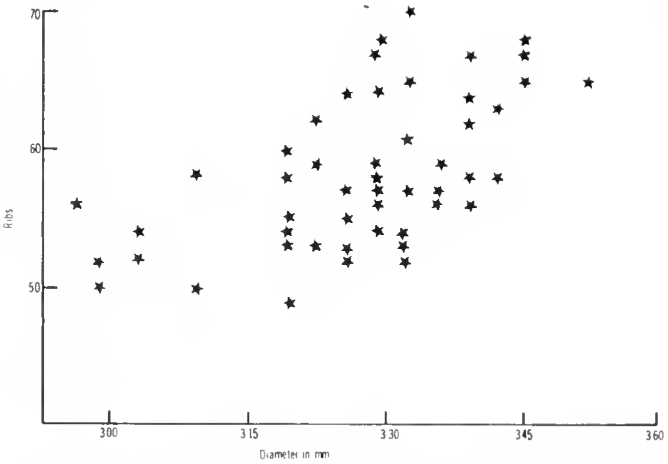


FIG. 33. Correlation between rib count and shell diameter in *Opanara areaensis areaensis* from Station 383.

There is also variation in the number of microradial riblets between each pair of major ribs. While the microradials often are close to the resolution limit for the stereoscopic binocular microscope at 100× magnification, they can be counted. Variation in major rib spacing adds to the variation in microrib counts. At the same time that major rib width in relation to the interstices was estimated, I counted the number of microradials present between crowded and more widely spaced ribs on the same portion of the body whorl (fig. 32b). The observed range is cited as "two to

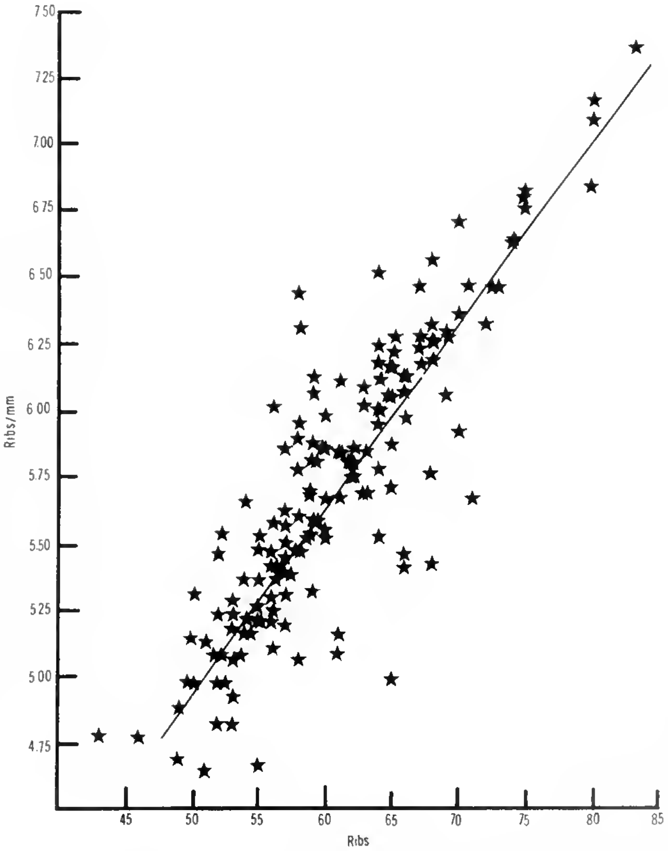


FIG. 34. Correlation of ribs and ribs/mm. in *Opanara areaensis* (all adult material).

TABLE XIV. - CORRELATION OF MICRORADIAL COUNTS WITH MAJOR RIB COUNTS AND SHELL DIAMETER IN THE ENDODONTIDAE

Estimated Number of Radial Riblets	Number of Taxa	Median Group Rib Count	Mean and Range of Group Rib Count	Median Shell Diameter in Group	Mean and Range of Shell Diameter in Group
1-2	3	250	231.7(195-250)	2.15	2.40(1.97-3.07)
2-4	4	150	145.1(60.8-225)	3.79	3.62(1.73-5.17)
3-5	19	113	114.1(61.8-250)	3.27	3.33(2.25-6.29)
4-6	27	94	97.8(60.6-178)	3.60	3.64(2.16-6.72)
5-8	36	78	85.9(40.3-202)	3.36	3.56(1.68-6.59)
6-10	18	67	70.2(41.0-108)	3.84	3.85(2.68-5.79)
8-12	25	61	58.9(19-109)	4.02	4.11(2.00-8.46)

four" or "five to eight" radial riblets and is based on observation of both specimens with visually crowded major ribs and visually more widely spaced major ribs whenever abundant material was available. The cited figures are estimates and do not represent averaged data.

In summary, basic data recorded for each specimen consisted of raw body whorl rib count and an index of rib spacing calculated from the shell diameter. For each species, based upon observations of a few specimens, estimates were made as to the number of microradials between each pair of major ribs and an estimate of relative rib-interstice width on the first portion of the body whorl. The presence or absence of secondary sculpture was noted and any progressive changes in the postnuclear sculpture during ontogeny were recorded in the written diagnoses.

TABLE XV. - SHELL DIAMETER AND RIB SPACING IN THE ENDODONTIDAE

Ribs/mm.	Number of Taxa	Median Shell Diameter	Mean and Range of Shell Diameter
LESS THAN 2	4	6.40	7.26(4.28-12.26)
2.00-2.99	9	4.98	4.91(3.06-7.30)
3.00-3.99	9	4.96	5.28(3.88-7.60)
4.00-4.99	11	4.51	4.60(2.77-6.59)
5.00-5.99	8	4.12	4.03(2.90-4.89)
6.00-6.99	19	3.74	3.61(1.87-4.73)
7.00-7.99	11	3.36	3.87(2.61-5.42)
8.00-9.99	20	3.07	3.32(1.79-6.72)
10.00-12.99	22	3.04	2.97(1.73-5.17)
13.00-19.99	15	2.84	2.97(1.68-4.61)
MORE THAN 20	5	2.15	2.49(1.83-3.43)

Although there is a general pattern of little difference between populations in respect to rib counts and rib spacing, variation within a particular population is rather large. Using material of *Opanara areaensis* as an example, Figures 33 and 34 indicate the typical situation. Rib count does increase with shell diameter (fig. 33), but the correlation (r = 0.56) is not significant. When rib spacing is correlated with raw rib count (fig. 34), the relationship is slightly tighter, but the variation is large enough that individual specimen measurements have little predictive value. The low inter-populational variation reflects the fact that nearly all species of Endodontidae are restricted to the leaf litter zone in dense undisturbed forests. Variation in the moisture and temperature environment under these conditions is minimal, hence ecophenotypic changes are predicted to be minor.

Correlated variations

While statistical treatment of data for individual populations was done in many cases, generally only the mean and range were calculated for each subspecies and species. Although considerable analysis of interspecific sculptural variation patterns has been undertaken, full elucidation of this will be deferred until data from the Charopidae and extralimital taxa are available for comparison. Relationships between shell size, niche and surface sculpture are complex. Only a few of the more obvious factors will be discussed at this time.[1]

A. *Rib spacing.* — Within the family Endodontidae, 140 species-level taxa retain major radial ribs on the entire body whorl. While in a few of these taxa only very worn or fossil shells were available, for the

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[1] Data on *Priceconcha* and *Thaumatodon spirrhymatum* (Solem, 1973d) are not included below.

TABLE XVI. - CORRELATION BETWEEN RIB SPACING AND SHELL DIAMETER IN THE ENDODONTIDAE

	Ribs/mm.										
$\overline{X}$ Diameter	Less Than 2	2.00-2.99	3.00-3.99	4.00-4.99	5.00-5.99	6.00-6.99	7.00-7.99	8.00-9.99	10-12.99	13-19.99	Over 20
1.50-2.00						1		1	4	2	2
2.01-2.50						1		2	2	4	1
2.51-3.00				1	1		5	6	5	2	
3.01-3.50		1				4	5	5	7	4	2
3.51-4.00		1	1	2	3	8	2	4	3		
4.01-4.50	2	2	2	1	2	4	4				
4.51-5.00		1	2	4	2	1	1			3	**b**
5.01-5.50		2		1			1		1		
5.51-6.00			1	1				1			
6.01-6.50		1	2			**a**					
6.51-7.00				1				1			
7.01-7.50		1									
7.51-8.00			1								
Over 8	2										

TABLE XVII. – SIZE AND DEGREE OF SCULPTURE REDUCTION IN LARGER ENDODONTIDAE

Major ribs present subapically, absent on lower spire and body whorl	$\bar{X}$ D
Kondoconcha othnius	4.06
Libera spuria	4.83
Nesodiscus taneae	4.89
Endodonta laminata	6.22
Libera tumuloides	6.51
Nesodiscus magnificus	11.19

Major ribs absent, microsculpture well developed	$\bar{X}$ D
Nesodiscus obolus f. obolus	4.76
Libera garrettiana	4.85
Nesodiscus f. acetabulum	5.12
Nesodiscus huaheinensis	5.17
Nesodiscus obolus f. celsus	5.50
Nesodiscus cretaceus	5.62
Nesodiscus fictus	6.47

Shell surface smooth except for growth wrinkles	$\bar{X}$ D
Endodonta concentrata	5.06
Nesodiscus fabrefactus f. piceus	6.06
Libera heynemanni	6.52
Endodonta lamellosa	6.61
Endodonta kamehameha	6.91
Endodonta marsupialis	7.20
Nesodiscus fabrefactus	7.46
Endodonta fricki	8.99
Nesophila tiara	11.29

great majority it was possible to record the basic data as outlined above. Tables XIV and XV present the results of tallying combinations of variables. In Table XIV species have been grouped as to the estimated number of radial riblets, then rib counts and diameters tallied for each group. There is a clear pattern for rib counts to drop drastically between groups with an increase in number of radial riblets. The same groups show very little change in shell size as measured by both mean and median diameter. Only where the number of riblets drops to one or two is there a marked decrease in diameter, and only where the number rises to between 8 and 12 is there an average increase in shell size.

TABLE XVIII. – SHELL SIZE AND SCULPTURE REDUCTION IN POLYNESIAN ENDODONTIDAE

Shell diameter	Total taxa	Taxa with reduced sculpture	Per cent of taxa with reduced sculpture
3.00 mm. or less	42	2	4.8
3.01-4.75	82	4	4.9
more than 4.76 mm.[1]	44	22	50.0

1. Two species, Pseudolibera lillianae and Kleokyphus hypsus, are based on single adults whose surface is so worn that ribbing pattern is unknown.

The relationship between rib spacing and shell diameter (tables XV and XVI) is not quite so tight. Although the median diameter shows a simple pattern of larger shells having fewer ribs/mm., the range within each group is large and mean shell diameter departs from the even scale.

Much of this departure can be explained through reference to Table XVI. Most species clump within a relatively narrow transverse zone. The exceptions in the area marked "B" are *Mautodontha boraborensis* (Garrett), *Australdonta pharcata,* and *A. ectopia.* All three are species at or near the *Nesodiscus* level of specialization, which is characterized by increased size, great rib crowding and reduction, plus umbilical widening. Other taxa on the *Nesodiscus* level lack major radial ribs on the body whorl and hence are not included on this chart. The 11 species in area "A" include eight *Libera, Gambiodonta grandis, Cookeconcha jugosus* (Mighels), and *Planudonta concava.* The *Libera* and *Gambiodonta* have greatly altered growth patterns because of brood-chamber formation. These changes produce a low diameter in relation to shell volume. The elevated spire and strong downward growth vector mean that the last few whorls show little increase in diameter when compared with a normally coiled shell. The offset in the chart of these species results from growth alteration. *C. jugosus* and *P. concava* are very large species with few and quite widely spaced radial ribs.

B. *Rib reduction.* – While major radial ribbing is present in most taxa, many species have the ribs reduced or absent. This state is arrived at in a number of different ways, the simplest being complete loss of both apical and postnuclear major radial ribs without any alteration in the microsculpture. This is restricted to the only Micronesian endodontid genus, *Aaadonta.* All nine taxa in this genus completely lack major ribbing, but retain typical microsculpture with no suggestion of size decrease.

In a few species, *Thaumatodon euaensis, T. subdaedalea, T. corrugata,* and *Libera subcavernula* (Tryon, 1887), the major radial ribs are prominent on the spire and usually well onto the body whorl, but before the actual beginning of gerontic growth they fade into irregularity and thus cannot be counted with any accuracy. Except for the *Libera,* these are quite small species.

Progressive sculpture reduction can be divided into three stages: 1) retention of major ribs on the upper spire with their loss on the lower spire and body whorl; 2) complete loss of major ribs but retention of a well-developed microsculpture that is clearly visible at less than 50× magnification; and, finally, 3) reduction or loss of the microsculpture producing a smooth surface, even at 50× magnification, except for gerontic growth wrinkles. Table XVII lists the species belonging to each category in ascending size order. While first glance suggests that this may be a pure phyletic phenomenon, since 20 of 22 taxa belong to *Nesodiscus, Endodonta,* and *Libera,* Table XVIII demonstrates

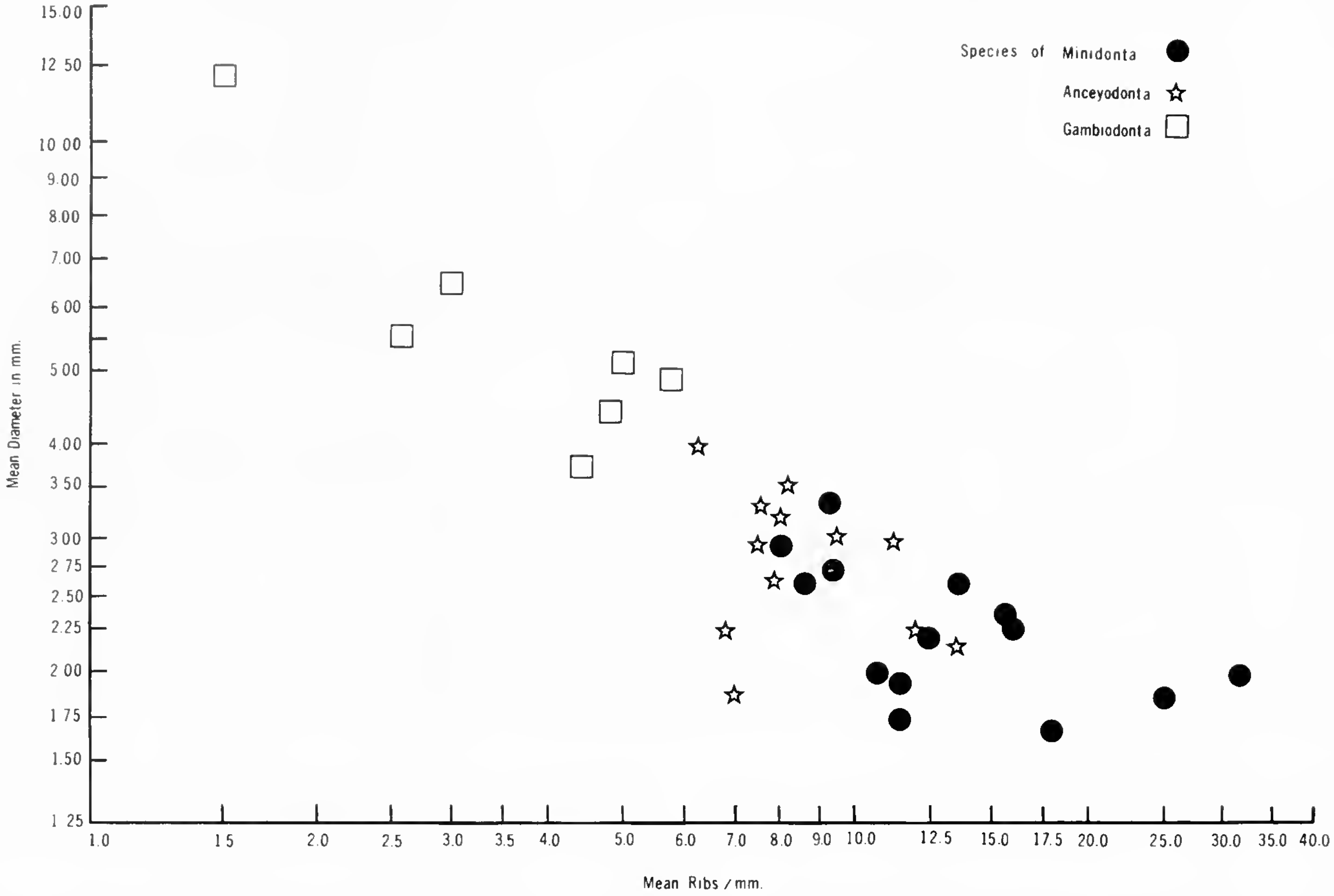

FIG. 35. Relationship of mean shell diameter to major rib spacing in species of *Minidonta, Anceyodonta,* and *Gambiodonta* on a double log scale.

that rib reduction is a size-correlated phenomenon. Of the 22 large species retaining prominent radial ribbing, there are 11 species of *Libera,* 5 *Gambiodonta,* 4 *Cookeconcha,* and single species each of *Taipidon* and *Planudonta.* Hence concentration of the species with reduced sculpture in a few genera parallels the restriction of large size to a few phyletic lines. Phyletic factors are involved, since only 4 of 15 large *Libera,* no large *Gambiodonta,* but all large *Nesodiscus* and *Endodonta* show sculpture reduction. The groupings in Table XVII represent similar stages in different phyletic series and no absolute correlation between size and stage of ribbing reduction was expected. Nevertheless the tendency for larger size to correlate with a greater degree of sculpture reduction in obvious. On an overall basis (table XVIII), major rib reduction clearly is size associated, since there is a tenfold increase in rib reduction frequency once a size of 4.75 mm. is surpassed.

Within the *Minidonta-Anceyodonta-Gambiodonta* lineage there is a clear pattern of change in rib spacing with size increment. When plotted on a double log chart (fig. 35), the pattern in the larger species is highly correlated, although in the smaller species there is greater scatter. The latter is the result of drastic alterations in shell shape, such as the flattened spire and widely open umbilicus of *Anceyodonta andersoni.*

The above discussion has been limited to situations where sculpture is reduced evenly over whorl surfaces on progressively larger parts of the shell. Sculpture reduction on only part of the whorl surface with retention of major ribbing on other sections is equally possible, but has occurred less frequently.

Two species, *Endodonta binaria* (Pfeiffer, 1856) from Kauai, Hawaii and *Kleokyphus callimus* from Makatea have the sculpture reduced above the body whorl periphery, but remaining prominent on the shell base. In *E. binaria* the broadly rounded major ribs are prominent on the upper spire, then gradually diminish in height, fading out well before the body whorl, but remaining prominent below the periphery up to the lip edge. *K. callimus* has normal ribbing below the shell periphery, but above the periphery the major ribs are scarcely larger than the microradials and do not change in size from the apex to lip edge.

Seven large species have the reverse situation, with major radial ribbing drastically reduced below the whorl periphery (table XIX). Except for *L. cookeana,* all these species have keeled or protruded peripheries. Such rib reduction is of obvious selective value. During growth the parietal wall callus must be deposited on the lower outer palatal surface of the preceding whorl. This callus either must be thick enough to cover completely the major ribs or else the ribbing must be absorbed prior to callus formation. Either tactic is wasteful in terms of energy utilization when the ribs are large. Rib building requires calcium extraction from the environment and then energy expenditure in deposition. Subsequent energy use to dissolve and resorb or to completely cover the ribs with additional calcium layers would be considerable. Size reduction of the subperipheral ribbing thus increases the snail's efficiency. Considering just the 14 largest species that retain major radial ribbing (table XIX), those with sub-peripheral rib reduction are noticeably larger than those retaining large sub-peripheral ribs. The disparity would be greater except for *Gambiodonta mirabilis*, which is the smallest species of the group, yet shows dramatic rib reduction (fig. 188c-d). The very high and prominent supra-peripheral ribs in this species and its development of very prominent protruded keels indicates the energy-use advantage in having the subperipheral sculpture reduced in size.

When the above data is combined with that in Table XVII, the extent of size correlated rib reduction is even more marked. Combining the seven species cited above with the 22 species over 4.75 mm. in diameter that show both sub- and supra-peripheral rib reduction, 29 of the 44 taxa (65.9 per cent) comprising the larger endodontid species show at least partial rib reduction. The six smaller species showing rib reduction referred to in Table XVIII consist of the three *Thaumatodon* with rib reduction on the last part of the body whorl, the two species showing only supra-peripheral rib reduction (*Endodonta binaria* and *Kleokyphus hypsus*) plus the peculiar Rapan species *Kondoconcha othnius*.

An exception to this pattern is seen in *Priceconcha tuvuthaensis* Solem (1973d). Here virtually all sculpture is absent from the apex and spire with only traces of micro-reticulations and vague larger peripheral irregularities suggesting major rib remnants on the body whorl. Since its maximum recorded size is only 4.54 mm., the extent and completeness of sculpture reduction is unusual. Probably this correlates with a habitat shift, since the live collected individuals were obtained on the trunks of trees up to 10 ft. above ground level. Only a few *Cookeconcha* and *Libera bursatella bursatella* have been taken above ground level, with the remaining species litter or subcortical forms.

Data concerning the reasons behind this pattern of rib reduction once a size of about 4.75 mm. is obtained will be presented elsewhere in conjunction with discussion of the Charopidae and taxa from other areas.

TABLE XIX. – SHELL SIZE AND SUBPERIPHERAL RIB REDUCTION IN LARGER ENDODONTIDAE

No subperipheral rib reduction

Species	$\bar{X}$ D
Libera fratercula fratercula	5.60
Libera recedens	5.66
Planudonta concava	5.79
Libera streptaxon	6.06
Cookeconcha jugosus	6.18
Libera fratercula rarotongensis	6.59
Libera gregaria	6.72

Average $\bar{X}$ D = 6.09

Subperipheral rib reduction	$\bar{X}$ D
Gambiodonta mirabilis	5.54
Gambiodonta tumida	6.18
Pseudolibera lillianae	6.42
Libera incognata	7.30
Libera cookeana	7.60
Libera jacquinoti	8.46
Gambiodonta grandis	12.26

Average $\bar{X}$ D = 7.68

In the above discussion of surface sculpture, two patterns emerge. First, that rib spacing is determined by an interaction of rib width, distance between ribs, number of microradial elements, shell size, and degree of spire protrusion in non-brood chamber taxa. Within broad limits and more closely within particular phyletic lineages, larger species will have fewer major radial ribs per unit distance on the periphery. Secondly, reduction or loss of both macro- and microsculptural elements is associated with increased size.

These trends can be seen in relation to particular phyletic situations. On Rarotonga *Libera fratercula* retains large radial ribs, *L. subcavernula* has ribbing reduced on the body whorl, and *L. tumuloides* has lost the major ribbing completely. The latter two species were restricted to interior valleys of Rarotonga and presumably derived from the coral boulder zone *L. fratercula*. While the Rarotongan shoreline race of *L. fratercula* is quite large (mean diameter 6.59 mm.), the nominate race from the offshore islets of Rarotonga and elsewhere in the Cook group is smaller (mean diameter 5.60 mm.) than *L. subcavernula* (6.29 mm.) and *L. tumuloides* (6.51 mm.). If *L. fratercula* originated on one of the other Cook Islands and *L. f. rarotongensis* is secondarily enlarged, then this forms a typical "rib reduction-size increase" series.

In Hawaii, the very small *Endodonta ekahanuiensis* (mean diameter 2.77 mm.) has prominent ribbing, which is reduced in the larger *E. binaria* (4.26 mm.), further reduced in *E. laminata* (6.22 mm.) and greatly reduced in the other described species, whose mean diameters range up to 8.99 mm. *Nesophila capillata* (Pease) (mean diameter 4.46 mm.) has fairly prominent radial ribs, while the much larger (mean diameter 11.29 mm.) *N. tiara* (Mighels) has weak ribs on the upper spire, but lacks major sculpture on most of the surface although showing growth wrinkles. A similar series is seen in the Society Island genus *Nesodiscus,* where the smaller species, *N. taneae* (Garrett) and *N. obolus* (Gould) (mean diameters 4.89 and 5.08 mm., respectively), retain vestiges or very crowded radial ribs; species of intermediate size, *N. huaheinensis* (Pfeiffer), *N. cretaceus* (Garrett), and *N. fictus* (Pease) have fairly prominent micro-sculpture; and the very large *N. fabrefactus* (Pease) is macroscopically smooth. Only the extremely large *N. magnificus,* known from a single very worn adult, departs from this pattern by apparently retaining moderate sculpture.

Functional significance of sculpture

Such a high percentage of the species probably is extinct that experimental field work concerning the relative efficiency of the several sculpture types no longer may be possible. The sculpture does serve to break up the shell surface with a series of narrow protrusions. These are more numerous and closer together in smaller species than in larger species. A series of narrow protrusions coming into contact with moist granular material in the environment is much less apt to adhere than is a relatively smooth surface. Since the Endodontidae live in the upper soil and litter layers, under stones or in rotting logs, and are constantly touching moist or wet granular materials, avoidance of surface debris accumulations is a major problem. The less-than-3-4 mm. species in particular have to cope with comparative "boulders" that, when coated with a water film, would tend to adhere strongly to any passing object. This adds not only to the weight of shell to be transported by the snail, but also would increase the volume of the shell and thus impede movement through narrow crevices. Although the complex sculpture increases *total* surface area of the snail shell, it drastically reduces effective *contact* surface area (fig. 24) between the shell and particles in the environment.

The surface sculpture of the endodontid land snails seems to be an adaptation to minimize accumulation of trash on the shell. Many minute arthropods accomplish this by use of waxy surface coatings. Investigation of the surface properties for the smooth "zonitoid"–like periostracum in such Holarctic taxa as *Retinella, Zonitoides, Vallonia,* and *Carychium,* whose basic niche is similar to that of the Endodontidae, but which belong to divergent families, in contrast to the periostracum of such sculptured taxa as *Discus, Punctum, Striatura,* and many pupillids — probably will yield important results. All litter snails must solve, or live with, the tendency to pick up particles from the environment. Prominent surface sculpture seems to be a primary means of minimizing particle accumulation.

OTHER EXTERNAL SHELL FEATURES

Analysis of body whorl descension and the pattern of sulcus occurrence require a few comments. As indicated previously (p. 11), the tendency of the body whorl to descend more rapidly is one of the characters used to separate adult shells from juveniles. This descension is a relative character. It must be measured against the rate of descension for the spire whorls. If the spire is secondarily elevated, then a greater degree of body whorl descension must occur before it becomes noticeable. If the spire is secondarily flattened, then the relative degree of body whorl descension will be magnified in comparison. No practical direct measure of body whorl descent was developed. Only relative coding was possible.

As a result, the few strong correlations between body whorl descension and shell parameters can be interpreted as the result of secondary modifications. The only species with abrupt body whorl descension are *Libera recedens* Garrett (figs. 170, 175e), *Libera retunsa* (Pease) (fig. 178e), and *Libera streptaxon* (Reeve) (fig. 179a). In these species the normal *Libera* shape is altered into a shell with flattened spire. The abrupt body whorl descension results from problems of umbilical narrowing during brood chamber closure. Those species with strong body whorl descension tend in part (*Rikitea insolens,* fig. 150; *Planudonta concava,* fig. 149a; *Australdonta pharcata,* fig. 137b) to be flat-spired taxa, although some (*Kleokyphus hypsus,* fig. 95e; *Mautodontha saintjohni,* fig. 75b; *Opanara*

TABLE XX. - BODY WHORL DESCENSION AND SHELL SIZE

$\bar{X}$ and SEM of:	Body Whorl Descension		
	None	Slightly	Moderately
Height	2.60±0.17	2.11±0.12	1.89±0.08
Diameter	4.75±0.28	4.03±0.21	3.52±0.13
H/D ratio	0.532±0.017	0.529±0.011	0.539±0.010
Whorls	6.01±0.14	5.64±0.10	5.44±0.09
Spire protrusion[1]	4.66	3.70	3.61
Number of taxa	44	67	57

1. $\bar{X}$ of code states, when "1" is depressed and "7" is spire protrusion greater than body whorl width

TABLE XXI. - BODY WHORL CONTOUR AND RATE OF DESCENT

Body whorl contour	Body whorl descension				
	Not	Slightly	Moderately	Strongly	Abruptly
Rounded	9	45	52	8	
Angled	3	9	2		1
Barely protruded keel	8	7	2		
Strongly protruded keel	22	4	1		2
Knife-edge keel	2	2			

altiapica, fig. 105c) have elevated spires and do show a major change in coiling pattern.

Those 44 species classified as showing no increase in body whorl descension (table XX) had significantly larger size, more whorls, and a higher spire protrusion/body whorl width ratio than those with slightly or moderately deflected body whorls. There was no alteration in the H/D ratio. This suggests that body whorl descension may be insignificant in its overall effect on shell proportions.

Further analysis (table XXI) shows that the size correlations are probably secondary to body whorl contour features. The combination of marked keel development and no body whorl descension is strikingly different from the pattern where a rounded body whorl is associated with slight to moderate body whorl descension. The two keeled taxa with abrupt body whorl descension are *Libera recedens* and *L. streptaxon*. In both cases there are space problems with brood chamber narrowing that require quick inward growth. This can be achieved most readily by abrupt body whorl deflection. Earlier (p. 23) it was shown that keel development led to larger size, so that the greater size increase should not be attributed to the descension correlation. From the standpoint of mechanical efficiency, attachment of the parietal-palatal margin to the keel edge of the previous whorl would be simplest. In *Planudonta concava* (fig. 146) the descent of the body whorl has resulted in partial transfer of the parietal wall onto the columellar wall region. Similarly the parietal wall sections in *Libera streptaxon* and *L. recedens* are detached and extend to narrow the umbilicus. Since parietal wall deposition involves smoothing the previous surface by either covering or partly resorbing the ribs, then secreting a relatively thin callus, the detached parietal wall areas are less substantial and complex than the normal columellar surfaces. Unless there are major advantages to this happening, maintainence of mechanical strength in the shell would favor retaining a whorl attachment that avoided parietal wall detachment. Following the keel edge accomplished this, and probably prompted the tendency for adult body whorl descension.

Sulci have developed in a number of taxa, usually in connection with keel formation. A major exception to this generalization is the peculiar subsutural sulcus found in several *Anceyodonta*. This is not always present in every specimen; for example see *A. sexlamellata* (Pfeiffer) (fig. 86a, c), and the distribution within the genus is not random. The sulcate species, *A. sexlamellata* (Pfeiffer), *A. soror, A. difficilis, A. obesa,* and *A. subconica* (figs. 81d, e; 83; 88a, c; and 89a) are rather high spired compared with other species in the genus (fig. 82, for example). Only *Anceyodonta ganhutuensis* (fig. 81a) among the high-spired forms lacks the sulcus. It is possible that this sulcus enables better attachment to the previous whorl by extending the parietal wall slightly upward, reducing the sutural depth, and avoiding any alteration in rib height at the suture. As such, this sulcus could have selective value for the particular species involved. Other high-spired taxa, such as the various *Nesodiscus* (figs. 159-161), *Libera* (figs. 174-178), and *Aaadonta* (figs. 203-204) have the spire whorl relatively flat sided, while in the sulcate *Anceyodonta* they are strongly rounded. Attachment without problems of rib height is far easier in the flat-sided whorl taxa than in *Anceyodonta*.

TABLE XXII. - CORRELATION BETWEEN SULCI AND BODY WHORL CONTOUR

Body whorl contour	Total taxa	Supraperipheral sulcus present	Subperipheral sulcus present
Rounded	114	8	1
Angled	15	8	2
Weak keel	17	16	12
Strong keel	29	27	28
Knife-edge keel	4	2	0

Formation of supraperipheral and subperipheral sulci is correlated with keel formation (table XXII). Virtually all species with keels have prominent supraperipheral and subperipheral sulci. Only when the keel becomes so narrow that it is "knife-edge," as in *Endodonta fricki* (Pfeiffer) (fig. 167g), does the subperipheral sulcus disappear completely. In those species with a rounded body whorl, very few show clear sulci. *Orangia cookei cookei* (fig. 123a) has a distinct supraperipheral sulcus, while other species in the same genus are distinctly keeled, for example *O. maituatensis* (fig. 123e). *Opanara duplicidentata* (fig. 102) is the only species in its genus to show a sulcus, as is *Mautodontha ceuthma* (fig. 72e) and *Anceyodonta sexlamellata* (Pfeiffer). Most *Australdonta* and all other *Aaadonta* are keeled, so that the sulci of *Australdonta pseudplanulata* (fig. 127e) and *Aaadonta pelewana* (fig. 207b) are not surprising.

It may be that the development of a supraperipheral sulcus is a preliminary to angulation followed by keel formation, but the evidence needed to solve this question is not available. I consider it quite possible that such round body whorl, sulcate taxa as those mentioned above could represent either states preliminary to keel formation or taxa that have secondarily rounded body whorls. Frequently juvenile examples will have much more sharply angulated or keeled peripheries than do adults of the same species. The concentration of sulcus formation in keeled taxa does suggest a causative relationship, but much more evidence is needed before the questions can be answered.

APERTURAL BARRIERS

Perhaps the most characteristic feature of the endodontid shell is the narrowing of the apertural opening by a series of ridge-like barriers. These are present even in late embryonic and newly hatched shells, extend from near or at the lip edge posteriorly for generally a fraction of a whorl, maintain this relative position throughout shell growth by a combination of anterior increment and posterior resorption, and have a very characteristic superior microdenticulation pattern.

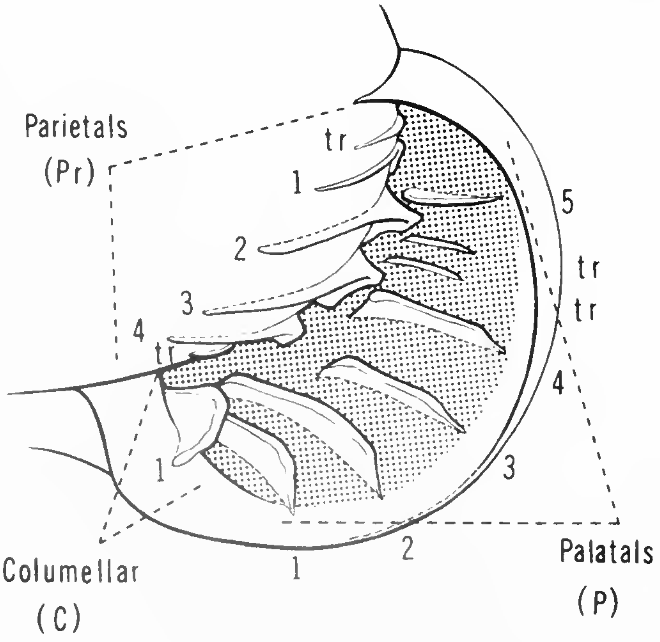

FIG. 36. Apertural barrier terminology and numbering system. Trace barriers are indicated by "tr."

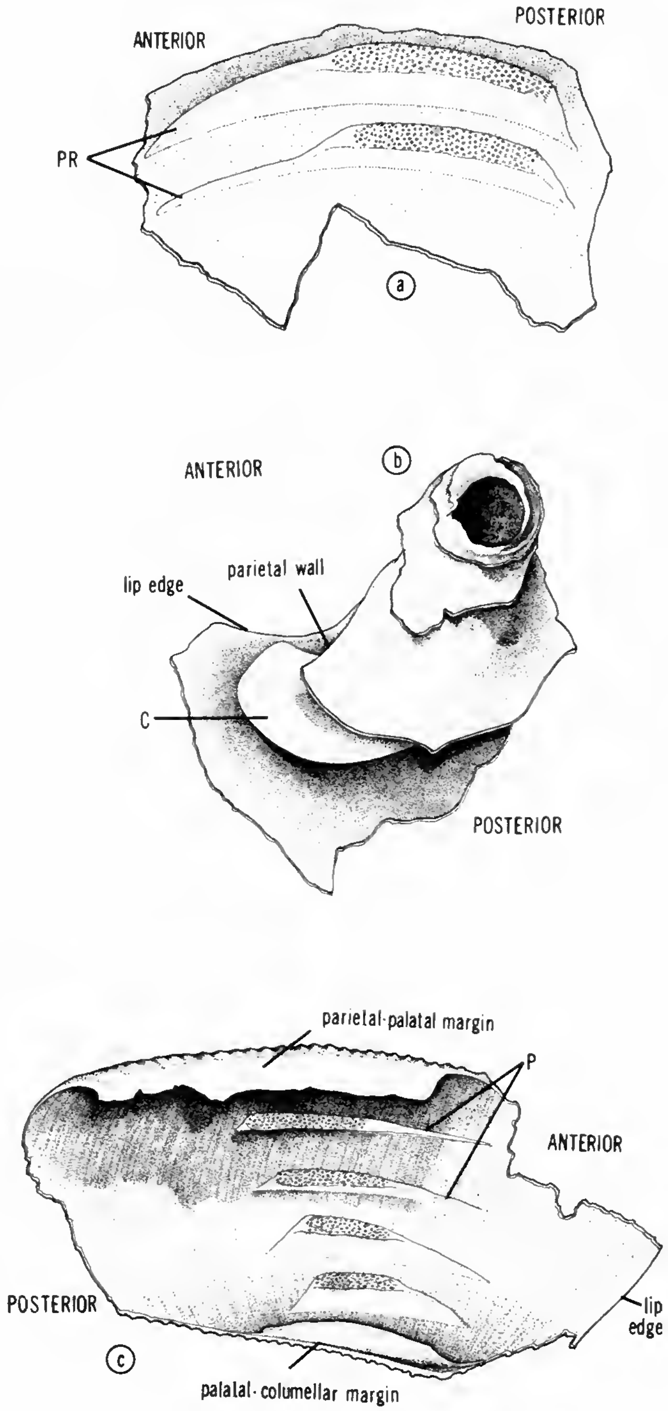

FIG. 37. Apertural barrier form in the Endodontidae: **a**, parietal wall fragment; **b**, columella with portion of basal lip and broken upper whorl fragments remaining; **c**, palatal wall section showing points of attachment to antepenultimate whorl. All greatly enlarged and based on *Orangia cookei montana*. Abbreviations are: PR - parietal lamellae; C - columellar lamella; P - palatal lamellae.

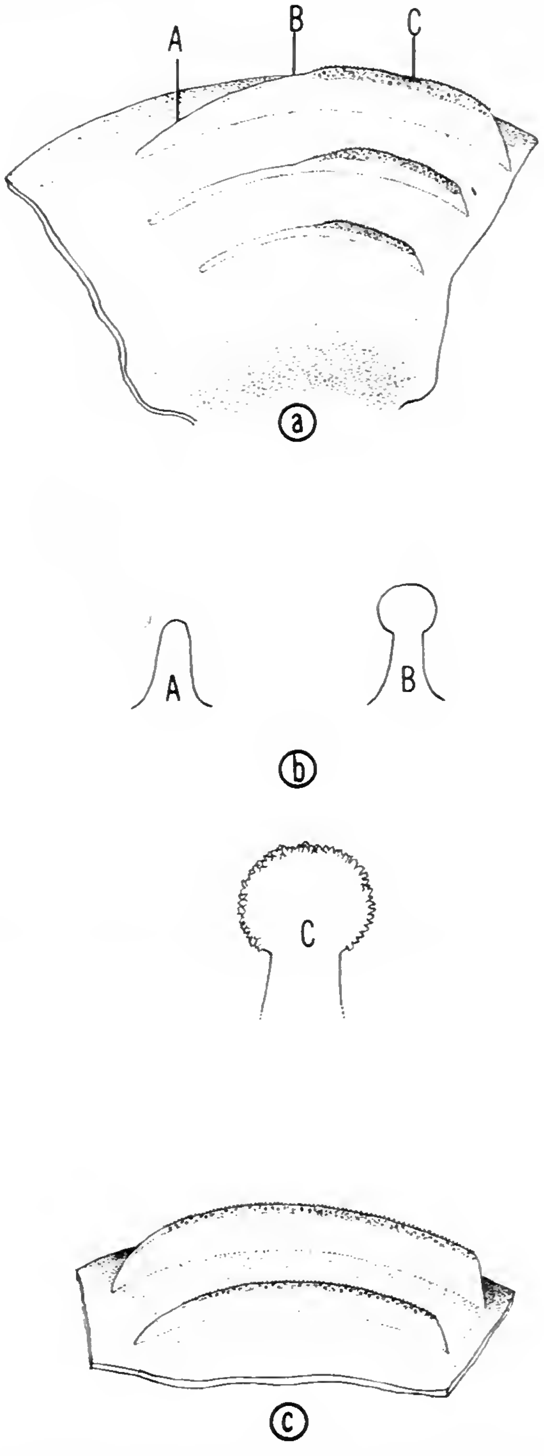

FIG. 38. Parietal barrier structure in *Australdonta degagei* (Garrett) and *Mautodontha aoraiensis:* **a**, **b**, *Australdonta degagei* from Station 839, Rimatara, Austral Islands (BPBM 149163); *a*, parietal wall in lateral view with anterior portion to left; *b*, cross-sectional views through 1st parietal barrier; **c**, *Mautodontha aoratensis* from Station 870, Mt. Aorai Trail, Tahiti, Society Islands (BPBM 145536). Parietal barriers with anterior end to left. (MM)

In a few extremely gerontic individuals (compare adult and gerontic *Minidonta simulata* in fig. 70a, d) the barriers may be greatly reduced from their normal size, while within both a few species (for example, *Ruatara oparica,* figs. 113, 114) and genera (*Nesodiscus,* figs. 152-161) there has been great reduction or even loss of the barriers. In many taxa there are trends for size reduction and splitting of the barriers (for example, *Mautodontha punctiperforata,* fig. 76d; *Opanara megomphala,* fig. 106a, c; *Australdonta radiella,* fig. 132a, c; *Taipidon centadentata,* fig. 144a, b; *Planudonta intermedia,* fig. 149c; and the Hawaiian *Nesophila*). The correlatives of these trends are discussed later.

These barriers are analogous to those found in other land-snail taxa (Solem, 1972c). Each major phyletic unit shows its own pattern as to ontogenetic time of appearance and persistence, number, relative position within the aperture, and terminology applied to the barriers. The complex barriers and plates of such groups as the Corillidae (Gude, 1914), Strobilopsidae (Pilsbry, 1948, p. 849, fig. 458), Polygyridae (Pilsbry 1940, p. 959, fig. 384), Pupillidae (Pilsbry, 1948, p. 869, fig. 469), camaenid genus *Labyrinthus* (Solem, 1966b, p. 39, fig. 9), and Tornatellinidae (Cooke and Kondo, 1960, p. 8, fig. 2) differ radically from those of the Endodontidae (figs. 36-38) and Charopidae. There is no evidence that they are not independently derived, although they perform the same inferred functions of reducing predation on the snails by making it more difficult or impossible for a predator to gain access to the retracted animal. Adoption of a uniform terminology for these diverse types of barriers would imply homology and serve no useful function, although retention of the standard apertural zonation descriptions is justified.

The numbering system and zonation used to describe the apertural barriers in both the Endodontidae and the Charopidae are shown in Figure 36. Those barriers located on the parietal wall are termed parietals (PR). They are numbered from upper right to lower left in sequence. Junctions of the parietal with columellar and palatal walls are obvious, but the point of separation between the palatal and columellar walls is difficult to define with precision. It is at the curvature change from basically axial descent (columellar) to paralleling the plane of coiling (basal section of palatal). In practice there normally is a rather sharp point of change that is easily identifiable, although in a few taxa there are changes in growth of shell or barriers that alter the positions. For example, the closed umbilicus of *Mautodontha imperforata* (fig. 76e, f) and strong lateral compression in *Opanara fosbergi* (fig. 107c) effectively shifted the columellar barrier onto the palatal lip. An equivalent shift of parietal barriers onto the columellar area would be possible under such growth distortions as occurred in *Planudonta* (fig. 146), *Nesodiscus taneae* (fig. 152), and several *Libera*. In several other taxa, such as *Anceyodonta soror, A. difficilis, A. labiosa, Opanara areaensis* (fig. 104a, c, e), and *Ruatara koarana* (fig. 113a, b), the columellar barrier's growth pattern results in its being deflected down onto the basal part of the palatal wall. The distinction between columellar and palatal barriers thus is partly subjective and requires careful attention to unusual alterations in shell form or barrier ontogeny before making comparisons with other taxa. In practice, there usually is little difficulty in recognizing homologous barriers within at least a genus. The numbering of palatal barriers (P) from lower left to upper right is for convenience.

A more arbitrary distinction is that used between barriers and traces (fig. 36, tr). The latter frequently are characterized by being much lower in height, significantly shorter, only half or a third as long, and lacking any trace of microdenticulations on the upper edge. In these circumstances, the distinction is simple and obvious. In species such as *Anceyodonta subconica* (fig. 81d), *A. difficilis* (fig. 83a), *A. soror* (fig. 83c, e), and *A. obesa* (fig. 89f), the traces are miniature replicas of the major barriers with microdenticulations above and similar cross-sectional shape. At the other extreme, species with reduced and split barriers, such as *Mautodontha punctiperforata, Opanara megomphala, Australdonta radiella, Taipidon centadentata, Planudonta intermedia,* and all species of *Nesophila* have the major barriers reduced in size nearly to that of the traces. In other species, such as *Priceconcha tuvuthaensis* Solem (1973d, p. 22), only the slightly raised microdenticulated section that starts three-eights of a whorl inside the aperture permits distinguishing the barriers from the traces.

Throughout the discussion and descriptions, major barriers are referred to as "1st, 2nd, and 3rd," while traces are called "first, second, and third" as a shorthand differentiation. Similarly, counts of major barriers are given in numerals as, 1, 2, 3; traces are spelled out.

Despite the above practical difficulties in discriminating between the major barriers and additional traces, the general distinction is highly useful and significant. Decisions in regard to any particular species involve comparisons with related taxa as well as direct observations on barrier size, shape, and microdenticulation.

The occurrence of traces is not random, but concentrated within a few taxa (table XXIII). Nine other genera, including such speciose taxa as *Australdonta, Nesodiscus,* and *Libera,* have no species with traces. Members of the *Minidonta-Anceyodonta-Gambiodonta* lineage have 76.5 per cent (26 of 34 species level taxa) with palatal traces, but only 47.1 per cent (16 of 34) with parietal traces, whereas the *Thaumatodon-Zyzzyxdonta-Priceconcha-Aaadonta* species have 40 per cent (8 of 20) with palatal traces and 60 per cent (12 of 20) with parietal traces. The *Cookeconcha-Endodonta* group has 33.3 per cent (8 of 24) with palatal traces, but none with parietals. The sporadic occurrence of traces in a few other genera is obvious. Size of shell does not correlate with trace presence or absence, since species with such traces include the genera that are smallest (*Minidonta, Anceyodonta*) and largest (*Endodonta, Gambiodonta*) in size. I have no explanation as to the functional significance of traces as opposed to barriers.

TABLE XXIII. - PRESENCE OF TRACE BARRIERS IN THE ENDODONTIDAE

Genus	Total species level taxa	Number with Parietal traces	Palatal traces
Minidonta	15	3	10
Mautodontha	17	2	5
Anceyodonta	12	7	9
Cookeconcha	16	0	2
Kleokyphus	2	1	1
Opanara	12	0	1
Taipidon	11	3	3
Planudonta	4	2	0
Kondoconcha	1	1	1
Endodonta	8	0	6
Gambiodonta	7	6	7
Thaumatodon	9	7	4
Zyzzyxdonta	1	1	0
Aaadonta	9	3	3
Priceconcha	1	1	1

Discussion of structural and size variations in the barriers found in each zone precedes analyses of barrier growth, microdenticulations, and the overall variation in barrier numbers and length.

Parietal barriers

The basic shape and positioning of the barriers are shown in Figures 37 and 38. The typical parietal barrier (fig. 37a) has the posterior third to half expanded above (fig. 38a, b) with most of the expanded section covered with microdenticulations (fig. 39d, e) that all point toward the apertural margin. The anterior half to quarter of the lamella has a slenderer form, is without denticulations, and descends towards the parietal surface. The manner of this descent varies with tooth position and between taxa. In *Orangia cookei montana* (fig. 37a) the 1st parietal (upper) descends very gradually until its tip, then plunges abruptly. The 2nd parietal (lower) has an abrupt descension just anterior to the denticulated area, then continues forward as a "thread-like" ridge to its anterior termination. The lower parietals in *Opanara areaensis areaensis* (fig. 39c) have an intermediate pattern of descension. *Australdonta degagei* (fig. 38a) shows a very characteristic pattern in which the 1st parietal (upper) is a high lamellar barrier and has gradual anterior descension; the 2nd (middle) has a shortened posterior denticulated section and a long "thread-like" anterior section; and the 3rd (lower) is shortened, lower in posterior height, and with a proportionately longer anterior extension. This progressive pattern of height reduction and shortening of the denticulated section is repeated in most species and is well demonstrated by *Gambiodonta grandis*

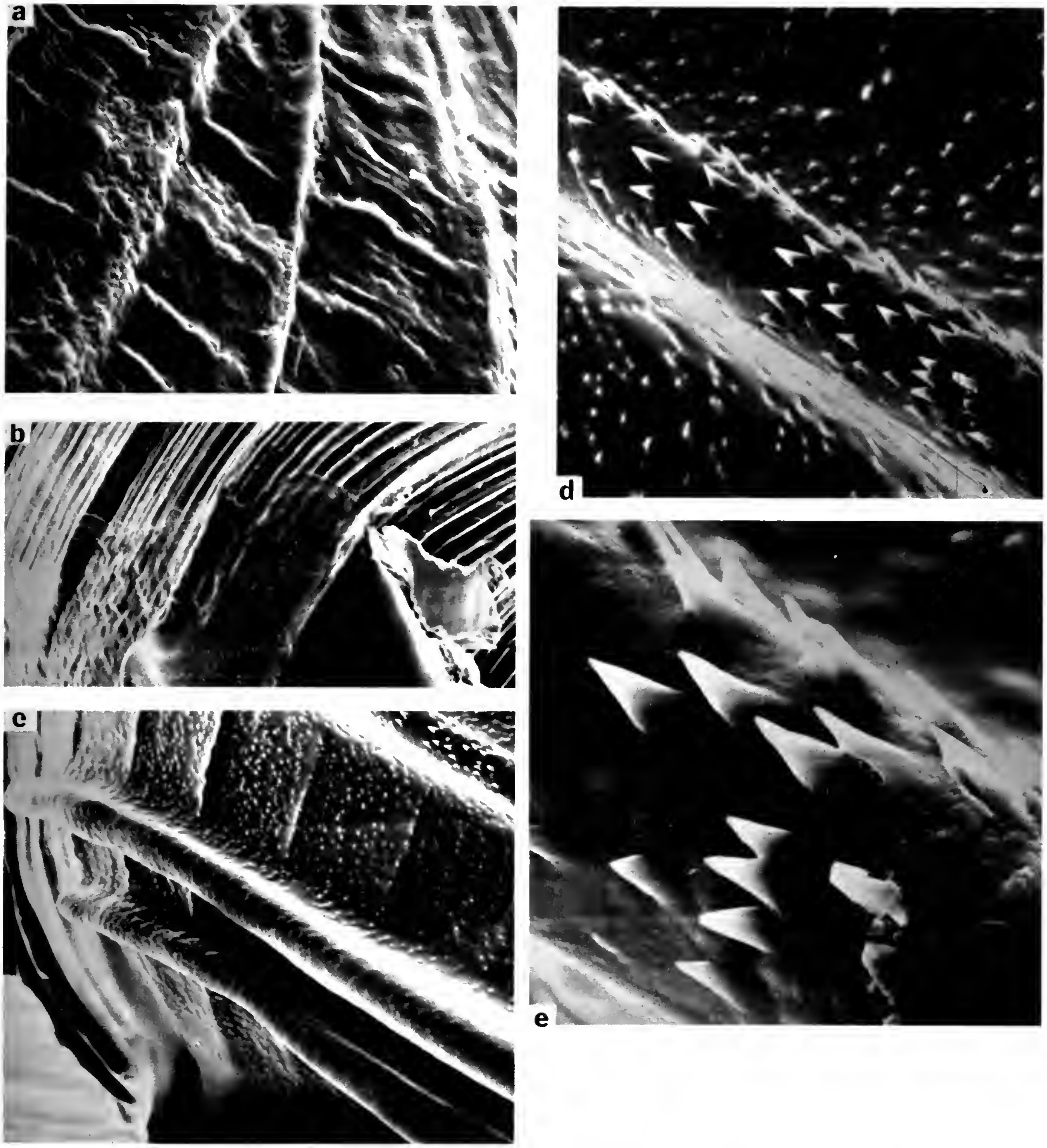

FIG. 39. Shell sculpture and denticle structure in *Opanara areaensis areaensis*. Station 474, Rapa Island. BPBM 144651: **a**, apical sculpture showing worn area (ca. 3,000×); **b**, anterior edge of parietal callus showing method of riblet covering (300×), note anterior edge of upper parietal lamella; **c**, anterior descension of 2nd and 3rd parietals with portion of 1st parietal showing serrations (300×); **d**, top portion of 1st parietal serrated section (ca. 1,000×); **e**, detail of serrations on 1st parietal (ca. 3,000×).

(fig. 189c). In contrast, some species such as *Mautodontha aoraiensis* (fig. 38c) have the denticulations extend to within a very short distance of the anterior end with sharp anterior descension.

Descension of the 2nd parietal barrier is a convenient index of variability. Table XXIV correlates the type of descension and number of major barriers present. There is a tendency towards more rapid descension with decrease in barrier number, but this is not nearly as strongly correlated as many other variations. This is not a size-correlated variable (table XXV). Larger species with only 2 parietal barriers tend to have either very sharp anterior descension or a very long threadlike portion. To some extent this is

TABLE XXIV. - CORRELATION BETWEEN NUMBER OF PARIETAL BARRIERS AND DESCENSION OF 2ND PARIETAL BARRIER

Number of parietals	Sharp anterior	Gradual from middle	1/4-1/3 is threadlike	3/8+ is threadlike
2	15	10	13	23
2-3	4	15	9	25
3-4	1	6	5	15
4-5				9
many				6
TOTALS	20	31	27	78

phyletically correlated, since of the 15 taxa with sharp anterior descension, 13 are Libera and two are *Cookeconcha*. Of the 23 taxa with long threadlike anteriors, 10 belong to *Cookeconcha* and *Endodonta*, three to *Mautodontha*, two to *Libera*, four to *Taipidon* and *Planudonta*, with the other four scattered among four genera. There is thus experimentation within genera.

The normal relation between the anterior termination of the 1st and 2nd parietals, excluding the 18 taxa where it is absent or data was unavailable, is for the 2nd to project slightly (fig. 37a). This occurs in 52.8 per cent (85) of the species. In 31.7 per cent (51 taxa) it is even with the 1st, while in 3.1 per cent (5) it is slightly behind, and in 12.4 per cent (20) it is deeply recessed. Recession of the 2nd parietal frequently is a prelude to loss of the barrier. A small, deeply recessed 2nd parietal normally occurs in *Nesodiscus taneae* and *N. huaheinensis*, only rarely in *N. obolus*, and is lost in the other *Nesodiscus* species. Thirteen taxa of *Libera* have a deeply recessed 2nd parietal, it is totally lost in *L. retunsa* and *L. tumuloides*, while only in the very small *L. umbilicata* and *L. micrasoma* are the 2nd parietals equal in size and length to the 1st. *L. gregaria* has 2 equal parietals and occasionally a 3rd. Other taxa with deep recession of the 2nd parietal include *Rhysoconcha*, *Opanara duplicidentata*, *Mautodontha maupiensis*, and *Taipidon petricola petricola*. All of these species have 3 to 5 parietal barriers. The *Opanara* and *Taipidon* are the only members of their genera that have 4 parietals. The "reduced 2nd" could be an added barrier in these two species, while the *Rhysoconcha* appear to be involved in secondary size reduction (pp. 255-256) and thus the significance of the deeply recessed 2nd parietal is uncertain.

TABLE XXV. - CORRELATION BETWEEN ANTERIOR DESCENSION OF 2ND PARIETAL BARRIER, DIAMETER, AND WHORL COUNT IN SPECIES WITH 2 PARIETAL BARRIERS

Type of descension	Number of taxa	$\overline{X}$ D	$\overline{X}$ W
Sharply	15	5.51±0.44 (1.86-8.46)	6.63±0.26 (4.00-7.675)
Gradually from middle	10	3.90±0.31 (2.28-5.10)	5.55±0.30 (4.125-6.950)
1/4 to 1/3 is threadlike	13	4.16±0.55 (1.79-8.99)	5.54±0.24 (3.625-6.500)
3/8+ is threadlike	23	4.72±0.25 (3.06-6.91)	5.73±0.19 (4.075-8.050)

Mautodontha maupiensis belongs to a genus in which many species have the basic 4 parietal compliment reduced to only 1 or 2 and thus may represent an incipient reduction series.

While no direct measurement of parietal barrier width was feasible, the relative degree of expansion for the microdenticulated area compared with the barrier shaft could be observed and special modifications noted. The data are summarized in Table XXVI. This variation includes both size-correlated and straight phyletic factors. The "beaded" structure (figs. 41a; 194d; Solem, 1973d, fig. 10) is characteristic of and restricted to the anatomically isolated *Thaumatodon-Zyzzyxdonta-Aaadonta-Priceconcha* complex. *Thaumatodon multilamellata* (Garrett) (fig. 192d, e) has separate, evenly spaced "hooks" developed on the denticles, but all the other species have this beaded structure. *Kondoconcha othnius* is unique in having accessory trace barriers mounted medially on each side of both major parietals (fig. 108c, d), which otherwise are only moderately expanded above. Formation of a bifid upper parietal has occurred in three lineages, a Hawaiian, an Austral Island, and a Gambier Island group. The Hawaiian *Cookeconcha nudus*, *C. thwingi*, *C. henshawi*, *Endodonta binaria*, *E. concentrata*, *E. lamellosa*, *E. marsupialis* (fig. 167a), *E. fricki* (fig. 167g), and *E. ekahanuiensis* form one apparently monophyletic assemblage. In these species the bifidity occurs because of a slanted lower addition to the upper parietal that may or may not be counterbalanced by a slight upward deflection of the main lamellar blade. The area between the two blades is partly filled in with calcareous deposition, giving a concave contour to the upper parietal. The Austral Island *Minidonta micraconica* (fig. 65b, d, e) and *M. gravacosta* (fig. 65g) have the same basic type of bifidity, except that the lower blade is inserted more directly on the lower surface and there is no deposition between the two blades. The angle at which the secondary blade is

TABLE XXVI. - CORRELATION BETWEEN DIAMETER AND SUPERIOR STRUCTURE OF PARIETAL BARRIERS

Barrier:	$\overline{X}$D	Number of taxa
Not expanded	4.84±0.30 (3.06-11.29)	28
Weakly expanded	4.40±0.19 (1.68-12.26)	80
Moderately expanded	3.14±0.15 (1.86-4.36)	26
Strongly expanded	3.11±0.28 (1.73-5.54)	14
Bifid	4.21±0.74 (1.79-8.99)	11
Beaded	3.42±0.20 (2.15-5.10)	17
Lateral extensions	4.06	1

attached is more nearly perpendicular in the latter species. The Mangarevan *M. taravensis* (fig. 71c) has the 3rd parietal bifid, probably by fusion, while *Anceyodonta andersoni* and *A. alternata* have the upper bifid posteriorly. Rarely the 3rd parietal is bifid in *A. obesa.* Bifidity of the upper parietal has thus occurred among the smallest (*Minidonta*) and largest (*Endodonta*) of the taxa, which is reflected in the large standard errors of the mean (table XXVI). The net effect of a bifid upper parietal is to widen the area along the parietal wall that is effectively narrowed by the barriers. In non-bifid species the vertical distance between the 1st and 2nd parietal is "empty space" and not narrowed. The other major variation occurs in *Rhysoconcha* (figs. 108a, b; 112) whose barriers are greatly distorted, probably as a result of secondary size reduction (pp. 255-256).

The above special variations have been excluded from analyzing the pattern of barrier expansion, since although the effect of these changes is the same as alterations in superior expansion, I could not equate these exactly with the stages in simple superior expansion. The latter were coded (table XXVI) as strongly expanded (fig. 83), moderately expanded (fig. 70a), weakly expanded (fig. 69e), and not expanded (fig. 144). The change from the moderately to weakly to not expanded states clearly is size correlated. Larger species have less superior expansion of the barriers than smaller sized taxa. Partly this is directly size correlated, but a large part of the "not expanded" category correlates with size reduction of the barriers. Of the 28 "not expanded" taxa, only the Marquesan *Taipidon semimarsupialis* (fig. 143e) has fairly prominent parietals. Yet these are reduced in size within the context of the genus (compare *T. analogica,* fig. 143a, d). The remaining taxa have the parietals reduced to threadlike traces, low ridges, or split into many threadlike traces. Often both the palatal and columellar barriers are lost or reduced greatly in number.

Strongly expanded barriers are characteristic of the *Minidonta-Anceyodonta* complex from the Gambier Islands, with two *Minidonta,* four *Anceyodonta,* the monotypic *Rikitea,* and one *Gambiodonta* included. Otherwise, there are *Minidonta rotellina* (Pease) from Aitutaki, Cook Islands, four Rapan taxa (*Rhysoconcha variumbilicata* and the *Orangia cookei* complex), and *Cookeconcha cookei* (Cockerell) from Oahu. The distinction between moderately expanded and strongly expanded is not sharp, with the latter condition usually indicating a bulbous expansion on part of the barrier, while the moderately expanded species tend more to have the entire microdenticulated section of the barrier expanded. These taxa are scattered more widely throughout the family, with 10 genera included.

Other noteworthy variations in the parietal barriers are a tendency for barrier size reduction to accompany splitting into numerous threadlike traces. In the unique *Minidonta extraria* (fig. 71d, f) each major parietal has several threadlike traces while retaining the strongly expanded denticulated sections. Species such as *Opanara megomphala* (fig. 106a, c), *Australdonta radiella* (Pfeiffer) (fig. 132a, c), *Taipidon centadentata* (fig. 144), *Planudonta intermedia* (fig. 149c), and *Gambiodonta tumida* (fig. 188a-b), show partial to near-total reduction to threadlike traces.

Columellar barriers

The larger or only columellar barrier may be (fig. 37b) a high C-shaped or blade-like structure extending from well inside the aperture to or near the lip edge. Sometimes (for example, fig. 86d, e) it may be partly to nearly buried by a heavy columellar callus in adult and gerontic individuals. In other taxa it is reduced to a thread-like trace (fig. 82a) and/or is very deeply recessed within the aperture (fig. 203b). In 61 taxa the columellar barrier is absent. The barrier, when present, may be parallel to the plane of coiling (fig. 123d), slanting downward from the coiling plane (fig. 86c), or (in extreme cases) deflected onto the basal lip of the shell (fig. 104).

In a few taxa there routinely is more than 1 columellar barrier. *Thaumatodon euaensis, T. multilamellata,* both subspecies of *Aaadonta fuscozonata, Anceyodonta sexlamellata,* and *Planudonta matauuana* have 2 columellar barriers. *Planudonta intermedia,* both races of *Opanara megomphala* and *Taipidon centadentata,* have many threadlike barriers. They, plus *P. matauuna,* represent taxa in which there has been splitting and reduction of the parietal and palatal barriers. The *Thaumatodon, Aaadonta,* and *Anceyodonta* are taxa with fully developed large barriers and thus show a different pattern of barrier addition. *Thaumatodon hystricelloides* and *T. vavauensis* have either 1 or 2 barriers, and thus can be viewed as potentially in the process of adding the second barrier. The *Thaumatodon-Aaadonta-Zyzzyxdonta* complex thus has six of 18 taxa with at least a strong tendency toward 2 columellar barriers, while only one taxon of the other genera, *Anceyodonta sexlamellata* (Pfeiffer), has 2 columellar barriers by other than a barrier size reduction process. Species in which the columellar barrier is infrequently absent are discussed in the text individually.

The pattern of columellar barrier loss is documented in Table XXVII. Such speciose taxa as *Anceyodonta, Endodonta, Taipidon, Gambiodonta, Thaumatodon,* and the Rapan genera show only a few species or are not listed, since these taxa retain prominent columellar dentition. In contrast, such taxa as *Nesodiscus, Nesophila, Rikitea, Pseudolibera,* and *Planudonta,* represent cases of great size reduction, splitting, and/or loss of barriers from the aperture. In these taxa many or virtually all of the species lack a columellar barrier. *Australdonta* has only one species, *A. raivavaeana,* that retains a weak, threadlike ridge in three-quarters of the examples, while all other *Australdonta* have no barrier on the columellar wall. It may be, however, that the extra palatal of

TABLE XXVII. - LOSS OF COLUMELLAR BARRIER

Genus	Total taxa	Columellar barrier Absent	Deeply recessed
Minidonta	15	4	3
Mautodontha	17	9	3
Cookeconcha	16	12	
Kleokyphus	2	1	
Opanara	12		2
Rhysoconcha	2		1
Ruatara	4		1
Australdonta	12	11	1
Taipidon	11	1	1
Planudonta	4	2	
Rikitea	1	1	
Nesodiscus	10	10	
Nesophila	2	2	
Pseudolibera	1	1	
Libera	19	6	8
Aaadonta	9	1	4

Australdonta may be a descended columellar. In *Mautodontha, Cookeconcha, Libera, Minidonta,* and *Aaadonta* up to two-thirds of the species lack a columellar barrier. If deep recession of the barrier is viewed as a prelude to its loss, then the phyletic linkage of barrier loss becomes even stronger (table XXVII).

Barrier size and relative position with respect to the lip edge are shown in Table XXVIII. The general agreement between the two variables, high lamella reaching near to lip edge and low threads or ridges deeply to partly recessed is obvious. The position of the barrier in relation to the lip edge is variable at a low taxonomic level, however. The subspecies of *Orangia cookei* (fig. 123a, c, d), for example, are identifiable by the degree of barrier recession alone. There also is an obvious relationship between barrier position relative to the plane of coiling and how nearly it approaches the lip edge (table XXIX). A change in barrier anterior growth generally involves just the tip at the callus area. The one species in which the barrier is both deeply recessed and deflected onto the basal margin, *Opanara fosbergi* (fig. 107c), is extremely compressed above and below, with the result that part of the columellar wall has, in effect, been moved onto the basal margin. The other species involving deflection show two distinct patterns. In *Ruatara koarana* (fig. 113b) and the three subspecies of *Opanara areaensis* (fig. 104), the barrier begins in normal columellar position, with terminal growth at adulthood deflecting the anterior portion downward. In four Gambier Island taxa, *Minidonta taravensis* (fig. 71a, c), *Anceyodonta labiosa* (fig. 87d, e), *A. difficilis* (fig. 83a), and *A. soror* (fig. 83e), the columellar barrier is extremely high and has rotated downward through a 90° arc onto the basal lip, with a slight inward twist at the anterior end. Thus deflection of the columellar barrier onto the basal margin has been accomplished in at least three different ways. A reverse variation is seen in *Mautodontha subtilis* (Garrett), where 25 per cent of the specimens have the 1st palatal shifted up onto the columellar wall.

Presence or absence and actual height of the columellar barrier are not directly size correlated (tables XXX, XXXI). The mean whorl count (table XXX) of species with and without barriers is virtually identical, but the diameter is significantly different ("*t*" is 2.5014 with 177 df). This conflicting pattern partly is a phyletic artifact. Most *Libera,* all *Gambio-*

TABLE XXVIII. - CORRELATION BETWEEN COLUMELLAR BARRIER HEIGHT AND POSITIONAL RELATION TO LIP EDGE

	Barrier height					
Barrier position	low rounded thread	low ridge	low lamella	high lamella, gradual descension	high lamella, sharp descension	Totals
Lip edge	0	3	5	17	14	39
Midway across callus	6	9	3	12	4	34
Top of callus	3	8	3	5	1	20
Deeply recessed	7	10	2	6	0	25
Totals	16	30	13	40	19	118

TABLE XXIX. - COLUMELLAR BARRIER POSITION AND RECESSION

Recession: barrier reaches-	Position: Parallel	Slanting down	Deflected onto basal margin
Lip edge	18	14	7
Midway across callus	19	14	1
Top of callus	15	5	0
Deeply recessed	22	2	1

donta, and all *Endodonta,* which have high whorl counts and have, or tend toward, brood chamber growth patterns, have proportionately low diameters relative to their whorl counts, since the growth vector has shifted (pp. 21-29). They retain prominent dentition. In contrast, taxa at or near the *Nesodiscus* level of specialization (p. 113), such as *Nesodiscus, Planudonta, Nesophila,* and *Rikitea,* combine high whorl count, wide umbilici, and reduced apertural barriers. The greater diameter of those taxa without columellar barriers reflects a difference in both growth vectors and the phyletic tendency toward general tooth reduction. Similarly (table XXX) there are no correlations between position of the columellar barrier relative to the lip edge and shell size.

Shell size and columellar barrier height (table XXXI) show only slight size correlation. Those taxa with either a low lamellar barrier, or a high lamellar barrier that descends gradually, average larger in diameter and whorl count than those with other barrier heights, but the differences are only marginally statistically significant and the overlap of ranges is extensive. Both categories include many brood-chamber taxa, with their increased whorl count. It is probable that the elongation of the lamellar barrier in these taxa is a simple correlative of the extra growth.

In summary, the columellar barriers show little direct size-correlated variation, but rather indicate phyletic linkages and patterns of variation rather closely. States of alteration in barrier position and size can be demonstrated to be derived in different ways and thus are convergent in nature.

TABLE XXX. - SHELL SIZE AND COLUMELLAR BARRIER POSITION

	Number of taxa	Diameter	Whorl count
Barrier:			
Present	118	3.91±0.15 (1.68-12.26)	5.74±0.08 (3 5/8-8)
Absent	61	4.58±0.22 (2.59-11.29)	5.67±0.12 (3 5/8-8)
Barrier position:			
Lip edge	39	3.78±0.29 (1.79-12.26)	5.58±0.11 (3 5/8-7 3/8)
Midway across callus	34	3.70±0.28 (1.68-8.99)	5.59±0.13 (4-7 1/8)
Top of callus	20	4.16±0.35 (1.73-8.46)	6.01±0.22 (4 1/2-7 5/8)
Deeply recessed	25	4.23±0.32 (1.97-7.30)	5.96±0.17 (4 7/8-8)

Palatal barriers

The palatal barriers (fig. 37c), have a typical pattern of change in shape, becoming progressively longer and lower from basal lip to upper palatal wall. Frequently the barriers will be well developed and prominent on the lower palatal wall, but with only a single reduced ridge present above the periphery, as, for example, in *Taipidon* (fig. 145a, c), *Libera* (fig. 184b, e), *Thaumatodon* (fig. 196b, e), and *Aaadonta* (fig. 206b, e). This is most common in taxa with angled or keeled peripheries. Equally common is the presence of supraperipheral traces (fig. 36), with or without a major barrier near the parietal-palatal margin (figs. 87, 88, 89, 140a, c). The absence or lower profile of palatal barriers in this upper sector of the aperture correlates with the tendency for the 1st parietal, which frequently is the highest of the parietal barriers, to lie opposite this region and protrude into the area. The low traces sitting opposite the largest parietal also preserve a space function, since the widest gap between opposing barriers occurs in this region. This space probably permits the buccal mass and foot to be withdrawn past the barriers through this open channel.

TABLE XXXI. - SHELL SIZE AND COLUMELLAR BARRIER HEIGHT

Barrier height	Number of taxa	Shell diameter	Whorl count
Low thread	16	3.45±0.23 (1.97-4.73)	5.38±0.14 (4-6 1/4)
Low ridge	30	3.41±0.27 (1.68-7.60)	5.58±0.16 (4 1/8-7 5/8)
Low lamella	13	4.34±0.55 (2.33-7.30)	6.15±0.29 (4 7/8-8)
High lamella, gradual descension	40	4.61±0.30 (2.58-12.26)	6.05±0.11 (4 3/4-7 1/4)
High lamella, sharp descension	19	3.36±0.24 (1.79-5.06)	5.36±0.18 (3 5/8-7)

Height variation in the palatal barriers partly correlates with the relative sizes of the lower parietal and columellar barriers. When these are small, as in Figure 143d, the 1st palatal will be higher than the 2nd. In taxa where the columellar (fig. 162b) and/or the lower parietal (fig. 71c) are very large, the 1st palatal will be slightly to significantly reduced in height. Similarly, where the 1st parietal is very large, as in *Minidonta taravensis* (fig. 71a, c), the palatal barrier lying on the opposite wall will be markedly reduced in prominence. Because this pattern differs quite widely within genera and is of complex origin, no satisfactory criteria for comparing relative palatal barrier height between species were formulated. Discussions of major variations in barrier shape, position relative to the lip edge, superior expansion, and correlatives of barrier loss and reduction precede consideration of correlations with parietal barrier features.

TABLE XXXII. - PALATAL BARRIER SHAPE AND LENGTH CORRELATIONS

Barrier shape	Barrier Length Under 1/8 whorl	1/8 whorl	3/16 whorl	1/4 whorl	To line of vision	Beyond line of vision
Crescentic	2	3				
Blade-like, sharp descension	5	2				
Blade-like, gradual descension	3	58	38	15	4	5
Low ridges	2	5		1		3
Threadlike	1	1		2		1

Barrier shape is relatively constant, with departures from the basic form (fig. 37c) correlated more with barrier length than any other factor (table XXXII). Shortening of the barrier may result in a crescentic form or one with much sharper anterior descension. Size reduction to a threadlike or low ridge status can correlate with either very short or very long barriers. All these changes may signal a tendency toward barrier loss, since the only taxa with crescentic palatals are three *Cookeconcha* and the two dentate races of *Ruatara oparica.* A high proportion of *Cookeconcha* and *Ruatara oparica reductidenta* have reduced or no palatals (table XXXVII), and the concentration of change to a crescentic shape in these taxa seems significant.

Position of the palatal barriers relative to the lip edge is far more variable than the position of the parietal barriers. The latter, without exception, extend essentially to the plane of the lip edge or slightly beyond, depending on the parietal callus protrusion. In contrast, the palatal barriers can extend to the lip edge (fig. 204a, c) or lie so deeply recessed that they are barely visible by tilting the aperture (fig. 189a). The pattern of this change is size correlated (tables XXXIII, XXXIV). Taxa with the palatal barriers at the lip edge or only slightly recessed (table XXXIII) do not differ significantly in size from each other ("*t*" = 1.5772 with 89 df) and their whorl count is identical. There are highly significant size and whorl count differences in going from "slightly" to "moderately" and then to "deeply" recessed palatal barriers. The changes in diameter, respectively, have "*t*" 's of 4.1558 with 78 df and 2.2751 with 56 df. The change in whorl count has, respectively, "*t*" 's of 2.1191 with 77 df and 3.6609 with 55 df. Since the change from "deeply recessed" to "barely visible" is only accentuating a basic trend, the lack of size change is expected. The slightly smaller size of taxa in which the barriers are lost reflects the diverse number of taxa in which this phenomenon has occurred (p. 62).

TABLE XXXIII. - PALATAL BARRIER RECESSION AND SIZE CORRELATIONS

Palatal barrier recession	Number of taxa	Diameter	Whorl count
Lip edge	39	[illegible].13 ([illegible])	5.40±0.11 (4–7 1/2)
Slightly recessed	[illegible]	[illegible]	5.46±0.10 (4–6 3/8)
Moderately recessed	[illegible]	[illegible]	[illegible]±0.12 ([illegible] 3/4–7)
Deeply recessed	[illegible]	[illegible]	[illegible] ([illegible] 1/4–[illegible])
Barely visible	[illegible]	[illegible]	[illegible]
Absent	[illegible]	[illegible] ([illegible]–11.[illegible])	[illegible]

Major recession of the palatal barriers is correlated with brood chamber formation and increased whorl count more than any other factor (table XXXIV). The clustering of these states in *Nesodiscus, Pseudolibera, Gambiodonta,* and *Libera* is obvious. *Orangia* has the highest mean whorl count of the Rapan taxa; and *Planudonta* represents an increase in whorl count over *Taipidon,* except for the brood chamber species, *T. semimarsupialis.* This correlation of deep recession with increased whorl count requires more analysis than available data permits. I have no information as to whether the normal pattern is for the deep recession to result from a sudden cessation of barrier growth followed by continued lip edge accretion; a slowing of barrier growth at some stage in development; or a gradual development throughout ontogeny. Examination of extensive growth series would permit at least partial solution of this problem, but the necessary material was not available for study. Young *Gambiodonta grandis* (fig. 189e) have the palatals only slightly recessed, but in adults (fig. 189a) they are barely visible. Since that species is the only *Gambiodonta* with deep recession, this is only suggestive of one situation.

The deeper recession of palatal barriers than parietals probably has direct functional significance.

TABLE XXXIV. - PHYLETIC CORRELATIONS OF PALATAL BARRIER RECESSION

	lip edge	slightly recessed	moderately recessed	deeply recessed	barely visible	absent
Cookeconcha	1	4	1	3		6
Endodonta		3	5			
Nesophila						2
Minidonta	5	7	2	1		
Mautodontha	3	6	4			4
Anceyodonta	6	5	1			
Kleokyphus	1	1				
Rhysoconcha	2					
Opanara	4	7	1			
Kondoconcha	1					
Ruatara		1	2			1
Orangia			4	1		
Taipidon	5	4	2			
Planudonta		1		2		
Thaumatodon	7	1				
Aaadonta	3	6				
Zyzzyxdonta	1					
Australdonta		7	1	1		3
Nesodiscus			1	1	6	2
Gambiodonta			3	4		
Libera			1	17		1
Rikitea						1
Pseudolibera						1

The basic microdenticulations on the upper barrier edge could be used as the gripping surfaces for mantle edge extension after deep retraction of the animal. Columellar and parietal surfaces would be used more extensively in this than the palatal wall, which is further from the shell axis. Hence retention of the parietal barriers to the lip edge presumably would continue to serve a significant function even after their apertural narrowing function had lessened. In contrast, there would be little selective value for extending the palatal barriers to the lip edge.

Palatal barrier expansion is partly size correlated (table XXXV), and parallels, but does not exactly follow the degree of parietal barrier expansion (table XXXVI). As in the parietal barrier expansion, a weak or slight expansion of the barriers is normal (table XXXVI). More than half of the taxa show this generalized condition. The proportion showing "typical" palatal barrier expansion is greater, probably since the palatal barriers are lost in so many taxa. Only one species, *Endodonta binaria* (Pfeiffer), has the palatal barriers bifid. All of the 12 taxa in which the palatal barriers are not expanded represent forms with great size reduction of the barriers. *Orangia sporadica* (fig. 123f), the three *Planudonta* that retain palatal barriers, the two subspecies of *Ruatara oparica* with palatal barriers, three of the four "Group III"

TABLE XXXV. - SIZE CORRELATION WITH PALATAL BARRIER EXPANSION

Barrier:	Number of taxa	Diameter	Whorl count
Not expanded	12	4.00±0.18 (2.98-4.98)	5.55±0.18 (4 1/4-6 3/8)
Moderately expanded	20	3.35±0.27 (1.97-6.60)	5.51±0.18 (4 1/4-8)
Strongly expanded	15	2.65±0.20 (1.73-5.06)	5.16±0.17 (3 5/8-6 3/8)

TABLE XXXVI. - PATTERNS OF BARRIER EXPANSION

State:	Number of taxa Parietal	 Palatal
No data		1
Absent	1	22
Not expanded	28	12
Weakly expanded	80	91
Moderately expanded	26	20
Strongly expanded	14	15
Bifid	11	1
Lateral accessory	1	0
Beaded expansion	17	17

Cookeconcha, Taipidon centadentata, and both subspecies of *Opanara megomphala* have obvious and extensive barrier size reduction. In mean size and whorl count they are average for the family (table XXXV), but are obviously and significantly larger than those taxa with moderately or strongly expanded palatal barriers. Strongly expanded palatal barriers are found in the smaller Hawaiian *Cookeconcha* and *Endodonta;* Mangarevan *Minidonta* and *Anceyodonta; Taipidon petricola petricola* (the smallest sized taxon in the genus); and both species of *Rhysoconcha,* which are secondarily reduced in size (pp. 255-256). These species are distinctly smaller in size and slightly lower in whorl count (table XXXV), but not all small species, by any means, have strong palatal barrier expansion. Moderate expansion of the palatal barriers is spread among 20 species belonging to 11 genera. These are intermediate in size, but have an average whorl count.

Loss of the palatal barriers (table XXXVII) has occurred in 22 (11.3 per cent) of the taxa, compared with total loss of the parietal barriers only in *Nesodiscus fabrefactus.* The palatal barrier loss is found in two monotypic genera, *Pseudolibera* and *Rikitea;* both species that I have examined of the Hawaiian *Nesophila; Planudonta concava,* which is the largest of the four species in that genus; only one subspecies, *Ruatara oparica reductidenta,* of the Rapan radiation; the two largest *Nesodiscus* species, *N. magnificus* and *N. fabrefactus; Libera retunsa* generally (9 of 11 specimens) lacks palatal dentition; and several taxa in *Cookeconcha, Mautodontha,* and *Australdonta* lack the barriers. The six *Cookeconcha* (*C. decussatulus, C. jugosus, C. thaanumi, C. paucicostatus, C. lanaiensis,* and *C. hystrix*) have a larger mean shell diameter (4.64 ± 0.44) than those with palatal barriers (3.45 ± 0.40). The difference is significant ("*t*" = 1.914 with 13 df) at the 5 per cent level. The several *Mautodontha* (*M. aoraiensis, M. consimilis, M. acuticosta,* and *M. unilamellata*) also show size reduction of the parietal barriers, but do not differ in size from those with well-developed barriers. Similarly, the three *Australdonta* (*A. ectopia* and both subspecies of *A. radiella*) do not differ significantly in size from the other species in the genus.

TABLE XXXVII. - REDUCTION AND LOSS OF PALATAL BARRIERS

Genus	Number of taxa	Barrier low ridge or threadlike	Barrier lost
Minidonta	15	1	0
Mautodontha	17	0	4
Cookeconcha	16	2	6
Opanara	1[illegible]	2	0
Ruatara	[illegible]	[illegible]	1
Orangia	[illegible]	1	0
Australdonta	[illegible]	[illegible]	3
Taipidon	11	[illegible]	0
Planudonta	4	3	1
Rikitea	1		1
Nesodiscus	[illegible]	[illegible]	2
Nesophila			[illegible]
Endodonta	3	1	[illegible]
Pseudolibera	1		1
Libera	[illegible]	1	1

Of the above taxa, the *Pseudolibera, Nesodiscus, Nesophila, Planudonta,* and *Cookeconcha* represent either large-sized species in general or the largest in their lineages. The correlation is not exclusively with large size, since most *Libera,* all *Gambiodonta,* and the Hawaiian *Endodonta* retain very large and prominent palatal barriers. In the case of the Hawaiian taxa, a habitat shift may have more to do with the barrier loss than size factors. *Cookeconcha* has been found on stumps and logs (Pilsbry and Vanatta, 1906, p. 783) or on mossy tree trunks (*personal observation*), while *Endodonta* is known from under twigs and dead leaves (Pilsbry and Vanatta, 1906, p. 783) or talus slopes (Cooke, 1928, p. 14). Species of *Endodonta* mostly are much larger than species of *Cookeconcha,* but by remaining in the ground strata, *Endodonta* may have reason for retention of large barriers. If the primary predators were ground strata hunters, then *Cookeconcha's* shift in habitat could significantly reduce the selective value of the barriers.

The reasons for palatal barrier loss in the *Mautodontha* species is unknown. Only *M. aoraiensis* (figs. 74e, f) retains prominent parietals, while in the other three (figs. 78b-g) the parietals also are greatly reduced in size. *Australdonta radiella* (fig. 132) has the parietals reduced to threadlike traces, but shows no unusual shape or sculpture features, while *A. ectopia* (fig. 137e) has only a single parietal trace remaining.

Reduction of the palatal barrier to a low ridge or threadlike state can be viewed as a prelude to barrier loss. Tallying reduction and loss together (table XXXVII) emphasizes that lineage is more important than size factors, since the reductions in *Cookeconcha, Taipidon, Planudonta,* and *Nesodiscus* account for 62.5 per cent of all palatal barrier size reductions. When combined, the loss or great reduction of palatal barriers is concentrated in *Mautodontha, Cookeconcha, Australdonta, Planudonta, Nesodiscus,* and

Nesophila, with 26 (68.4 per cent) of 38 taxa clustered in these six genera.

Parietal and palatal barrier trace and expansion correlations

Tables XXIII, XXXVI, and XXXVIII give some indications of semi-independence in barrier characteristics on the two main apertural walls. The presence of palatal traces (table XXIII) does not correlate, in most cases, with similar parietal traces, and only 15 of 24 genera have such traces. Only palatal traces occur in the Hawaiian lineage, the *Thaumatodon* complex of genera tends to have both, while members of the *Minidonta - Mautodontha - Anceyodonta - Gambiodonta* complex have both in varying proportions. If allowance is made for the much greater loss of palatal barriers (table XXXVII), then the more conservative pattern of palatal barrier expansion is obvious. Bifid parietals will, in effect, be broadly expanded. When the patterns of parietal barrier expansion are correlated with unusual palatal barrier expansions (table XXXVIII), the departures from a "one-to-one" relationship are obvious.

TABLE XXXVIII. - CORRELATION OF UNUSUAL PALATAL BARRIER EXPANSION WITH PARIETAL BARRIER EXPANSION

Parietal expansion	Palatal expansion not	moderately	strongly
not	5		
weakly	5	5	2
moderately	2	6	3
strongly		7	7
bifid		4	3

Further comparisons of palatal and parietal barriers are deferred until after discussion of barrier growth and microdenticulation patterns.

Barrier growth

The apertural barriers in most species retain their same position relative to the aperture from hatching through old age. There thus has to be a pattern of incremental anterior growth and posterior resorption coordinated with increased shell size. The pattern of this growth can be deduced through scanning electron microscope studies of anterior deposition and posterior resorption areas. *Opanara areaensis areaensis* (fig. 39) can serve as an example. It has high profile sculpture on the shell surface, thus requiring change in the normal pattern of parietal callus and wall deposition (fig. 39b). In smooth-shelled taxa, such as zonitoids, the parietal callus can be deposited directly onto the previous shell layer. Probably at most there is dissolution of the periostracum to permit better bonding of the calcareous shell layers. In *Opanara* there is obvious dissolution not only of the overlying periostracum, but also a significant part of the underlying calcareous ridge structure prior to deposition of the initial thin callus layer (see lower left of fig. 39b). Such adsorption is not total (fig. 39c), since the remnants of the radial ribs are clearly visible as contours in the parietal callus between the 1st and 2nd parietal barriers. The increase in rib visibility from right to left in Figure 39c is only partly an artifact of increasing curvature. It mainly comes from increasing thickness in the parietal callus which tends to "even out" the surface and gradually eliminate the surface irregularities that reflect rib position on the previous whorl. This is most easily explained by assuming that as the callus is extended anteriorly as a single layer (fig. 39b), a similar thin layer is deposited over the inner surface of the callus and barriers at least up to the point at which the superior microdenticulations occur. Evidence for such a pattern of layering is found by examining the posterior margin of the barriers (figs. 40, 41). In *Thaumatodon hystricelloides,* which has a very thick palatal callus, the multi-layered nature of the callus is evident at the resorption surface (left of fig. 41a). Although less prominent, the same layering can be seen in *Opanara areaensis* (Solem, 1973b, lower left of fig. 10). Deposition and resorption of the denticulated portions of the barriers is a more complex matter. While the anterior threadlike and non-denticulated barrier surfaces apparently are added to in multiple increments, the denticulated portion remains stable in height and has a very complex surface in the Endodontidae. The lower portion of each barrier shows layering on the resorption surface (fig. 40) just below the denticulated bulge, but the latter shows no traces of layering at much higher magnification. Below the obviously layered section is a slanted resorption facies with grooves etched into the barrier. This suggested that the mantle tissue secretes a weak acid that effectively dissolves the barrier and callus. Very probably the mantle gland extensions onto the pallial roof (figs. 163e; 171e, MG) control both aspects of growth. The lack of layering in the denticulated bulge suggests that this is deposited as a single "cap" around the multi-layered barrier and then not further involved in the process of callus and barrier formation until resorption.

The pattern is quite different in the Charopidae, where the denticulated surfaces can be seen on the anterior slope of the barrier (Solem, 1973b, fig. 17) and thus layered deposition is possible. Even in a species with comparably shaped barriers, such as the St. Helena Island *Helenoconcha,* the denticulated surfaces are deposited in successive layers (Solem, in press A). The latter pattern probably reflects the lowered whorl count and thus more rapid increase in whorl cross-section found in the Charopidae as opposed to the Endodontidae. In the latter there would be less rapid change in barrier height needed to maintain the same absolute degree of apertural narrowing and thus single denticulated layer formation with gradual anterior increment would be effective. In the Charopidae, where more rapid barrier height increment per unit of whorl growth would be required, the multiple layer pattern of denticulation would be effective and efficient.

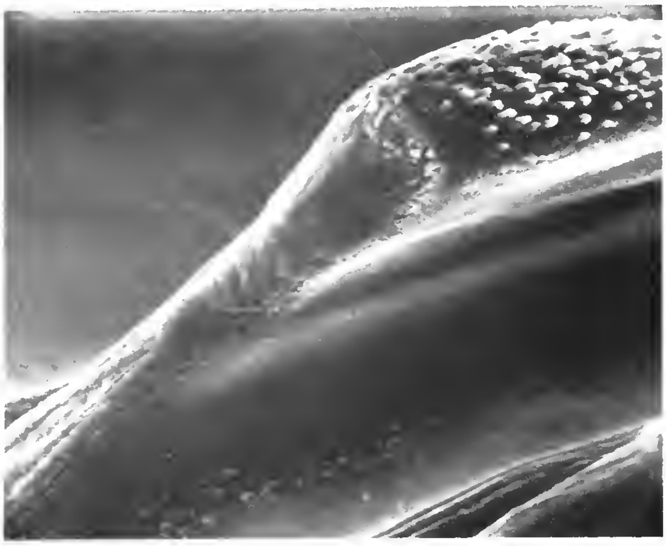

FIG. 40. Palatal barrier resorption surface in *Thaumatodon spirrhymatum*. 780×.

While the layered nature of growth in the barriers has been established, there is no direct evidence of growth and resorption sequence. Simple observation shows that the length of the barriers varies slightly within a population, generally within less than a sixteenth of a whorl. The difference is in the whole row of barriers. Except for teratological examples, the entire row will be added to or resorbed equally. In juveniles there are clear differences in the distance from lip edge to anterior barrier termination, suggesting that there is no one-to-one correlation in shell increment and barrier increment. Putting these observations together suggests a simple pattern of postembryonic barrier growth and resorption, in which there is first posterior resorption and barrier shortening. This is followed by subsequent anterior additions to the callus and barriers. The exact correlation with shell edge increments is unknown. Such a sequence would be efficient in terms of energy budget, since calcium resorbed from the barrier posterior could be deposited at the anterior end. The alternate sequence of anterior addition followed by posterior resorption would require an extra energy load on the snail. In addition, extra calcium would have to be accumulated from the environment to support the anterior addition, then calcium resorbed from the posterior would have to be stored until needed for the next growth increment. This would be highly inefficient. Whether there is linkage or not between parietal and palatal growth changes is unknown.

The above data on growth do serve to explain the layered nature of the barriers and provide an explanation for the variation observed in barrier length. Because the length generally had to be judged by obtuse-angled viewing into the aperture, exact length measurements could not be obtained. The cited differences of barrier length must be treated as relatively crude estimates. In a few taxa, such as *Australdonta degagei*, however, the barriers were clearly visible through the palatal wall and their

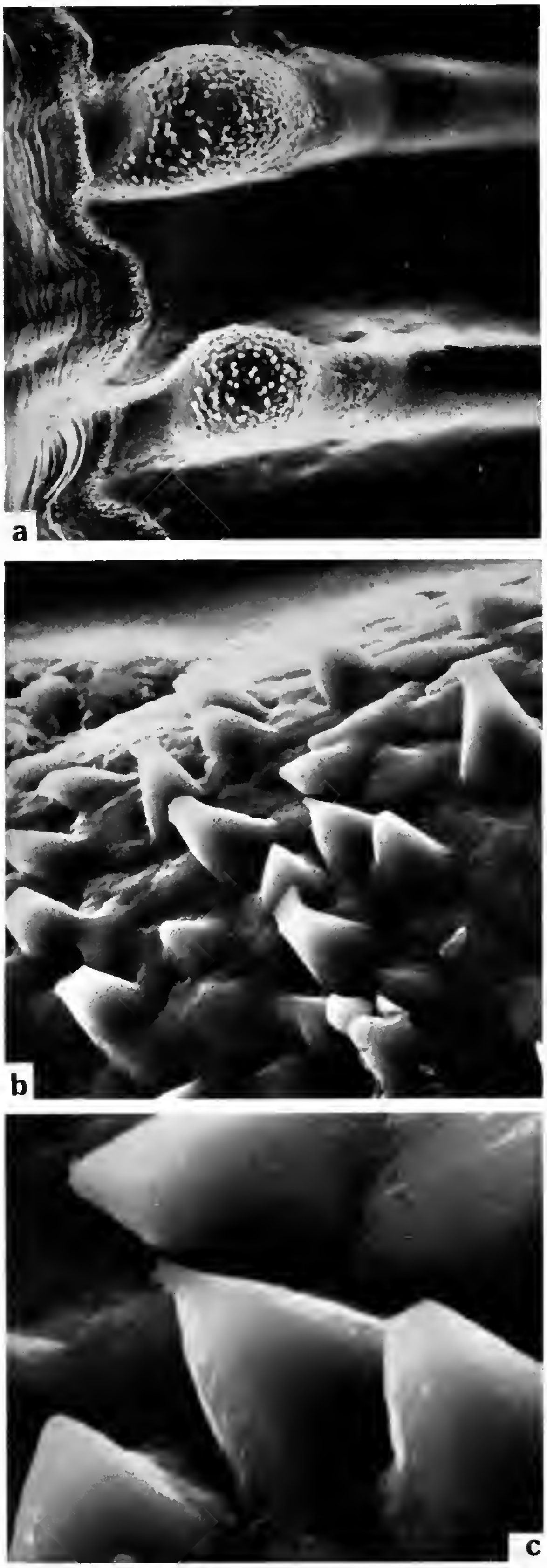

FIG. 41. Palatal barrier sculpture in *Thaumatodon hystricelloides* (Mousson). Station 19, Lake Lanuto'o, 2,500 ft., Upolu, Samoa. FMNH 153452: **a**, fractured edge of palatal callus and two palatal lamellae with single beads on each, 300×, note even nature of layering beneath palatals; **b**, top of single palatal bead at 3,000×; **c**, individual barbs at 10,000×.

length could be measured directly. Barriers of adult *A. degagei* showed about a 10 per cent range in barrier length. In juvenile specimens this reached an observed maximum of 25 per cent although most variations were in the 15-20 per cent range.

Microdenticulations

Under optical examination, the upper, posterior edges of the barriers are seen to have minute "serrations." Under the scanning electron microscope, these are seen to consist of elongately triangular microdenticles, generally sharp pointed (fig. 39d, e), but sometimes blunt tipped (fig. 41b). All of these point in the same direction, toward the apertural opening. Elsewhere (Solem, 1972c) I have discussed the possible original function of such microstructures and their origin from micropustulations. The latter are visible on the callus of *Opanara areaensis* (figs. 39c, d). From a microgripping surface useful in extending the retracted snail, more sophisticated and sharper microdenticles provided added protection against arthropod predation. The basic form and orientation of these denticles are the same throughout the Endodontidae. This contrasts with the Charopidae (Solem, 1973b), where the denticles are of many types, leading me to suggest that barriers originated many different times in the Charopidae, but that the extant Endodontidae share a common ancestor in which microdenticulated barriers were present.

Within the Endodontidae, there are relatively simple patterns of denticle variation. In the vast majority of taxa, they are evenly distributed along the upper expanded edge of the major barriers, but absent from the lower and/or non-expanded anterior sections. The microdenticulations do not occur on the callus trough or threadlike portions of the barrier, but are replaced by the micropustulations. In four genera, *Thaumatodon, Zyzzyxdonta, Priceconcha,* and *Aaadonta,* the barrier shape is altered. Superior expansion is restricted to a series of relatively widely (*Thaumatodon spirrhymatum,* Solem, 1973d, fig. 10) to quite closely spaced (*T. hystricelloides,* fig. 194d, e) "beads." These beads may be simple swellings (fig. 41a) or variously laterally twisted (fig. 194d). The number of such beads depends upon both their spacing and the total barrier length. In one species, *T. multilamellata* (Garrett), the barriers are topped with recurved hooks (fig. 192d) or simple vertical points (fig. 192e).

Another variation has been observed in the larger Endodontidae from Hawaii. Microdenticulations in both *Endodonta* and *Cookeconcha* (fig. 42) may be blunt tipped or even truncated (fig. 42f) on top of the barrier, although retaining the basic triangular form on the sides of the expanded portion (fig. 42a, b, e). They thus have the basic form of the microdenticulations found in the Charopidae (Solem, 1973b, figs. 15, 16, 19, 21, 22) on the barrier top, but the pattern of attachment (fig. 42a) shows that these are derived from the basic endodontid pattern. All of those specimens agree in having the uniform pattern of microdenticulations. This suggests quite strongly that the triangular points are the generalized condition in this group. Even when the barrier expansion is changed to "beaded" patterning, the character of the microdenticulations is constant.

Barrier numbers and length

Variation in the number of parietal and palatal barriers shows a combination of both size and phyletic factors. Previously (pp. 52-58, 62-63). I have discussed the pattern of loss and size reduction in these barriers. Although generally there is a normal number of barriers for all specimens of a given species, a substantial number of taxa (39 of 179) show variation in numbers of parietal (table XXXIX) and/or palatal (table XL) barriers. In a few cases, the material available permitted study of such variations between populations of the same species. In *Ruatara oparica* (fig. 115) there are geographic differences in the barrier number changes. In *Anceyodonta hamyana* (table LXXIII) the proportions fluctuate widely between populations, while in *Opanara bitridentata* (table LXXVIII) the limited data suggests a more consistent variation pattern. Species of *Australdonta* (fig. 126) show a variety of patterns.

The percentages listed in Tables XXXIX and XL are based on a few to many specimens and/or populations. Their reliability as being truly indicative of the overall pattern in a species is low, but they do suggest the variety of experimentation that exists and hint at its nature. Percentages in taxa such as

TABLE XXXIX. - PERCENTAGE DISTRIBUTION OF PARIETAL BARRIER NUMBERS

Species	Number of parietal barriers				
	1	2	3	4	5
Mautodontha daedalea			67.7	32.3	
M. punctiperforata		71.4	28.6		
M. parvidens		92.9	7.1		
M. rarotongensis		36.4	63.6		
M. consimilis	9.1	90.1			
M. acuticosta	23.4	76.4			
Anceyodonta hamyana			45.9	54.1	
A. densicostata			15.0	85.0	
A. labiosa			36.4	63.6	
Opanara bitridentata		61.8	38.2		
O. a. areaensis			93.7	6.3	
Rhysoconcha atanuiensis			98.0	2.0	
Ruatara o. oparica		21.1	71.0	7.9	
R. o. reductidenta	1.3	8.2	77.7	11.4	1.3
Australdonta degagei			75.0	24.3	
A. pseudplanulata			87.5	12.5	
A. tapina			28.6	71.4	
A. yoshii			90.9	9.1	
A. raivavaeana			73.2	22.1	
Tairidon fragila	60.0	40.0			
T. varidentata	75.0	25.0			
T. marquesana		25.0	75.0		
T. woapoensis		25.0	75.0		
T. petricola decora			15.0	85.0	
Thaumatodon euaensis			38.1	61.9	

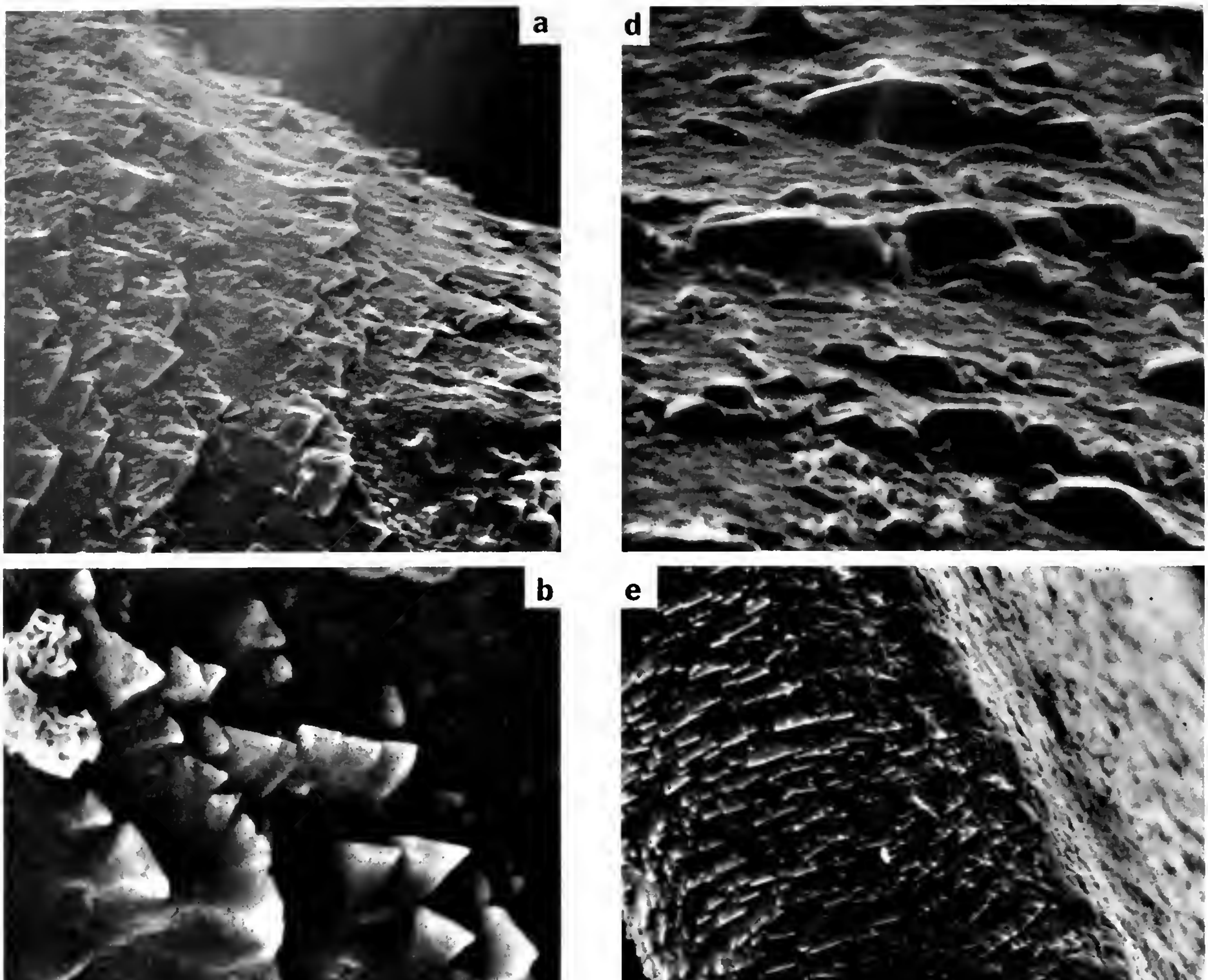

FIG. 42. Palatal barrier sculpture in Hawaiian Endodontidae: **a-d**, *Endodonta fricki* (Pfeiffer). Waianae Mts., Oahu, Hawaii. BPBM 128063. *a*, lateral view of 2nd palatal at 2,250×; *b*, top view of 2nd palatal at 11,000×; *c*, view from aperture of 2nd palatal lamellar sculpture at 2,750×; *d*, same at 6,800×; **e-f**, *Cookeconcha nudus* (Ancey). Kaiwicki, 2,500 ft. elevation, Hilo, Hawaii. FMNH 90319. *e*, top view of 2nd palatal at 1,000×; *f*, same at 5,000×. Photographs courtesy of Engis Equipment Company, Morton Grove, Illinois.

TABLE XL. - PERCENTAGE DISTRIBUTION OF PALATAL BARRIER NUMBERS

Species	Number of palatal barriers						
	0	1	2	3	4	5	6
Mautodontha parvidens				7.0	86.0	7.0	
M. rarotongensis			66.7	33.3			
M. boraborensis					88.2	11.8	
Opanara bitridentata					78.1	15.1	6.1
Rhysoconcha atanuiensis						98.0	2.0
R. variumbilicata						96.0	4.0
Ruatara o. oparica			5.3	7.9	86.3		
R. o. normalis				19.2	73.6		
Orangia sporadica					82.0	13.0	5.0
Australdonta degagei					3.5	93.6	
A. pseudplanulata				25.0	75.0		
Taipidon woapoensis				12.0	88.0		
Libera b. bursatella	5.1	5.1	89.8				
L. b. orofenensis	6.3	25.0	62.4	6.3			
L. spuria			3.2	9.7	87.1		
L. garrettiana				4.6	95.4		
L. heynemanni				86.7	13.3		
L. incognata			64.7	11.8	23.5		
L. jacquinoti				3.8	96.2		
L. subcavernula			95.3	4.7			
L. tumuloides		94.8	5.2				
Thaumatodon multilamellata						66.7	33.3

Australdonta degagei, Ruatara, Rhysoconcha, and *Libera bursatella* are based on quite significant specimen numbers. The low frequency deviants presumably thus reflect rare mutants or developmental accidents. Other situations, as in the *Australdonta,* hint at classic Mendelian dominance as the underlying basis of variation. In discussing the correlatives of barrier numbers, the varying extent of departures from a uniform number presented practical difficulties. Species were classed as having significantly variable barrier counts only if one-third or more departed from the standard number. Otherwise the species is grouped with those taxa having the predominant character state condition. While this underemphasizes the total extent of variation, it does facilitate making comparisons.

Most genera have a clear majority or nearly all species showing a constant number of parietal barriers (see table XLI). Only in *Mautodontha, Anceyodonta, Australdonta,* and *Taipidon* are there massive experimentations in barrier numbers. Genera such as *Minidonta, Cookeconcha, Nesodiscus, Gambiodonta,* and *Thaumatodon* show some variations. The genera with strong variations are also those in which there is a great range in the degree of apertural narrowing achieved by the barriers (table XLVIII). Both size and number reduction of the barriers are involved in this pattern.

Genera with a predominance of 2 parietals include *Cookeconcha* and *Endodonta* from Hawaii, *Orangia, Taipidon,* and *Libera. Minidonta, Australdonta, Opanara,* and *Aaadonta* have mostly 3 parietals, while *Thaumatodon* has 4 parietals, and the Mangarevan *Anceyodonta* and *Gambiodonta* tend to have 4 or 5 barriers. All the taxa with many parietals involve extreme cases of size reduction for the barriers. Thus the number of parietal barriers is tied to phyletic units and also is involved in the degree of apertural narrowing. Raw data on the size correlations of

TABLE XLI. - PHYLETIC CORRELATION OF PARIETAL BARRIER NUMBERS

	Number of parietals								
	0	1, 1-2	2	2-3	3	3-4	4, 4-5	5	many
Minidonta			2		12		1		
Mautodontha		1	6	1	3	1	5		
Anceyodonta					2	2	4	4	
Cookeconcha		4	12						
Kleokyphus					1		1		
Opanara				1	8		1		2
Rhysoconcha					1		1		
Ruatara				1	3				
Orangia			5						
Australdonta		1	1		5	1	2		2
Taipidon		1	5	1	2		1	1	
Planudonta		1	3						
Rikitea		1							
Nesodiscus	1	7	2						
Nesophila									2
Kondoconcha			1						
Endodonta			8						
Pseudolibera		1							
Libera		2	17						
Gambiodonta			1		1		3	2	
Thaumatodon					2	1	6		
Zyzzyxdonta					1				
Aaadonta			1		8				
Priceconcha								1	
TOTALS	1	19	64	4	49	5	25	8	6

parietal barrier number (table XLII) require interpretation. The larger size of those taxa with only 1 parietal reflects the concentration of this state in species of *Cookeconcha* and *Nesodiscus* in which the apertural narrowing function has, for all practical purposes, been lost. Similarly, the larger size of those taxa with 2 parietals results from the phyletic units *Endodonta* and *Libera* clustering there. The large standard errors of the mean show that there are not significant size differences between barrier numbers, but that this relates more to phyletic unit and degree of apertural narrowing.

The number of palatal barriers is basically 4 in the Endodontidae (table XLIII), with changes to 3, 5 or total loss of palatal barriers the most common alterations. Addition of a 5th palatal has happened in several different ways. Most *Aaadonta, Kleokyphus callimus* (fig. 95b), *Endodonta lamellosa,* and *E. marsupialis* (fig. 167a) have an extra subperipheral barrier; in *Australdonta* (fig. 127a, b) it is possible that descent of the former columellar barrier onto the lower palatal wall has been completed; *Rhysoconcha* (fig. 112) and *Minidonta micraconica* (fig. 65b) have extra supraperipheral barriers; while

TABLE XLII. - SIZE CORRELATION OF PARIETAL BARRIER NUMBERS

Number of parietal barriers	Number of taxa	$\bar{X}$ D	$\bar{X}$ W
0	1	7.46	7+
1, or 1-2	19	5.31±0.41 (2.90-11.19)	5.94±0.23 (4 3/8-8)
2	64	4.66±0.20 (1.79-8.99)	5.88±0.13 (3 5/8-8)
2 or 3	4	3.63±0.29 (3.01-4.33)	5.40±0.18 (5-5 3/4)
3	49	3.22±0.13 (1.68-6.60)	5.33±0.09 (4-8)
3 or 4	5	3.41±0.25 (2.54-3.98)	5.69±0.25 (5-6 1/2)
4	22	3.81±0.46 (2.00-12.26)	5.76±0.19 (4-7 1/2)
4 or 5	2	3.08±0.15 (2.93-3.23)	6.00±0.43 (5 1/2-6 1/2)
5	7	3.40±0.42 (2.20-5.07)	6.03±0.19 (5 3/8-6 3/4)
many threadlike	6	4.98±1.28 (3.21-11.29)	5.40±0.17 (4 3/4-5 7/8)

Kondoconcha othnius (fig. 162b) has both enlarged the upper palatal and added another supraperipheral palatal barrier. Reduction to only 3 palatal barriers generally involves loss of the supraperipheral barrier, as in *Minidonta inexpectans* (fig. 62d) and some *Aaadonta* (fig. 206b), or by elimination of a subperipheral barrier, as in many *Libera* (figs. 173d).

Unlike the number of parietal barriers, there is a rather clear size correlation with the number of palatal barriers (table XLIV). Although the large standard errors of the mean for the diameters indicate a large amount of variability, the trend itself is obvious.

Table XLV reviews the correlations between numbers of parietal and palatal barriers. There is generally central clustering. The pattern of reductions in both sets has been described above.

Barrier length is a difficult measurement to make and one that is subject to considerable error, since the distance must be judged by looking into the aperture at an angle. In addition, the growth pattern outlined above would mean that the length of barriers would vary according to the stage in the growth cycle at which the animal died. Given the above factors, the cited lengths should be taken for what they are, estimates of relative length and not firm figures. Figure 43 shows how length was estimated, as an arc of a circle to the nearest sixteenth. The pattern of the parietals, normally extending anteriorly of the lip edge, permits seeing slightly more than one-fourth of a whorl from its anterior termination. If the sharp posterior descension could be spotted, but not the actual posterior margin, it was scored as "to the line of vision" or "one-quarter whorl," depending on the degree of anterior extension. Extending the same principle to measuring the palatal barrier length was simple, but this means that comparisons of parietal and palatal lengths is not possible, since the two arcs are at different distances from the shell axis. In Figure 43, the solid lines indicate the arc for a one-quarter-whorl long parietal barrier, while the dotted lines indicate the length of a palatal barrier, in this case about one-eighth whorl long.

TABLE XLIII. - PHYLETIC CORRELATION OF PALATAL BARRIER NUMBERS

	Number of palatals						
	0	1, 1-2, 2	3	3-5	4	5	many
Minidonta		1	3		9	2	
Mautodontha	4	1			10	2	
Anceyodonta					12		
Cookeconcha	6		3	1	4	2	
Kleokyphus					1	1	
Opanara					9	1	2
Rhysoconcha						2	
Ruatara	1				3		
Orangia					5		
Australdonta	3		1	1	2	5	
Taipidon		1	1	1	7		1
Planudonta	1		1		1		1
Rikitea	1						
Nesophila	2						
Nesodiscus	2	3	3	2			
Kondoconcha						1	
Endodonta					6	2	
Pseudolibera	1						
Libera	1	7	6		5		
Gambiodonta			2		5		
Thaumatodon				1	6	2	
Zyzzyxdonta			1				
Aaadonta			2	2	1	4	
Priceconcha						1	
TOTALS	22	13	23	8	86	25	4

TABLE XLIV. - SIZE CORRELATION OF PALATAL BARRIER NUMBERS

Number of palatal barriers	Number of taxa	$\bar{X}$ D	$\bar{X}$ W
0	21	5.03±0.52 (2.90-11.19)	5.28±0.18 (4-7)
1-2	14	5.68±0.60 (1.97-11.29)	6.50±0.28 (4 3/4-8)
3	22	4.99±0.47 (1.68-12.26)	6.00±0.24 (4-7 5/8)
3-5	8	4.16±0.35 (2.70-5.17)	5.51±0.14 (5-6 1/4)
4	85	3.71±0.14 (1.73-8.99)	5.65±0.08 (3 5/8-7 5/8)
5	24	3.51±0.26 (1.97-7.20)	5.46±0.14 (4 1/4-7 1/2)
many	4	3.76±0.34 (4.13-5.77)	5.98±0.10 (5 3/4-6 1/4)

TABLE XLV. - CORRELATION OF PARIETAL AND PALATAL BARRIER NUMBERS

Number of parietals	Number of palatals: no data	0	1	1-2	2	2-3	3	3-5	4	5	5-6	many
0		1										
1		8	4				3	1				
1-2		2									1	
2	2	5		1	4	1	12	3	28	6		2
2-3						1			3			
3		1			1		6	2	30	9		
3-4									3	2		
4							1	2	13	6	1	
4-5									2			
5									7	1		
many, a few high						2						
many, none high		3									1	

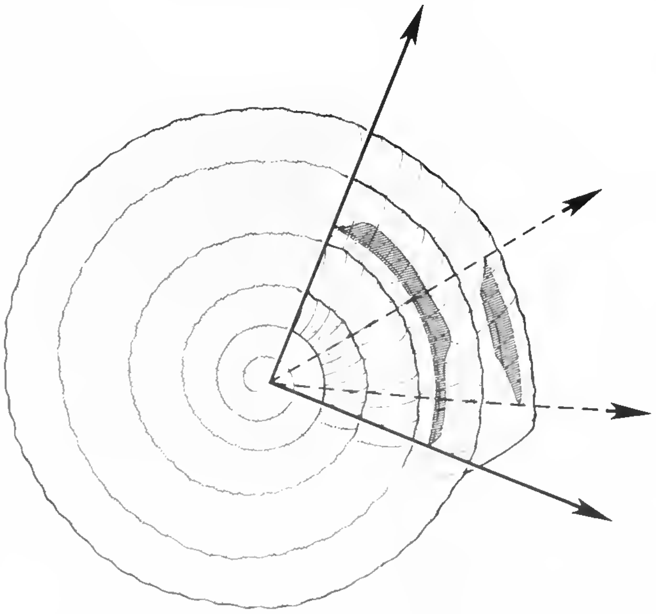

FIG. 43. Method of measuring parietal (solid line) and palatal (dotted line) barrier lengths.

TABLE XLVI. - PARIETAL BARRIER LENGTH AND SIZE CORRELATIONS

Length of parietal barriers	Number of taxa	$\bar{X}$ diameter	$\bar{X}$ whorl count
1/8th whorl	1	3.88	5.25
less than 3/16ths	11	3.46±0.44	5.28±0.37
3/16ths	34	3.78±0.25	5.46±0.17
less than 1/4th	21	3.91±0.29	5.73±0.14
1/4th	33	3.52±0.22	5.18±0.11
more than 1/4th	18	3.26±0.16	5.57±0.14
to line of vision	16	4.14±0.28	6.78±0.18
beyond line of vision	44	4.92±0.34	6.06±0.13

TABLE XLVII. - PALATAL BARRIER LENGTH AND SIZE CORRELATIONS

Length of palatal barriers	Number of taxa	$\bar{X}$ diameter	$\bar{X}$ whorl count
less than 1/8th	13	3.64±0.29	5.16±0.18
1/8th	69	4.14±0.22	5.77±0.11
3/16ths	38	4.10±0.24	5.85±0.14
1/4th	18	3.57±0.21	5.71±0.12
line of vision	4	3.21±0.42	6.04±0.19
beyond line of vision	9	3.87±0.58	6.05±0.36

TABLE XLVIII. - DEGREE OF APERTURAL NARROWING BY BARRIERS

Genus	Total taxa	Apertural narrowing			
		Strong	Moderate	Weak	Not
Minidonta	15	2	8	5 (2→)	
Mautodontha	17		5	6	6
Anceyodonta	12	8 (1→)	(←1) 4		
Cookeconcha	16	2 (2→)	3	(←2) 4	7
Kleokyphus	2		2		
Opanara	12	2	8 (2→)		2
Rhysoconcha	2	1 (1→)	1		
Ruatara	4	1	1 (1→)	1	1
Orangia	5		4 (1→)	1	
Australdonta	12		5 (5→)	3	4
Taipidon	11	1 (1→)	(←1) 7 (1→)	1	2
Planudonta	4				4
Rikitea	1		1		
Nesophila	2				2
Nesodiscus	10				10
Kondoconcha	1	1 (1→)			
Endodonta	8	6	(←1) 1	1	
Pseudolibera	1				1
Libera	19		(←1)10 (1→)	(←3) 7	2
Gambiodonta	7	7			
Thaumatodon	9	2	(←4) 7 (1→)		
Zyzzyxdonta	1	1			
Aaadonta	9	2 (1→)	(←4) 7		
Priceconcha	1	—	—	1	—
	181	36 (7)	(12)74 (12)	(5)30 (2)	41

There is no major correlation of parietal barrier length and size (table XLVI) until the very elongate barriers are encountered. Those that extend to or beyond the line of vision are found in species with higher whorl counts (and thus larger size). Most probably this is a simple release pattern. Whatever triggered the adding of additional whorls also slowed the posterior resorption phase of barrier growth, or the barriers simply lengthened proportionately to the increment in whorls. Palatal barrier length correlates probably more with palatal barrier shape changes (table XXXII) than it does with size (table XLVII). Short barriers are a prelude to loss of the barriers.

Degree of apertural narrowing

The most fundamental functional significance of barriers is the degree to which they effectively narrow the aperture. Ideally this should have been quantified in some manner. An obvious procedure would have been to measure the cross-sectional area of the aperture in a plane through the expanded portions of the barriers, subtract from this the area that is open between the barrier tips, and then calculate the per cent of the aperture that is walled off by the barriers. Unfortunately, this proved to be impractical, since sufficient material to permit sectioning each species through the barriers was not available. In many species, such as *Libera* (fig. 182) and *Gambiodonta* (figs. 187a, c), the elevated portions of the barriers are recessed essentially beyond the line of vision from the aperture. Thus even direct visual estimates of the degree to which the apertures are narrowed become subjective.

The degree of narrowing obviously varies widely. In all *Nesodiscus* and taxa with reduced barriers, such as many *Mautodontha* (fig. 78) and *Cookeconcha* (fig. 94), the aperture is virtually unimpeded by the barriers. In contrast, taxa such as most *Anceyodonta* (figs. 81, 82, 83) and *Endodonta* (fig. 167) have the aperture almost closed by the thicket of protruding barriers.

An estimate of relative closure is tallied in Table XLVIII. The number of taxa that are intermediate in character have been indicated in parentheses and are accompanied by directional arrows. Genera such as *Anceyodonta* and *Gambiodonta* share common ancestry, with the latter retaining strong apertural constriction despite their large size, as do the Hawaiian ground-dwelling *Endodonta,* although many *Cookeconcha* that are almost equivalent in size have almost completely lost their barriers. Where a variety of relative constrictions is found in a genus, such as *Minidonta, Mautodontha, Cookeconcha,* and *Taipidon,* there has been drastic size reduction of the barriers (table XXXVII). As an indication of the different states, reference is made to species of *Minidonta,* which range from strongly restricted to nearly no major narrowing. *Minidonta micra* (fig. 63a) is strongly narrowed; *M. micraconica* (fig. 65b), moderately; *M. hendersoni* (fig. 63c), weakly; and *M. planulata* (fig. 69b) tends towards virtually no effective apertural narrowing, a state achieved in such species as *Mautodontha subtilis* (fig. 77d).

At least one additional factor is involved, the body whorl contour (fig. 14A-E). Species with the body whorl laterally compressed (fig. 14A), such as *Mautodontha maupiensis* (fig. 76a), will have the aperture more constricted than species with an evenly rounded periphery, such as *Mautodontha subtilis* (fig. 77d), even though the actual height of the barriers may be virtually identical in the two species. The probable extent of this correlation is shown in Table XLIX.

TABLE XLIX. - CORRELATION OF APERTURAL NARROWING AND BODY WHORL CONTOUR

	Apertural narrowing			
Body whorl	Strong	Moderate	Weak	Not
Compressed laterally	10	19	4	5
Evenly rounded	6	15	12	12
Keeled	14	23	5	8

Taxa with evenly rounded peripheries tend to have much less apertural narrowing than do those taxa with either laterally compressed or keeled peripheries. Formation of a keel would automatically tend to accentuate the degree of apertural narrowing by the barriers, as would the lateral compression of the body whorl. But the latter change may be directly selected for because of the aperture narrowing, while keel formation (pp. 21-23) may be more of a means of lessening shell height, with the apertural narrowing a secondary feature.

Some of the largest (*Endodonta, Gambiodonta*) and some of the smallest (*Minidonta, Cookeconcha*) taxa have strongly narrowed apertures, so data on overall size are not presented. Often, within a particular genus, species with strongly constricted apertures will be smaller in adult size than those with little or no apertural narrowing. This is obvious in *Anceyodonta,* where the eight species with strongly constricted apertures have an average mean adult diameter of 2.54 mm., while the four species with only moderately constricted apertures have an average mean diameter of 3.42 mm. *Taipidon petricola petricola,* the only species in that genus with a strongly constricted aperture, is the smallest in the genus. Similarly, the shift from "moderately" to "weakly" to "not constricted" in *Australdonta* is size correlated, the respective average mean diameters being 3.38 mm., 3.95 mm., and 4.19 mm. Thus within a lineage there may be a tendency for barrier constriction reduction to correlate with size increase, but there is no overall pattern.

Summary of barrier variation

Much of the variation in structure, reduction, and numbers of apertural barriers in the Endodontidae is correlated with phyletic factors rather than size. There is no equivalent in respect to the apertural barriers to the apparent triggering size of 4.75 mm. after which drastic radial rib reduction occurs (pp. 47-49). The degree of superior expansion to the barriers does correlate partly with small size, but lack of any expansion is a correlative of barrier reduction rather than of shell size. Relative expansion of the parietal and palatal barriers is not closely correlated. Recession of the palatal barriers does correlate with size change, but shape and form of the barriers correlate with each other, not shell size. Similarly, there are correlations in form and position of the columellar barriers, but these are independent of shell size.

Within phyletic lines there are tendencies toward barrier size reduction and lessened degree of apertural constriction, both of which correlate to some extent with increased size within that lineage. But this varies from lineage to lineage in terms of what size is reached before major barrier reduction occurs. As a result of the above data, I have confidence that apertural barriers carry a high information content for phyletic deductions.

GROSS ANATOMY

This monograph covers 185 species-level taxa. No material was seen of six previously described species. The dissections include 58 taxa, whose phyletic

TABLE L. - PHYLETIC REPRESENTATION OF DISSECTED TAXA

Genus	Total taxa	Number seen	Number dissected
Minidonta	15	15	1
Mautodontha	17	17	2
Anceyodonta	12	12	
Cookeconcha	18	16	3
Kleokyphus	2	2	
Opanara	12	12	11
Rhysoconcha	2	2	2
Ruatara	4	4	2
Orangia	5	5	4
Australdonta	12	12	2
Taipidon	11	11	6
Planudonta	4	4	3
Rikitea	1	1	
Nesodiscus	8	8	2
Nesophila	4	2	1
Kondoconcha	1	1	
Endodonta	10	8	3
Pseudolibera	1	1	
Libera	19	19	6
Gambiodonta	7	7	
Thaumatodon	9	9	4
Zyzzyxdonta	1	1	
Priceconcha	1	1	1
Aaadonta	9	9	5
Totals	185	179	58

distribution is summarized in Table L. Partial specimens of *Opanara areaensis microtorma, Orangia cookei tautautuensis,* and *Kondoconcha othnius* were also seen, but the material was too fragmentary or poorly preserved for successful illustrations to be prepared or measurements made. The major phyletic gaps in the coverage are in the Mangarevan radiation (many *Minidonta,* and all *Anceyodonta, Gambiodonta,* and *Rikitea*), *Minidonta, Mautodontha,* and *Kleokyphus.* Cooke (1935, pp. 41-42) reported that the complete destruction of native forest on Mangareva had occurred prior to 1934, although obviously live collected native land snails from the island were added to museum collections as late as 1872. Similarly, the collections on the Tuamotus have yielded virtually no living endemics in this century. The faunas of these two areas include *Pseudolibera,* both *Kleokyphus, Mautodontha daedalea,* five species of *Minidonta,* all *Anceyodonta,* all *Gambiodonta,* and *Rikitea insolens,* for a total of 30 species-level taxa. If these groups are eliminated, then 38.9 per cent (58 of 149) species-level taxa were dissected at least in part. This section includes data on *Thaumatodon spirrhymatum* and *Priceconcha tuvuthaensis,* the species described in Solem (1973d).

Because of the fragmentary material available for dissection in many species, information concerning apical organ systems frequently is lacking. For example, the origin of the penial retractor muscle could be observed in only 40 of the 58, the length of the pallial cavity in 35, and the character of the ovotestis in 37 taxa. Penial length was measurable, however, in 54 of the 58 taxa. Within these limitations of materials and successful observations, the following pages review the observed patterns of variation in structure, delineate the topographic anatomy of the body, compare and contrast these features with equivalent structures as observed in the Pacific Island Charopidae, and occasionally add comparative remarks from dissections of Australian, New Zealand, New Caledonian, and Lord Howe Island taxa. These additions are background data necessary to establish the importance assigned variations in structure against the context of a broader scope investigation. While comparisons of the endodontid shell variation with the Charopidae have been deferred until the second monograph, the anatomical data are presented here.

The sequence of structures places the genital system first because of its higher information content concerning phylogeny within the family.

GENITAL SYSTEM

The terminology used below is modified from that of H. B. Baker (1938b, pp. 6-10, 92), since it more adequately reflects the apparent functioning of the system than does the terminology used by English workers such as Rigby (1963, 1965). The latter system was developed by forced comparisons of prosobranch and very advanced pulmonate taxa. It is not transferable to description of less specialized pulmonate taxa. Many of the fusions and specializations found in the advanced taxa have not taken place in the more generalized families. A recent commentary (Bayne, 1973) also basically adopts the Baker terminology. The abbreviation used in the illustrations follows each term.

OVOTESTIS (G) – The hermaphroditic gland or ovotestis is located above the reflexion of the intestine from the stomach apex. Typically it consists in the Endodontidae of many multilobate alveoli strung along a single collecting tubule. Typical patterns are shown in Figure 164a for the sequential relations of the alveoli along the collecting tubule and Figure 165e for the palmately clavate branching pattern of a single unit. The collecting tubule runs along the lower parietal wall of the whorl cross-section, ascending for one-third to two-thirds of a whorl, depending on the length of the ovotestis. I have no data on seasonal variation in development of individual follicles or length of the entire organ. Preservation in this area of the animal generally was poor. This dictated drawing only that portion which could be extracted easily, so that apparent differences in ovotestis lengths shown in the drawings are artifacts of dissection resulting from preservation problems. In the Endodontidae there is a single characteristic pattern of ovotestis orientation.

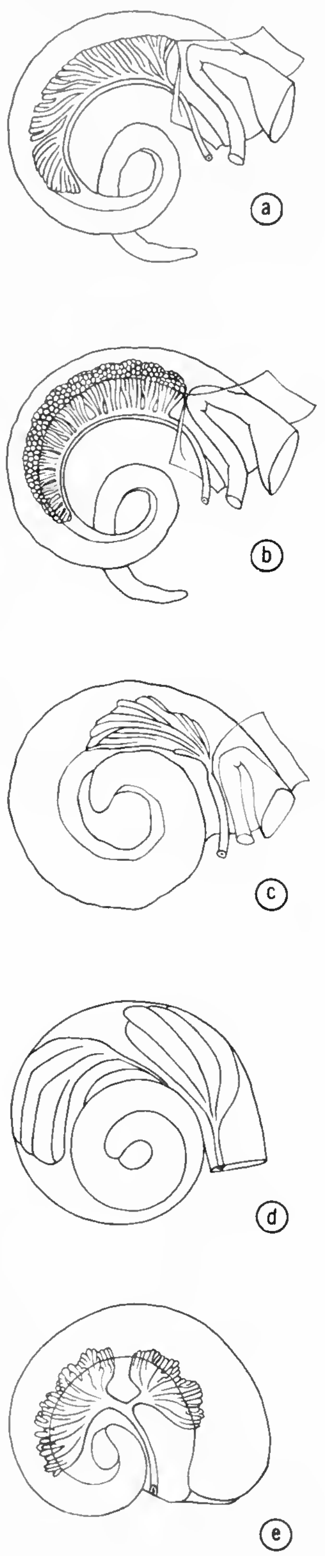

FIG. 44. Ovotestis structure and position in the Endodontidae (*a-b*) and Pacific Island Charopidae (*c-e*): **a**, typical pattern as seen in *Endodonta fricki*; **b**, pattern after nuclear whorl enlargement as seen in *Nesophila tiara*; **c**, typical pattern in the Pacific Island Charopidae as seen in the Tongan species usually known as "*Charopa*" *vicaria* (Mousson, 1871); **d**, pattern seen in *Aeschrodomus stipulata* (Reeve, 1852) from Pelorus Bridge, Marlborough, New Zealand (FMNH 165395), probably correlated with changes in coiling pattern and whorl size; **e**, pattern seen in *Thalassohelix propinqua* (Hutton, 1883) from Weka Pass, Waikari, South Canterbury, New Zealand (FMNH 165399) and associated with size increase of the whorl cross-section. (CK)

This is shown in Figure 44a. The follicles extend upward and outward at an acute angle to the shell axis. Often they reach from the lower parietal to the upper palatal margin, being imbedded in digestive gland tissue. Up to a full whorl or whorl and a half of digestive gland tissue extends above the ovotestis apex.

This is modified in only three of the dissected taxa. In *Nesophila tiara* (Mighels) and *Cookeconcha jugosus* (Mighels) (figs. 165d, h; 44b) the follicles have a right angle radial orientation to the shell axis, instead of sitting at an acute angle, while in both species of *Rhysoconcha* (p. 255) the follicles are reduced in number and lie essentially parallel to the plane of coiling. *Cookeconcha jugosus* is 25 per cent larger in diameter than an apparently related species, *C. hystricellus* (Pfeiffer), with virtually identical whorl count. The latter species (fig. 165j) retains the normal positioning of the ovotestis. *Nesophila tiara* has a mean shell diameter of 11.29 mm. with an average of slightly less that 5½ whorls, while the other studied *Nesophila, N. capillata* (Pease), has a mean diameter of 4.46 mm., with slightly less than 4⅞ whorls. Visual inspection of these four species shows that the apical whorls of the pair with altered ovotestis orientation are significantly larger than those of their smaller relative. The ovotestis orientation in *N. capillata* is unknown. The shell size increase in these taxa resulted not from the addition of more whorls, as is the pattern in *Nesodiscus* and *Libera*, but from proportionate change in whorl size without increase in whorl number. Thus the shift of ovotestis orientation in the *Nesophila* and *Cookeconcha* probably reflects the sudden availability of extra space in the upper whorls, and not any shift in genital structure itself. As presented elsewhere (pp. 255-256), the change in follicle orientation seen in *Rhysoconcha* is one of the features that led me to propose that this is an example of secondary size reduction.

The Pacific Island Charopidae have ovotestis patterns that stand in great contrast to those found in the Endodontidae. The typical charopid pattern (fig. 44c) is for one or two clusters of palmately clavate alveoli to extend virtually horizontally from the stomach apex toward the apex of the viscera. A single clump will extend as shown; the second clump, when present, will lie apicad of the first, separated from it by a distinct zone of digestive tissue. In such taxa as *Aeschrodomus stipulata* (Reeve, 1852) (fig. 44d) from New Zealand, which have an altered shell shape with high spire, the two clumps may nearly fill the whorl. Only the narrowest strips of digestive gland tissue extend anteriorly. Multiple experiments in size increase have occurred in the Charopidae, with forms such as the New Zealand *Thalassohelix propinqua* (Hutton, 1883) (fig. 44e) showing nearly right angle to the shell axis orientation for the follicles. The basic two-clump format is clearly visible, despite the convergence to the endodontid patterns (fig. 44a, b). In regard to Micronesian, Polynesian, and Melanesian taxa, the difference in ovotestis structure is diagnostic at the family level.

The Charopidae not only have fewer and proportionately larger alveoli in the ovotestis, but they are oriented and clumped differently from the follicles found in the Endodontidae. Observed changes in the follicles seen in the Endodontidae correlate with major shifts in growth pattern, either increase in whorl cross-sectional area (*Nesophila* and *Cookeconcha jugosus*) or probable secondary size reduction (*Rhysoconcha*).

HERMAPHRODITIC DUCT (GD) – This is an expanded continuation of the joined collecting tubules of the ovotestis follicles that extends to the carrefour region. In nearly all generalized shell-bearing pulmonates, this tube extends along the parietal or lower parietal margin of the whorl beneath or adjacent to the stomach. The function of this tube is to transport sex products. Its existence as a separate organ may be the result of simple space problems. The stomach occupies the same part of the visceral hump as the hermaphroditic duct, the space-consuming ovotestis lies above the stomach expansion and initial intestine reflexion, while the large albumen gland occupies the area below the stomach. The hermaphroditic duct provides an essential narrow passageway through the zone occupied by the main expansion of the digestive tract. In 32 of the examined Endodontidae, the hermaphroditic duct is a simple expanded tube (fig. 45a). The outer edge may have a few humps or wrinkles in it, but the inner surface is smoothly and evenly curved. Inspection of the drawings scattered through the systematic section shows major differences in degree of expansion and the extent to which it is obviously reflexed anteriorly before joining the carrefour. The expansion differences probably vary with the state of reproductive activity, while the exact degree of reflexion more probably reflects the state of contraction of the animal when preserved. The existence of a slight reflexion in the talon area is normal, but this often is accentuated in contracted animals. Presumably this is caused by apical movement of the pallial apex forcing the albumen gland and intestinal loops slightly above the stomach expansion by compressing the early part of the stomach. The permanent bend in the hermaphroditic duct permits varying lengths to be reflexed upward. Artificial straightening of the reflexed section can happen quite easily while pinning out a dissection for drawing. Thus apparent changes in this section of the genital system as illustrated have no significance.

What does seem to have significance is the degree to which the duct is kinked or partly coiled. This is shown most completely by *Aaadonta kinlochi* (fig. 45d) and only slightly less so in *Ruatara oparica normalis* (fig. 64h) and *R. o. reductidenta*. In *Cookeconcha jugosus* (fig. 165h) the middle half of the duct is kinked, while in *Thaumatodon euaensis* (fig. 195c) and *Aaadonta fuscozonata fuscozonata* (fig. 199e) the upper half of the duct is kinked. In *Thaumatodon hystricelloides* (fig. 45b) the top quarter is coiled, as is the top third in *Aaadonta c. constricta* (fig. 45c). The differences between the several states are shown and suggest that a progressive pattern of kinking from the apex is normal. The normal pattern in the Charopidae from the Pacific Islands also is for a simple hermaphroditic duct, but coiling occurs in many Austrozelandic taxa, such as *Allodiscus dimorphus* (Pfeiffer, 1853). Generally the duct in the Charopidae is thicker, shorter (corresponding with a general tendency toward fewer whorls in that family), and appears more highly iridescent than those from endodontid species.

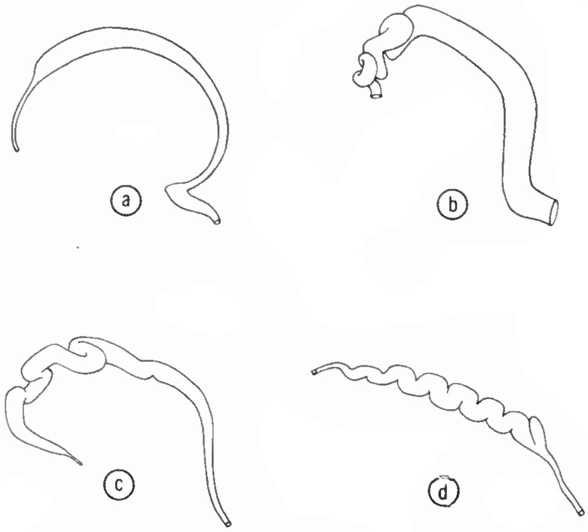

FIG. 45. Hermaphroditic duct variation in the Endodontidae: **a**, typical pattern; **b**, slight kinking as in *Thaumatodon hystricelloides;* **c**, moderate kinking as in *Aaadonta constricta;* **d**, extensive kinking as in *Aaadonta kinlochi*. In each drawing the ovotestis would be on the left and the reflexion to the carrefour on the right. (CK)

Viewed within the context of their lineages, the few endodontid taxa with coiled or kinked hermaphroditic ducts show no clear shell correlations with each other. Kinking has occurred in flat-spired, large species (*A. kinlochi* and *C. jugosus*), relatively small species with spires that protrude much higher than normal (*A. c. constricta, A. f. fuscozonata, T. euaensis,* and *R. o. reductidenta*) and species with a median spire projection (*T. hystricelloides* and *R. o. normalis*). The phenomenon is not associated with whorl increase and high spire, as in *Libera* and *Nesodiscus,* but with spire protrusion while retaining a normal, or even slightly lowered whorl count (*A. kinlochi, T. euaensis, A. c. constricta*). In the Austrozelandic Charopidae, kinking is, in general, associated with visceral hump reduction, changing in coiling patterns of the shell, and major size increments.

Thus kinking of the hermaphroditic duct in the Endodontidae should be viewed as having occurred independently in each genus. The presence of a kinked duct in an endodontoid genus should be taken as a signal that changes have occurred from the visceral hump coiling or protrusion pattern found in its ancestors. The reasons for kinking rather than simple shortening of the duct is unknown. There could be functional significance requiring a minimum duct length. It could be merely an accident of development, with the trigger that results in shortening the stomach failing to influence the development of the duct itself.

Although no measurements were taken as documentation, simple observation confirms that the longer the stomach, the longer the hermaphroditic duct, since it serves to convey sex products from a large organ above the stomach to a large complex of organs below the stomach.

TALON (GT) and CARREFOUR (X) – Considerable controversy exists concerning the structure and function of organs in this area. Many English workers refer to this as the "receptaculum complex" (Rigby, 1965, pp. 455-457), have called the lower portion of the hermaphroditic duct a "seminal vesicle," and inferred that there are functional divisions into a "fertilization sac" and two "receptacula seminis" in *Succinea* and zonitids such as *Oxychilus* (Rigby, 1963, pp. 328-329, fig. 7). In the Bulimulidae, Van Mol (1972, pp. 199-202) reported a highly complex talon structure, part of which is a fertilization chamber. In other taxa, such as the Australian camaenid genus *Craterodiscus,* there is no differentiated structure in the area where the hermaphroditic duct joins the albumen gland, prostate, and uterus (Solem, 1973c, p. 379, fig. 1, d). Similarly, in the Tornatellinidae (Cooke and Kondo, 1960, pp. 31-33) the structures can be greatly reduced (as for example in *Tekoulina,* Solem, 1972b, p. 101, fig. 3, *b*) or with an accessory, very large organ (Cooke and Kondo, 1960, pp. 31-33, fig. 8). In contrast to this, both the Endodontidae and the Charopidae have a relatively simple structural arrangement. The talon (GT) is a bulbous expansion sitting on a shaft that may be extremely short (most Charopidae) to usually quite long (many Endodontidae) and that emerges from the carrefour (X) apex. There is no external indication of any subdivision to the talon. In several exceptionally well-preserved specimens it was possible to examine this region in some detail.

The Endodontidae have variation in the talon shaft length. Of the 41 taxa in which this could be observed, 25 had a long shaft, as in *Endodonta fricki* (fig. 164b); seven had a medium length talon shaft, as in *Aaadonta c. constricta* (fig. 199c); and nine had a short talon shaft, as in *Thaumatodon euaensis* (fig. 195c). These variations are only partly phyletically associated. Of the genera in which two or more species could be scored, *Cookeconcha, Rhysoconcha, Orangia, Australdonta,* and *Libera* had only long talon shafts. Both *Planudonta* in which the talon could be observed had short shafts, but the four *Taipidon* had two with short and two with long shafts. *Opanara* has species showing all three states, while *Aaadonta, Thaumatodon,* and *Taipidon* have species with two states.

The situations involving mixed shaft types within genera or involving derivative genera (*Taipidon* and *Planudonta*) require special examination. In *Opanara,* short shafts are possessed by *O. bitridentata* (fig. 96c) and *O. duplicidentata* (fig. 96g); medium-length shafts by two subspecies of *O. areaensis* (fig. 96j); and long shafts by *O. altiapica* (fig. 97a) and *O. megomphala tepiahuensis* (fig. 97e). These are the only species in that genus for which this character was observed. *O. areaensis microtorma, O. duplicidentata,* and *O. bitridentata* are sympatric at Stations 446 and 451 on Mt. Perahu, while the nominate race of *O. megomphala* occurs with *O. areaensis* at Station 477. *O. duplicidentata* and *O. bitridentata* differ markedly in penial length (1.5 and 2.65 mm. long, respectively), pilaster pattern (figs. 96d, h), and origin of the columellar retractor muscle. *O. areaensis* has the penis length and columellar muscle origin of *O. bitridentata,* but modified pilasters (fig. 96k). The other *Opanara* mentioned above also differ in penis size and pilaster patterns.

Of the Marquesan species, *Taipidon semimarsupialis* (fig. 139a), *T. fragila* (fig. 138e), *Planudonta intermedia* (fig. 147a) and *P. concava* (fig. 147c) have short talon shafts, while *T. petricola petricola* (fig. 138a), *T. p. decora* (fig. 49a), and *T. centadentata* (fig. 139e) have long talon shafts. Both *Planudonta, T. semimarsupialis,* and *T. centadentata* are sympatric on Mt. Ooumu, Nukuhiva Island. *Taipidon fragila* from Hivaoa essentially is sympatric with *T. varidentata,* a species whose talon length is unknown, while the two races of *T. petricola* are the only endodontids known from Eiao and Hatutu Islands.

The several *Thaumatodon* and *Priceconcha* are all allopatric, but they have short, medium, or long talons. In *Aaadonta constricta* and *A. fuscozonata,* which were collected together at Station 203 on Peleliu and Station 221 on Koror, there are apparent differences in talon length.

Because of the allopatric variability in *Thaumatodon* the evidence is not fully conclusive, but there is a strong correlation of talon shaft length variations occurring under conditions of congeneric sympatry. This suggests that this feature may be involved in species isolating phenomena. Much more study is needed before this can be stated as a fact or disproved. Certainly the variations are repeated in several phyletic units, so that selection on a relatively low level would be involved. Because of its numerical frequency and broader geographic distribution, I conclude that the long talon shaft is the generalized state in the Endodontidae.

The carrefour (X) is a barely noticeable to prominent swelling in the gonoduct that usually lies partly buried in the surface of the albumen gland (GG). It receives ducts from the hermaphroditic duct (GD), talon (GT), and albumen gland (GG). Separate ducts exit to the uterus (UT) and prostate (DG). In several taxa, preservation was excellent and the apparent relationship of these ducts could be observed using transmitted or reflected light at 64×-100× magnification. Generally the albumen gland tissue was teased away, the ducts of the uterus and prostate separated, then the isolated carrefour area placed in a temporary glycerine mount on a depression slide for study. The species for which such detailed observations were made are *Opanara duplicidentata* (fig. 103a, b), *Taipidon petricola petricola* (fig. 138b), *Endodonta fricki* (fig. 164b), *Libera micrasoma* (fig. 171g), *Thaumatodon euaensis* (fig. 195c), and *Aaadonta constricta constricta* (fig. 199c). Inspection of these figures shows that the talon inserts either directly on the head or slightly to one side of the head of the carrefour. The hermaphroditic duct uniformly inserts laterally on the side of the carrefour, either just below (*O. duplicidentata*) or well below the carrefour head. The albumen gland duct is drawn as entering opposite the hermaphroditic duct in *Opanara duplicidentata,* but this needs confirmation. Since it was the first of these species studied and illustrated, this structure could have been misinterpreted. The other species show the albumen gland duct entering after the uterine duct has separated from the prostate. In *Libera micrasoma* and *Aaadonta c. constricta* it was possible to indicate the internal duct passageways. These appear in transparency to be simple tubes.

The situation in the studied Charopidae is quite comparable, with different species having short or long talon stalks, but generally the talons of charopids have a distinctly circular head, resembling a golf ball on a tee, while that of the Endodontidae is elongately ovate, and there is a greater tendency for the carrefour not to show any expansion in the Charopidae. Histological studies are needed to work out the significance of these reported differences and to establish the exact structures involved.

ALBUMEN GLAND (GG) – This mass of alveolar tissue is situated just above the pallial cavity apex and nestled in the loop of the intestines just below or at the point where the narrow esophagus widens to form the stomach. The albumen gland varies greatly in size from individual to individual, often has its surface indented by the head of the spermatheca and intestinal loops, and fragments upon handling. Most typically, whether the snail is contracted or expanded, a well-developed albumen gland lies next to the upper parietal wall. It will be broadest at the base, tapering to a narrow rounded tip just before the stomach expansion reaches the upper parietal margin. The spermathecal head lies at its base, next to the parietal wall, and between the albumen gland base and the kidney base. The intestinal loop that indents the kidney margin lies between the spermathecal head and the palatal wall. When reduced in size, the albumen gland may lie in the midwhorl section rather than being pressed against the parietal wall. Because of its variability in size, the necessity to remove tissue in order to examine the talon, and its general delicacy of structure, no attempt was made to show the albumen gland in complete form.

Compared with the Charopidae, the alveoli were smaller and the shape less variable in the Endodontidae. Charopid taxa have the albumen gland tightly jammed between the intestinal loops with the surface deeply indented by other structures. The gland has distinctly larger alveoli and is more ovoid than elongated in shape. Probably this relates to the fact that the Charopidae from Pacific Islands have a median whorl count of 4⅛– compared with a median of 5½+ for the Endodontidae. Shortening of the visceral hump coiling resulted in less space for "stringing out" the organs and hence greater compaction in the area between the pallial cavity apex and the stomach expansion.

PROSTATE (DG) and UTERUS (UT) – Most European workers have preferred the term "spermoviduct" for this region, reflecting the fact that in most European pulmonates there is a morphologically united common duct that is physiologically differentiated into male and female tracts. Good descriptions of the tract histology for this area in advanced land snails are given by Van Mol (1972, pp. 202-207) for the Bulimulidae and by Rigby (1965) for the Succineidae. The Charopidae agree with this pattern in having the ducts fused, but with a simpler pattern of differentiation than was seen in the above mentioned groups (Solem, *unpublished*). The Endodontidae differ in having the prostate and uterus entirely separate tubes that are very loosely bound together by a few connective tissue strands. Elsewhere (Solem, 1972b, pp. 108-112) I have reviewed the pattern among pulmonate snails of variation in fused *versus* separate pallial gonoducts (= prostate and uterus), and concluded that fully separated ducts are the basic pulmonate condition, with fusion of the tracts a derived character state and advanced condition that has evolved several times.

Throughout the Endodontidae, the prostate is a small, thin-walled tube into which one (fig. 191a), two (fig. 199c), three (fig. 164d), or even four or five (fig. 165a) rows of alveoli attach individually. Normally the prostate lies on top of the uterus, with the spermathecal shaft lying loosely attached on top of its duct. The prostatic alveoli are bent toward the outside of the whorl across the top of the uterus. The whole bundle of genital ducts (prostate, uterus, spermathecal shaft), esophagus, and columellar muscle occupy the lower palatal and columellar portion of the whorl margin, while the pallial cavity extends to the palatal margin. The hindgut occupies the upper parietal-palatal margin.

In the Charopidae, the prostate tissue is fused to the uterus, with an internal channel slightly to strongly demarcated from the uterine lumen. The prostatic tissue is composed of even fewer and often more elongated alveoli that show no patterned arrangements, rather than the large, rather short alveoli placed in even rows that are characteristic of the Endodontidae.

Structure of the uterus in the Endodontidae is far more complicated, but the histological studies needed to work out the details could not be undertaken. Depending upon the species, there is evidence of from two to four sections in the uterus. These range from an always present division into a simple, thin-walled, narrow upper chamber (fig. 164a, UT_1) and a broader, thicker walled, glandular chamber (UT_2) in the lower section, to the situation seen in *Thaumatodon hystricelloides* (fig. 191b). This species has a clump of glandular tissue, clearly different in texture from that of the albumen gland, around the head of the uterus (UT_1); the typical thin-walled, rather narrow tube (UT_2); the expanded zone with thick glandular walls (UT_3); and a narrower tube with very fine glandular tissue (UT_4) that lies below the termination of prostatic alveoli and before the start of a simple tube that I interpret as the free oviduct (UV). Presumably the upper zone of the uterus is the section associated with enclosure of the embryo with nutritive material and membranes, while the lower glandular section secretes the egg capsule. No eggs were seen inside the uterus of any specimen dissected during this study. Whether the more complex uterine area of *T. hystricelloides* reflects a change in structure or merely better preservation (this material initially was placed in 95 per cent alcohol after drowning) is unknown. The uterine area tended to swell quickly in liquids of lowered alcohol content and few detailed observations were made on this area, since after initial illustration and handling it often had burst or split open.

In the Charopidae, the uterus is much more sharply divided into two zones, with the lower chamber having thick glandular walls and often appearing as an ovoid structure grafted onto the prostate surface. The difference between having totally separate *versus* fused pallial gonoducts is a highly significant one and another key character separating the Endodontidae from the Charopidae.

Inspection of the drawings suggests that there may be differences in the number and actual size of the prostatic alveoli, but whether this is a variation correlated with reproductive cycle stage or has phyletic significance is unknown.

TERMINAL MALE GENITALIA – This complex includes the vas deferens (VD), epiphallus (E) (when present), penis (P), penial retractor muscle (PR), and the atrium (Y). Differences are substantial, primarily because species recognition presumably has great selective influence on this region. Because of this, description of the structural variations cannot be separated completely from a consideration of sympatric interspecific variation.

The vas deferens, when prostate and uterus are separate, must be defined as the prostatic duct below the end of the alveoli. Its appearance varies with preservation and possibly between taxa, but data are meager on this latter aspect. In some taxa it appears that the tube becomes thicker walled and reflects light more strongly almost immediately, but in others this change seems to occur gradually as the vas deferens descends to the penioviducal angle. The vas may or may not be loosely bound to the angle before reflexing upward along the penis itself. It is effectively held in the angle by the right ommatophoral retractor muscle that passes through the peniovidual angle. The ascent of the vas deferens is on the columellar side of the penis to a point that is usually distinctly below the head of the penis (fig. 46), although the exact point of entry varies within rather narrow limits for any single lineage. The entry into the chamber of the penis is a simple pore, normally distinctly below the point of apical union for the pilaster. The situation in *Endodonta* (figs. 164a, c; 165a, d, g) is typical. *Taipidon p. decora* (fig. 49a) shows an exceptionally low entrance. The basic two pilasters of the penis chamber unite at its apex and while drawing tech-

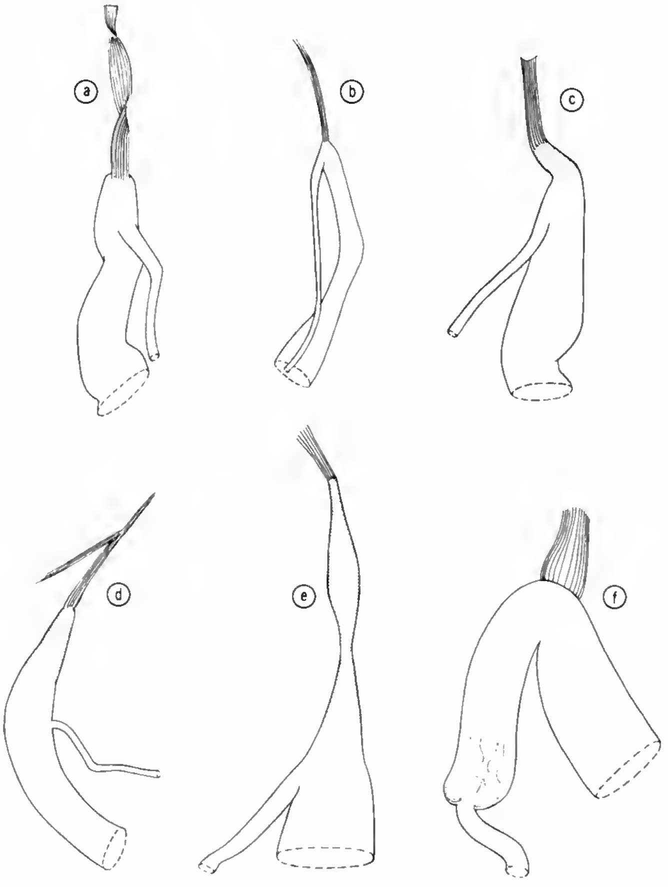

FIG. 46. Vas deferens entrance and penial retractor muscle insertion patterns: **a**, typical (based on *Cookeconcha jugosus*); **b**, apical vas deferens entrance (based on *Ruatara oparica normalis*); **c**, some added tissue to penis apex (based on *Opanara megomphala*); **d**, moderate extra tissue (based on *Opanara bitridentata*); **e**, much extra tissue (based on *Planudonta intermedia*); **f**, formation of a penial epiphallus and valvular vas deferens entrance (based on *Aaadonta c. contricta*). (CK)

niques may suggest that the pore (EP) lies opposite the point of union or on the same side as the point of union in generalized taxa, this is an artifact of drawing technique rather than an indication of structure. In forms with altered pilaster arrangement, such as *Cookeconcha hystricellus* (fig. 165j, k), the pore often is located just below the point of pilaster union, although externally (fig. 165j) it may appear to be apical in its insertion. In *Taipidon fragila* (fig. 138e) the penis is only 1.5 mm. long, compared with a 2.5 mm. long penis in its sympatric congener, *T. varidentata.* The former has a distinctly more apical insertion of the vas than does the latter. In *Rhysoconcha variumbilicata* (fig. 64f, g) the vas deferens entrance is almost apical, and in *R. atanuiensis* it is apical. The two dissected races of *Ruatara oparica* (figs. 46b; 64h-j) have the vas entering "just below the apex." These situations probably are indicative of size reduction.

The above changes represent positional minor shifts. In contrast, there is a major change in the *Thaumatodon-Priceconcha-Aaadonta* lineage. In these genera the vas deferens enters through a pair of "lips" or a "valve" (fig. 46f; 199d) into a reflexed zone of the penis that lies well below the point of attachment for the penial retractor muscle. Two pilasters extend from this point, in varying degrees of prominence (figs. 199d; 200c; and Solem, 1973d, fig. 20, b), up to the penis head and then into the main chamber. The length of the reflexed portion varies, being about one-third the penis length in *Thaumatodon decemplicata, T. hystricelloides,* and *T. spirrhymatum,* one-half the penis length in *T. euaensis* and all dissected *Aaadonta,* and two-thirds the penis length in *Priceconcha tuvuthaensis* (Solem, 1973d, fig. 20, *a*).

The homologies of this area and appropriate terminology present some difficulties. An epiphallus usually is defined as an expanded portion of the vas deferens that is functionally apical of the penis head. Normally, in advanced taxa, it is involved in spermatophore or sperm packet formation. Presumably in less advanced taxa it secretes fluids to carry and provide life support for the sperm during transport. It is not eversible and is very different from the penial structures. Frequently, in such groups as the Helicarionidae (Solem 1966a, figs. 6, *b*; 19, *a*; 22, *a*), there are accessory flagella or caeca on the epiphallus, and in Indian Helicarionidae (Blanford and Godwin-Austen, 1908) highly complex and spined spermatophores are formed in the epiphallus and its appendages. It also is possible for an epiphallus to develop from the penis itself and thus be a non-eversible apical chamber of the penis. The latter situation probably applies to the *Thaumatodon-Aaadonta* lineage. The altered zone lies topographically below, although functionally above, the penial retractor muscle and is reflexed anteriorly in all specimens. It is extremely difficult to see how this could be everted successfully. If this area is not everted during copulation, it would be functionally a "penial epiphallus." On the other hand, the reflected, probably non-eversible area has the typical penial pilasters found in the other Endodontidae. It is clearly of penial origin and probably of recent origin. The valvular arrangement at the point of vas deferens entrance is the "new" structural feature, while the change in penial retractor attachment, or equally possibly the growth of the penial chamber past the retractor muscle attachment, is a minor shift in position. The pilaster patterns are typical of the family. I have concluded that this is a functional penial epiphallus of recent origin and use the term epiphallus for the structure throughout this report and in an earlier publication (Solem, 1973d).

The adoption of a valvular entrance from the vas deferens and alteration of the upper penial chamber into an epiphallus represents the most striking change seen in the genital anatomy of the Endodontidae.

In contrast to this, the Charopidae normally have a vas deferens-derived epiphallus, with the entrance from the vas highly complex and variable, often involving sphincter pilasters and/or plug-like structures. The epiphallus normally is sharply differentiated from the penis and there are highly complex and varied patterns of transition between the two areas. In lineages that are undergoing visceral hump reduction in the Charopidae, such as the "flammulinid" genera *Flammulina* and *Maoriconcha,* the epiphallus may be shifted forward into the penial complex, thus giving an external appearance of no epiphallic differentiation (Solem, *unpublished*). One group of Micronesian Charopidae departs from the pattern in having direct entrance of the undifferentiated vas deferens into the penis head after passing partway through the U-shaped insertion of the penial retractor muscle (Solem, *unpublished*). There is no trace of any epiphallic differentiation.

The penis in the Endodontidae is basically an elongated tube with two pilasters extending from a union at the apex of the penis almost to or even into the atrium. Differences in penis length, pilaster pattern, and structure of the pilasters are highly influenced by interactions with sympatric congeners. Discussion of these factors follows preliminary review of some phyletic alterations. The Marquesan genera *Taipidon* and *Planudonta* are unique in the family because of developing a pustulose zone in the penis (figs. 49b; 138h; 147b, d). The extent and position of this glandular zone differs in the various species, ranging from perhaps two-thirds of the penis length in *T. semimarsupialis* to just the basal area in *T. petricola decora.* This is an additive feature to the genitalia and has no equivalent in other geographic areas.

Attachment of the penial retractor muscle (PR) to the penis itself is variable (fig. 46). In all dissected *Minidonta, Mautodontha, Cookeconcha, Rhysoconcha,* *Ruatara, Australdonta, Nesodiscus, Nesophila, Endodonta,* and *Libera* the penial retractor attaches directly onto the penis apex (fig. 46a). Upon opening the penis there is no indication of any extra thickness to the penis apex at or near the point of muscle attachment. In *Orangia, Planudonta,* several *Taipidon* (*T. centadentata, T. fragila,* and *T. varidentata*), and all *Opanara* except *O. depasoapicata* and *O. caliculata,* there is a "fleshy extension" to the penis apex that extends for a variable distance upward before the penial retractor attaches (figs. 46c-e). This partly glandular zone does not surround the muscle, but is a new zone between the muscle and the penis apex. The varying extent and prominence of this zone within a genus can be seen quite clearly in Figures 96 and 97. The typical apical insertion of *O. depasoapicata* (fig. 96a, b), weak extension in *O. altiapica* and *O. megomphala* (fig. 97a-d), moderate extension in *O. m. tepiahuensis, O. fosbergi,* and *O. perahuensis* (fig. 97e-h), and stout extension in *O. bitridentata* (fig. 96e, f) compare with a much more even extension in the species of *Orangia* (fig. 121). *Taipidon* shows great variability, with direct attachment in *T. petricola* (fig. 49a) and *T. semimarsupialis* (fig. 139a, b), a long but narrow attachment zone in *T. centadentata* (fig. 139e, f), and very prominent attachment zone in *T. fragila, T. varidentata* (fig. 138e, g), and the *Planudonta* (fig. 147). In all of the above taxa, both the union of the pilasters and apex of the penis lie a significant distance below the penial retractor attachment point. The function of the added zone is not known, but a logical possibility for investigation would be secretion of fluids equivalent to that normally provided by the epiphallus in more advanced taxa.

The different patterns of penial retractor attachment and vas deferens entrance are summarized in Figure 46. In essence, these seem to represent at least two separate kinds of experiments in providing the functional equivalent of an epiphallic zone: interposition of glandular tissue between the penis apex and penial retractor muscle in several groups, and then formation of a non-eversible section of the penis by reflexion in the *Thaumatodon-Priceconcha-Zyzzyxdonta-Aaadonta* complex. The addition of glandular tissue to the penis apex is found in Rapan and Marquesan genera, but not in taxa from other geographic areas.

Much more variability is seen in the shape of the pilasters. This is complicated in analysis by changes in relative size shown by the two basic pilasters, and some variability in pilaster number. Figure 47 shows the basic cross-sectional pilaster types: low and rounded (*a*); medium in elevation (*b*); or high and lamellate (*c*). In *Australdonta* (fig. 125b, e) the two pilasters are complexly folded and split into portions, so that they do not fit into any of the above categories. In *Ruatara* (fig. 64i) there is only a single rugose pilaster for most of the penis length, which becomes bifurcated basally, suggesting that it is a secondary modification from the basic two-pilaster pattern.

The low and rounded pilasters are characteristic of the few *Minidonta, Mautodontha, Endodonta,* and *Aaadonta* that have been dissected, plus such species as *Cookeconcha jugosus* (fig. 165h), *Taipidon centadentata* (fig. 139f), and *Planudonta intermedia* (fig. 147b). Those taxa in which the pilasters are higher than wide, but rounded above if not secondarily altered, include all *Thaumatodon, Planudonta subplanula* (fig. 147g), *Nesophila tiara* (fig. 165g), *Nesodiscus* (fig. 154), the other *Cookeconcha, Rhysoconcha, Opanara perahuensis* (fig. 97i), and *Orangia sporadica* (fig. 121k). The latter two species probably represent secondary modifications from the normal pattern in these genera, since the remaining *Orangia* and *Opanara* all have high, lamellate pilasters. These also are the normal condition in *Libera,* the remaining *Taipidon, Planudonta concava, Kondoconcha othnius* (p. 368), and *Priceconcha tuvuthaensis* (Solem, 1973d, fig. 20, *b*). Whether the pilasters unite both apically and before the atrium, as in *Endodonta*; extend routinely into the atrium, as in *Thaumatodon* and *Aaadonta*; or are variously altered is selected for at a low taxonomic level. There is a general tendency for those taxa with low pilasters to have union apically and basally, while for those with very high and lamellate pilasters there can be absence of any union (*Libera,* fig. 171b) or typical union apically (*Planudonta,* fig. 147b, d; and *Priceconcha,* Solem, 1973d, fig. 20, *b*).

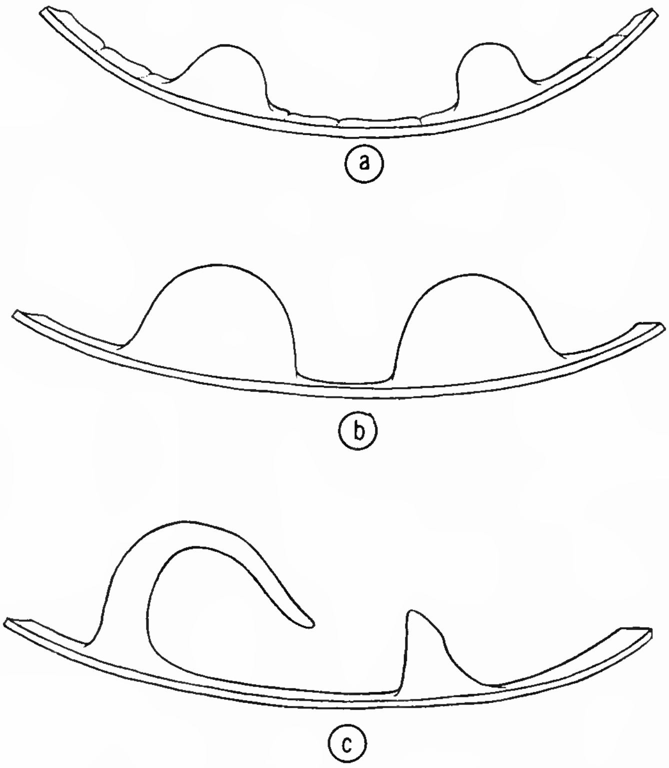

FIG. 47. Pilaster cross-sectional patterns in typical Endodontidae: **a**, low and rounded; **b**, elevated but rounded; **c**, high and lamellate (main pilaster) with reduced pilaster flattened or otherwise altered. (CK)

The relative size of the two pilasters is partly phyletically correlated and partly influenced by sympatric factors. The two pilasters are equal or nearly equal in size for dissected *Minidonta, Mautodontha, Rhysoconcha, Australdonta, Nesodiscus, Nesophila, Endodonta,* and all *Libera* except *L. cookeana.* Species of *Orangia, Planudonta, Thaumatodon, Priceconcha, Aaadonta,* and *Taipidon* (except two special cases) have the pilasters grossly unequal. Species of *Cookeconcha* and *Opanara* have a nearly equal mixture of both types. *Ruatara oparica* (fig. 64i) is unique in that the pilasters apparently fused into a single rugose structure that is split basally. There is no significant correlation between pilaster shape and relative size of the two pilasters (table LI), although a tendency exists for the low and rounded pilasters to be equal in size, with the higher pilasters more likely to be unequal.

TABLE LI. - CORRELATION OF PENIAL PILASTER SHAPE AND RELATIVE SIZE

Pilaster shape	Pilaster relative size	
	Equal	Subequal
Low and rounded	9	6
Intermediate	5	8
High and lamellate	9	15

The gross data on this variation should be checked with the patterns of sympatric variations summarized in Tables LII through LIV. Unfortunately, I had available for study only one example of sympatric congeners where low and rounded pilasters were involved. These two Tahitian *Mautodontha* (table LIII) differed grossly in penial size, but not in pilaster pattern. Their shell features (fig. 74) also are grossly different, so that there is no question of their being valid species. With high and lamellate pilasters, obviously there is much more room for experimentation. Overall the genus *Opanara* has six taxa with unequal pilasters and five with essentially equal pilasters. Listing several sympatric *Opanara* (table LII) shows that both penis size and pilaster changes occur. *Orangia* shows equivalent shifts. In the Tahitian *Libera* (table LIII) there is still a relatively simple pattern of penis size and pilaster proportion shifts, but in the Marquesan species (table LIV) the addition of a pustulose zone in the penis increased the options for change. The two *Planudonta* show size, pilaster length, and pustulose zone location variations, while the *Taipidon* show a unique pattern of change. On two different islands sympatric congeners have diverged in penial structure by one species having the pilasters broken up into a series of low bumps (figs. 138f, h; 139b, f).

The relatively few examples cited in these tables represent all the situations in which the anatomy of sympatric congeners could be studied. They have a greater importance by demonstrating the extent and ways in which these structures can be altered by interspecific selection phenomena. They also suggest that the size and shape variations seen in the penes of the few *Endodonta* and *Cookeconcha* dissected during this study (figs. 164, 165), none of which are sympatric, do not have great systematic importance. Rather it is probable that these variations hint at the extent of sympatric diversity in the essentially unstudied Hawaiian endodontid fauna. Similarly, they suggest that the wild variations seen in the terminal genitalia of New Zealand and New Caledonian taxa have to be interpreted in terms of such character displacement reactions.

At the same time, a note of caution must be injected here. Some of the outlined situations may be oversimplified. In the species accounts of *Libera bursatella bursatella* and *L. b. orofensis* reference is made to differences between and within populations in regard to penis size. Whether this is dimorphism, sibling species, or an apparent reversal of character displacement under conditions of exact sympatry is unknown. The *L. b. bursatella* with generally longer penes came from Station 863, where *L. cookeana* (penis length 5.9 mm.) occurred, but not *L. micrasoma,* with a penis length of 3.9-4.1 mm., which occurred with *L. b. bursatella* (penis length 4.3-4.5 mm.) at Station 866. Since there are clear-cut pilaster differences between the three species, the possible tendency toward closer similarity in penial length with sympatry of the different species is of very uncertain significance. Further work on these problems will depend upon new collecting efforts, since yet another complication exists. At Station 863, there were 169 *L. b. bursatella* and only one *L. cookeana,* while at Station 866, there were 90 *L. b. bursatella* and six *L. micrasoma.* The extent to which such disparate numbers would affect character displacement is unknown.

The Pacific Island Charopidae normally have a verge or vergic papilla and sophisticated circular or pocket-like stimulatory pads or pilasters. In the absence of these structures (epiphallate Micronesian genera), there is a combination of added muscular sheaths to the penis and epiphallus, plus a radiation of numerous fine lamellar pilasters from the epiphallic pore into the penis interior, where they coalesce into three large longitudinal pilasters.

Origin of the penial retractor muscle is yet another variable feature in the Endodontidae. In 29 of the 40 taxa in which this could be observed, the muscle originates from the diaphragm. While in one case the penial retractor is attached as low as the middle of the pallial cavity (*Aaadonta fuscozonata*) normally it attaches opposite the pallial cavity apex. *A. fuscozonata* has a sharply increased whorl count in comparison with other *Aaadonta,* so there may have been a forward shift of the muscle. In *Aaadonta kinlochi* and *A. constricta,* the attachment is just below the apex. It is slightly above the apex in *Orangia cookei* and *Opanara areaensis,* while in

Minidonta hendersoni the penial retractor attaches just at the point of stomach expansion.

This variability serves to indicate how gradual apical shift of the penial retractor origin could lead to the transfer of the muscle from the diaphragm to the free muscle system, generally the columellar muscle. This state is known in 11 taxa, including all dissected *Endodonta* and *Australdonta*. Both *Planudonta* for which the origin of the retractor muscle is known have it coming from the columellar muscle. The same state is found in both subspecies of *Taipidon petricola,* the smallest species in its genus, although other *Taipidon* have the more normal retractor muscle origin. In *Opanara duplicidentata* the penial retractor attaches to the tail fan just before this is joined by the buccal retractors. In *Nesodiscus fictus* the penial retractor attaches partly to the columellar muscle and partly to the diaphragm.

TABLE LII. - SYMPATRIC VARIABILITY IN PENIS SIZE AND PILASTER PATTERNS IN RAPAN TAXA

Species	Penis length in mm.	Pilaster pattern
Opanara		
bitridentata	2.65	both equal
duplicidentata	1.5	one split
areaensis	2.65	one reduced
megomphala	2.0-2.7	both equal
altiapica	1.8-2.1	one greatly reduced
Orangia		
cookei	2.0-2.1	unequal, both high, one split
sporadica	2.3	subequal, both widened, shorter
maituatensis	3.6	subequal, both split
Ruatara		
oparica	3.3	only one corrugated, split basally
Rhysoconcha	1.6-1.9	both equal

This shift of the penial retractor muscle origin has no obvious correlatives, but does have a significant result. Since the columellar muscle extends much further apically than the diaphragm, which attenuates as connective tissue at the level of the stomach, this shift in origin permits lengthening of the penis (fig. 56). A long penis is not a prelude to this shift, since *Opanara duplicidentata,* the only species in that genus to show the change in penial retractor origin, also has the smallest penis in the genus. In both *Planudonta* and two of the three *Endodonta,* penis length exceeds the shell diameter. In most other taxa it is considerably less. Only *Taipidon semimarsupialis* of the taxa with diaphragm origin of the penial retractor has the penis longer than the shell diameter. This probably is an accident caused by the secondarily changed growth pattern (fig. 143e) associated with brood-chamber formation in that species. In *Libera micrasoma* shell diameter and penis length are

TABLE LIII. - SYMPATRIC VARIABILITY IN PENIS SIZE AND PILASTER PATTERNS IN TAHITIAN SPECIES

Species	Penis length in mm.	Pilaster pattern
Mautodontha		
zimmermani	2.0	both equal
aoraiensis	0.6	both equal
Libera		
micrasoma	3.9-4.1	equal, simple
b. bursatella	4.3-4.5	subequal, folded
cookeana	5.9	one greatly reduced and only on lower half of penis

TABLE LIV. - SYMPATRIC VARIABILITY IN PENIS SIZE AND PILASTER PATTERNS IN MARQUESAN SPECIES

Species	Island[1]	Penis length in mm.	Pilaster pattern
Planudonta			
intermedia	N	4.6	small pilaster shorter, pustulose zone lower in penis
concava	N	6.0	small pilaster longer, pustulose zone more medial
Taipidon			
centadentata	N	4.3	split into bumps
semimarsupialis	N	4.9-5.3	unequal, high
fragila	H	1.5	unequal, high
varidentata	H	2.5	split into bumps

[1] N=Nukuhiva; H=Hivaoa

virtually identical. This is another brood chamber situation.

In the Pacific Island Charopidae, the penial retractor muscle inserts in a U-shaped fan on the penis-epiphallus junction, on the head of the highly complex epiphallus in the epiphallate Micronesian genera, or on the head of the penis with the vas deferens passing through the muscle in the third major group of taxa.

The atrium (Y) is formed by the union of the penis and terminal female genitalia (spermatheca, vagina, free oviduct) to form a common channel to the gonopore. Generally this is quite short, but in *Australdonta, Endodonta,* and *Aaadonta* the atrium is noticeably longer than normal, and in *Minidonta hendersoni, Taipidon varidentata, Planudonta concava,* and *Nesophila tiara* there is some lengthening present compared with related taxa.

The above discussion of variations in the male terminal genitalia can be summarized rather simply. The vas deferens normally enters the penis laterally through a simple pore, but in a few taxa more apical entry is obtained. In one lineage, the *Thaumatodon-Aaadonta* sequence, experimentation in development of a penial epiphallus has been accompanied by adoption of a valvular vas deferens entrance. In other groups accessory tissue on the penis apex may serve an epiphallic secretory function. The penis itself normally has two longitudinal pilasters that may be low and rounded, elevated and rounded, or very high and lamellate. The pilasters may be equal in size or sharply different, frequently depending on character displacement interactions with sympatric congeners. Major changes in *Ruatara* and two species of *Taipidon* apparently result from this phenomenon. The penial retractor muscle normally attaches to the diaphragm, but can shift to the columellar muscle just above the point where it is formed by union of the tail fan and buccal retractors. A few genera show a significantly elongated atrium, but most are short. The only additive structures to the terminal male genitalia are the pustulose zone found in the two Marquesan genera: the valvular entrance of the vas deferens seen in *Thaumatodon, Aaadonta,* and *Priceconcha*; and the added tissue on the penis apex in *Orangia, Planudonta,* many *Taipidon,* and some *Opanara.* The other variations are quite minor modifications on a unitary theme.

The Charopidae present a considerable contrast in having an epiphallus originating from the vas deferens, frequently a verge or vergic papilla, usually quite complex and extensive pilaster arrangements in the penis, often a very short penial retractor muscle that inserts in quite a different fashion, and radical changes in structure from group to group of the Pacific Island taxa. Even the isolated penis would be sufficient to indicate if a species belonged to the Endodontidae or Charopidae, and often what genus or group of genera.

TERMINAL FEMALE GENITALIA – This includes the post-uterine tubes, which are quite simple and uncomplicated in the Endodontidae. The normal pattern in land snails is for a thin-walled or muscular tube to lead from the glandular uterine section of the spermoviduct (if it shows a fused prostate-uterus) or uterus for a short-to-medium distance. This is the free oviduct (UV) and may be highly complex internally. It is joined by the shaft of the spermatheca (S). The combined tubes then extend forward to the atrium as the vagina (V). In the Charopidae, for example, the vagina may have almost as complicated a set of pilasters as is found in the penis of that group, the lower part of the spermathecal shaft may be enormously swollen because of high pilasters extending from the upper vagina, with the free oviduct opening reduced to a narrow pore. The upper portion of the free oviduct may have thick walls and be glandular in nature, while the spermathecal shaft narrows to a thin tube at the anterior end of the uterus, ascending along the latter to a typically ovate expanded head. There are numerous characters to use in systematic analysis, and in taxa from New Zealand and Australia it seems probable that the terminal female genitalia, as well as the male genitalia, are involved in species recognition.

The Endodontidae, in contrast, have extremely simple terminal female genitalia. A thin tube, without prominent internal features, extends from the lower section of the uterus to the atrium. It may be joined by the spermathecal shaft (which is a uniformly undifferentiated tube for its entire length) slightly to moderately above the atrium, thus technically forming a short vagina, or the spermatheca may insert on the penioviducal angle, effectively entering the atrium directly. In a few taxa, mainly the *Thaumatodon-Aaadonta* assemblage, the spermatheca actually inserts on the penis itself, slightly above the atrium. Regardless of where the spermatheca inserts, there are no indications of structural differentiation in the female tubes, nor even recognizable pilasters. They are extremely simple ducts.

The pattern of spermathecal insertion is primarily phyletic, with some convergences having occurred. Penial insertion of the spermatheca (fig. 48a) is characteristic of *Thaumatodon, Aaadonta,* and *Priceconcha.* The entrance is on the inside of the penioviducal angle, distinctly above the point where the penis separates from the atrium. There is no special internal structure evident. In *Rhysoconcha* (fig. 64g) the same pattern is seen. Atrial (fig. 48b) insertion of the spermatheca is normal in *Minidonta, Australdonta, Orangia, Libera, Taipidon, Planudonta,* all *Opanara* except two, and *Mautodontha aoraiensis.* Oviducal insertion (fig. 48c) occurs in *Nesodiscus, Nesophila, Cookeconcha, Endodonta, Ruatara, Opanara depasoapicata, O. bitridentata,* and *Mautodontha zimmermani.* The distance shift is not great and I question whether this makes any functional significance. Atrial and oviducal insertion occurs in

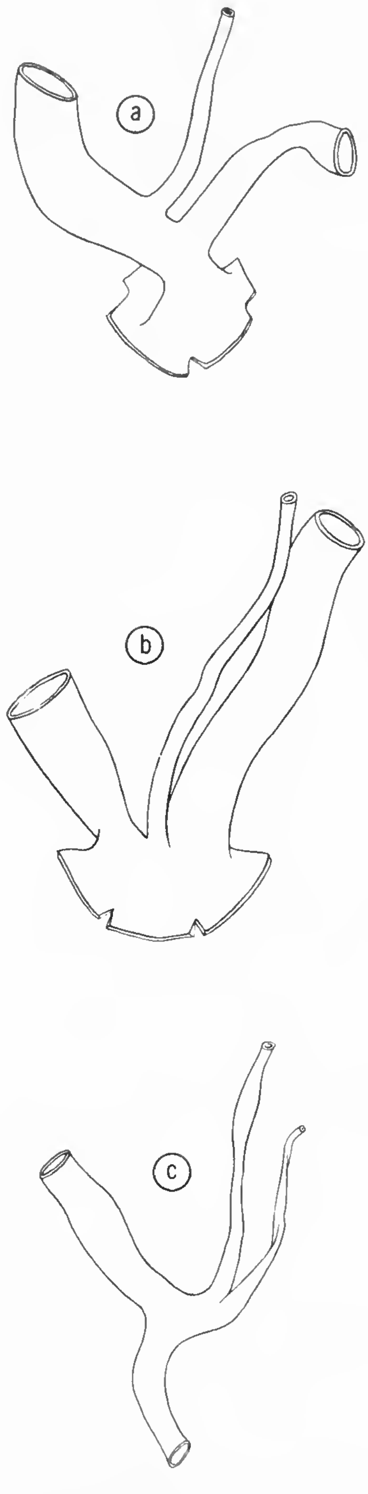

FIG. 48. Spermathecal insertion patterns: **a**, penial insertion (based on *Thaumatodon euaensis*); **b**, atrial insertion (based on *Libera cookeana*); **c**, oviducal insertion (based on *Endodonta fricki*). (CK)

both *Mautodontha* and *Opanara*, but otherwise there is phyletic correlation.

In all Endodontidae and Charopidae the spermathecal head extends past the pallial cavity apex. It is an elongately bulbous structure that lies next to the base of the albumen gland (fig. 49a) along the parietal wall and then next to the kidney base. It is sometimes lost during dissection of charopids because the artery passes over the spermathecal stalk to bind it into the apical viscera, but in all Endodontidae this appears to be free of this loop and thus dissects out easily. In order to show the relationships of this organ, *Endodonta fricki* was drawn with the organs pulled slightly apart. The perspective in this drawing (fig. 163d) might be interpreted as indicating that the spermathecal head lies below the pallial cavity apex, but this is an artifact. Many spermathecae seen in this study contained compact masses of sperm, but these were not enclosed in a membrane. There is no evidence of any spermatophore formation.

The above discussion of the genital system surveys patterns of variation and features observable after teasing apart the separate organs. It is useful to have one drawing in which the organs are portrayed as they are dissected out in early stages of study. Figure 49a attempts to show the just-excised genitalia. The material of *Taipidon petricola decora* was received for study long after the main systematic section had been completed. Hence it was decided to draw this showing the typical position of the organs when first dissected out, rather than as separated, to show all origins and insertions. This permits showing one apparently quite characteristic feature of the family. The shaft of the spermatheca (S) lies first on top of the free oviduct, then it sits directly on top of the vas deferens (VD) and prostatic duct for about the lower half of the prostate (DG). About the middle of the prostate, the spermathecal shaft shifts in position to lie on top of the prostatic acini and parallels the prostatic duct for the upper third. This is the typical position for the spermathecal shaft. The penis (P) has been shifted laterally in this view and is unusual primarily for the very low entrance of the vas deferens.

The above account concludes discussion of the structural and topographic variations seen in the genital anatomy of the Endodontidae. The differences from the Charopidae are substantial and obvious if even a fragmentary part of the genitalia is available. These are summarized in Tables LVIII, LIX following discussion of the other organ systems. Discussions of some size correlated variations in anatomical proportions are deferred, since several organ systems are involved.

Pallial complex

In the Endodontidae this area shows a simple and relatively uniform structural pattern, whose variations are mostly correlated with size, whorl count, and features of the palatal barriers. The typical configuration is shown in Figure 49c. A more detailed view is presented in Figure 195a. The most significant features for phylogeny are the weakly bilobed kidney (K) that reaches the hindgut (HG), the short reflexed ureter (KD) that opens in a ureteric pore (KX) just at the anterior tip of the rectal kidney arm, the simple pulmonary vein (HV), and the variable pattern of a mantle gland extension onto the pallial roof being present (fig. 171e) or absent (fig. 49c). The total absence of any secondary ureter or urinary groove leading from the ureteric pore (KX) to the pneumostome is a feature of major phyletic importance (p. 103).

The functional significance of this is that excretory products must exit onto the pallial roof surface. Water must then be used to flush out the waste products. In the typical sigmurethrans there is either a highly vascularized channel (many Bulimulidae and other holopodopid taxa) or a closed secondary ureter (Limacacea, Camaenacea, Helicacea) through which the excretory products pass. This divergence in the Sigmurethra was pointed out by H. B. Baker (1962a; 1963, p. 220). The secondary ureter seems to function primarily in water resorption. Elsewhere I (Solem, 1974) have postulated that the evolution of a secondary ureter was a necessary preadaptation to the evolution of land slugs from shelled ancestors. The exact level of classification required to recognize the third type of structure seen in the Endodontidae, a closed primary ureter, but no trace of any secondary groove or tube, cannot be considered here.

It is quite probable that the difference in median mean whorl count between the Endodontidae (5½+) and Charopidae (4⅛–) relates to the fact that the former lacks a ureter, and thus needs a greater pallial cavity area for holding a water reservoir (Blinn, 1964) than does the Charopidae in which there is a secondary ureter present. The only charopid known to me that may lack a secondary ureter is the Tasmanian species *Planilaoma luckmanii* (Brazier, 1877). The material available of this species was very limited and this observation (Solem, *unpublished*) needs to be confirmed by more dissections. To date, this is the only Indo-Pacific taxon seen that might be in any way transitional from the pallial cavity states of the Endodontidae to the Charopidae.

The normal pattern in the Charopidae is for an evenly bilobed kidney (secondarily altered with accentuation of either rectal or pericardial arms in different taxa); a complete secondary ureter opening lateral to the anus at the pneumostome; only very rarely (in Micronesian and Melanesian, but not New Zealand taxa) any mantle gland invasion of the pallial roof; the rectal kidney arm extensively overlapping the hindgut (often both dorsally and ventrally); and the heart much more deeply indenting the kidney. The difference of the secondary ureter in the Charopidae is the fundamental distinction. This means that even the smallest anterior fragment of the pallial cavity is sufficient to decide to which family the species belongs on the basis of ureter presence (Charopidae) or absence (Endodontidae) by the hindgut just inside the pneumostome.

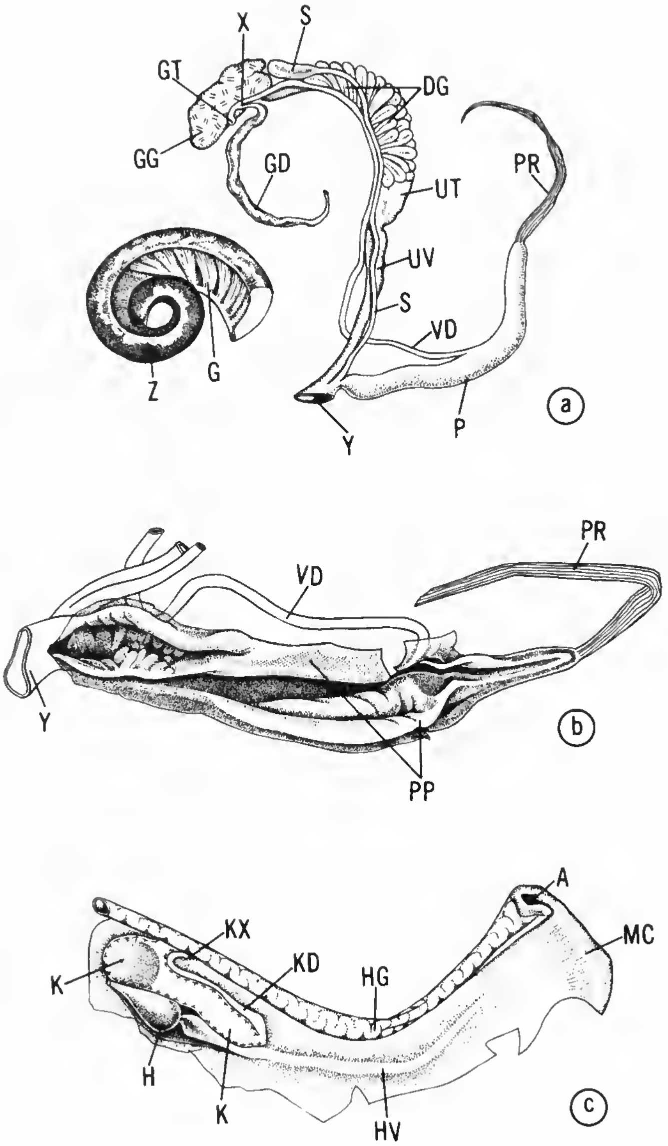

FIG. 49. Anatomy of *Taipidon petricola decora*. North side of Vaituha Valley, 600 ft. elevation, Eiao, Marquesas. BMNH: **a**, genitalia; **b**, interior of penis; **c**, pallial structures. Scales lines equal 1 mm. (CK). (See Appendix for explanation of abbreviations.)

Variation in the pallial region concerns the presence or absence of a glandular extension from the mantle collar onto the pallial roof, the relative length and prominence of the kidney arms, and the actual length of the cavity itself. The correlatives of these changes, which recur sporadically throughout the family, are not strong. The mantle collar extension involves shifting of some glandular materials from the collar itself posteriorly onto the pallial roof. The thickness and obvious nature of the extension varies rather widely, perhaps indicative of the stage in glandular activity. This area presumably is involved in the secretion and resorption of the palatal barriers. In swollen state this could be indicative of recent posterior barrier resorption, while in reduced state this could be indicative of recent deposition of calcareous material. Thus variation from individual to individual could be expected. Because specimens had been preserved mostly for long periods in alcohol of uncertain strength and acidity, retention of calcium residue in the glandular areas could not be depended on and no tests for calcium were made. The mantle collar extensions were obvious in *Australdonta degagei,* but not in *A. raivavaeana*; prominent in *Endodonta* (fig. 163e) and *Nesodiscus* (fig. 154b); prominent (fig. 171e) to absent (fig. 172e) in the illustrated *Libera* (but clearly present in other examples of *Libera fratercula*); present in most *Thaumatodon* and all *Aaadonta*; and also seen in *Taipidon semimarsupialis.* No traces of any pallial roof glands were seen in specimens of *Minidonta, Cookeconcha, Opanara, Rhysoconcha, Orangia,* the other *Taipidon, Planudonta,* or *Nesophila.* Many of those taxa with mantle roof gland extensions have long and/or deeply recessed barriers (10 taxa). The shift in mantle gland tissue under these conditions has obvious value in permitting barrier resorption and deposition activities with less complete animal retraction. *Taipidon semimarsupialis* and *Thaumatodon euaensis,* in contrast, have short (one-eighth whorl) barriers at the lip edge, the two *Australdonta* and *Endodonta lamellosa* have equally short, slightly recessed barriers, while the other two *Endodonta* have moderately recessed, short barriers. Taxa with such long barriers as *Priceconcha* (Solem, 1973d, p. 23) show no trace of mantle gland extension. While 10 taxa with mantle gland extensions have extra long and/or deeply recessed barriers, six do not, and some taxa with deeply recessed or very long barriers lack any trace of such an extension.

The variation in kidney width was not quantified, but obviously varies, as can be seen by comparing the very narrow, folded kidney of *Libera b. bursatella* (fig. 171d) with the far broader kidney of *Aaadonta c. constricta* (fig. 199a) and the average kidney shape of *Thaumatodon euaensis* (fig. 195a) or *Taipidon petricola decora* (fig. 49c). The broadened kidney in *Aaadonta* probably correlates with the comparatively great palatal wall distance from the parietal-palatal margin to the high second palatal barrier (fig. 203b), while in *T. euaensis* (fig. 194b) and *T. petricola decora* (fig. 140c) this same zone is distinctly narrower. Barriers would not be a factor in *Libera b. bursatella,* but the extreme deflection of the last few whorls (fig. 174a) has shortened the upper palatal wall (that portion above the weak peripheral keel) quite drastically. The extreme narrowing of the kidney in this species can be a byproduct of this space change.

Relative length of the kidney lobes was scored as the rectal lobe (that next to the hindgut) being distinctly less than half the length of the pericardial lobe (that next to the heart), or essentially half the length. Often the difference is quite striking, as in *Aaadonta constricta* and *A. fuscozonata* (figs. 199a, f), even though both of these are scored as having the "short" rectal lobe. The longer type rectal lobe is found in a variety of taxa, such as *Nesodiscus* (fig. 154b) and various *Libera* (figs. 171d; 172e) with elongated pallial cavities and high whorl counts, but also in *Opanara, Ruatara,* and some *Cookeconcha* with typical or possibly slightly reduced whorl counts. The relative position of the lobes can be altered by retraction of the body resulting in pushing the hindgut rectal lobe further apically than the pericardial lobe, thus distorting the apparent length relationship. No intrinsic significance can be attached to this variation.

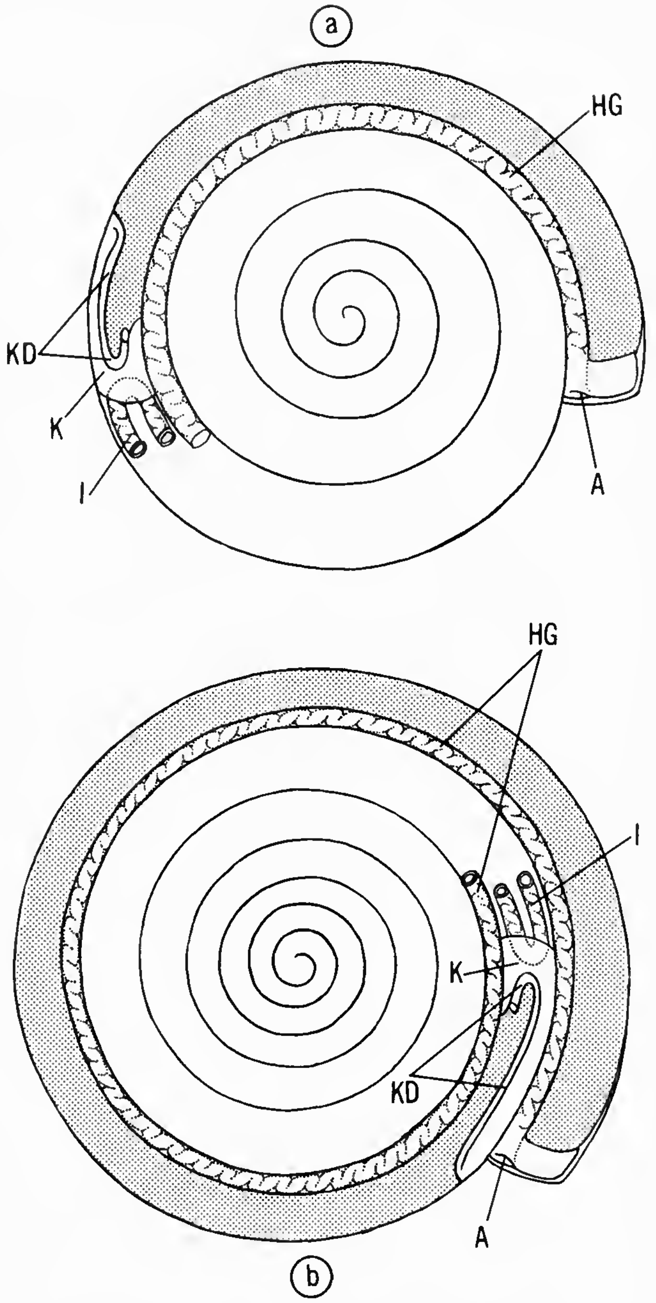

FIG. 50. Pallial cavity length variation, based on the typical (**a**) and an elongated (**b**) condition. (See Appendix for explanation of abbreviations.)

The major variation in appearance and size is change in length of the pallial cavity. This could be measured in 35 taxa and usually is expressed to the nearest one-eighth whorl. Flattened length measurements are subject to greater inaccuracy and give a less functionally correlated indication of length. The most frequent states were between five-eighths and three-fourths of a whorl, found in a total of 19 taxa (fig. 50a). Variation within a population was tested on a sample of *Libera f. fratercula* from Motutapu Island off Rarotonga (FMNH 152742). Whorl counts of the shells ranged from 6¼ to 7, with pallial cavity length varying from five-eighths to slightly less than a full whorl. Part of the variation was an artifact of contraction. Specimens deeply retracted into the shell had a cavity length at or near the high range of the variation. By pulling back up to a quarter whorl from the aperture, the linear length needed to occupy a full whorl was reduced. This makes the increased length an artifact of spiral distance rather than a change in actual measurement. This artifact in the data prevented meaningful statistical treatment. The median pallial cavity length in the *Libera* sample was three-fourths whorl.

Allowing for this variability, the significant departures from the average pallial cavity length in adult specimens were comparatively few. *Planudonta concava* had a three-eighths whorl-long cavity, despite the shell reaching a 6⅝ whorl count, which is significantly over the family median of 5½+. Presumably this involved no proportionate change in pallial cavity length, despite the raised whorl count. A number of species had one-half whorl pallial cavities – *Minidonta hendersoni, Mautodontha zimmermani, Cookeconcha jugosus, Opanara areaensis densa, Thaumatodon spirrhymatum, T. hystricelloides,* and *Aaadonta constricta.* These agree in that the dissected specimens have 5 to 5⅝ whorls, with a mean of 5¼+. This compares with a mean of 5⅝+ for those species with average pallial cavity lengths. Elongation of the pallial cavity (fig. 50b) is to essentially one whorl in *Taipidon semimarsupialis, Nesodiscus fictus,* and *Endodonta fricki*; 1⅛ whorls in *Aaadonta f. fuscozonata*; and between 1¼ and 1½ whorls in *Libera micrasoma* and *L. b. bursatella.* These are either brood-chamber taxa or the species with the highest whorl counts in their genus, averaging one-fourth (*Aaadonta*) to seven-eighths (*Nesodiscus*) whorl more than any other species in their genera. It is reasonable to look upon these species as showing proportionate elongation of the pallial cavity as the whorl count increased. The dissected specimens of these taxa had a mean whorl count of 6⅞ –, substantially above the other groups. The general elongation of the cavity correlates with the extremely shortened rectal lobes seen in *Aaadonta fuscozonata* (fig. 199f), *Taipidon semimarsupialis* (fig. 139c), and *Endodonta fricki* (fig. 163e). It is not the only correlative, since in *Nesophila tiara* (fig. 165c) the rectal lobe is virtually absent, possibly as a result of the dramatic overall size increment to over 11 mm. shell diameter in this species. The much larger whorl cross-section would provide adequate kidney volume space along the upper palatal wall without the thickness of the lobes seen in *Libera* (fig. 171d).

Basically the variations in kidney size, shape, and pallial cavity length should be looked on as representing space compromises. Presumably there is an effective kidney-volume/body-volume ratio that has to be maintained. The changes in shell growth that alter the palatal wall barrier configurations result in adjustment as to the kidney shape and lobe lengths. The available material did not lend itself to comparing foot length, shell whorl count, and pallial cavity length to see if the increase of length in the pallial cavity might be required to provide extra space for foot withdrawal. There is no question but that most of the length increase comes through extension of the relative area occupied by the respiratory surface between the anterior tip of the kidney and the pneumostome (see, for example, fig. 199a, f comparing one-half whorl and 1⅛ whorl pallial roofs, respectively).

Other features in the pallial complex show no significant variations in those taxa dissected. The heart (H) generally is slightly more than half the length of the kidney (K) and lies almost exactly parallel to the hindgut (HG). The hindgut extends only slightly apicad of the kidney base before departing from the parietal-palatal margin (fig. 163d). It then shifts onto the palatal wall and continues apically past the stomach expansion. In most dissected specimens there are at least traces of the mantle retractor muscle (fig. 199a, MD) present, but this feature has been omitted from most drawings.

In summary, the pallial complex in the Endodontidae is quite uniform in structure and differs significantly from that of the Charopidae in its lack of any secondary ureter. Changes in pallial cavity length correlate partly with whorl count alterations. Changes in the kidney shape and proportions correlate with changes in the upper palatal wall proportions. While the pallial complex has high information content as to family affinity, it yields little information on relationships within the family.

Digestive system

Descriptions and figures (figs. 163, 164) of *Endodonta fricki* serve to illustrate the basic structures of the digestive tract and associated glands. The buccal mass (fig. 164e, B) is uniform in shape throughout the family and has a very small generative sac visible posteriorly. Often the buccal ganglion (BGN) remains attached after dissecting out the buccal mass and muscles. The two salivary glands (OG) touch above the esophagus (BE) but are not united. Their ducts (OGD) enter the top of the buccal mass on either side of the esophagus. The buccal retractor muscles (BR) insert in a U-shaped fan on the buccal mass base. The esophagus is another "space saving" organ, since it passes from the buccal mass to past the pallial cavity apex, preserving the space function of the pallial cavity for retraction of the head and foot. Expansion of the digestive tube into a stomach (fig. 164f, IZ) starts perhaps one-eighth whorl above the pallial cavity apex and is completed one-eighth whorl later. The stomach extends from one-half to more than one whorl apically, then reflects into the narrow intestine (I) that passes forward into the typical complicated looping pattern between stomach and pallial cavity apex that is characteristic of pulmonates. One loop of the intestine

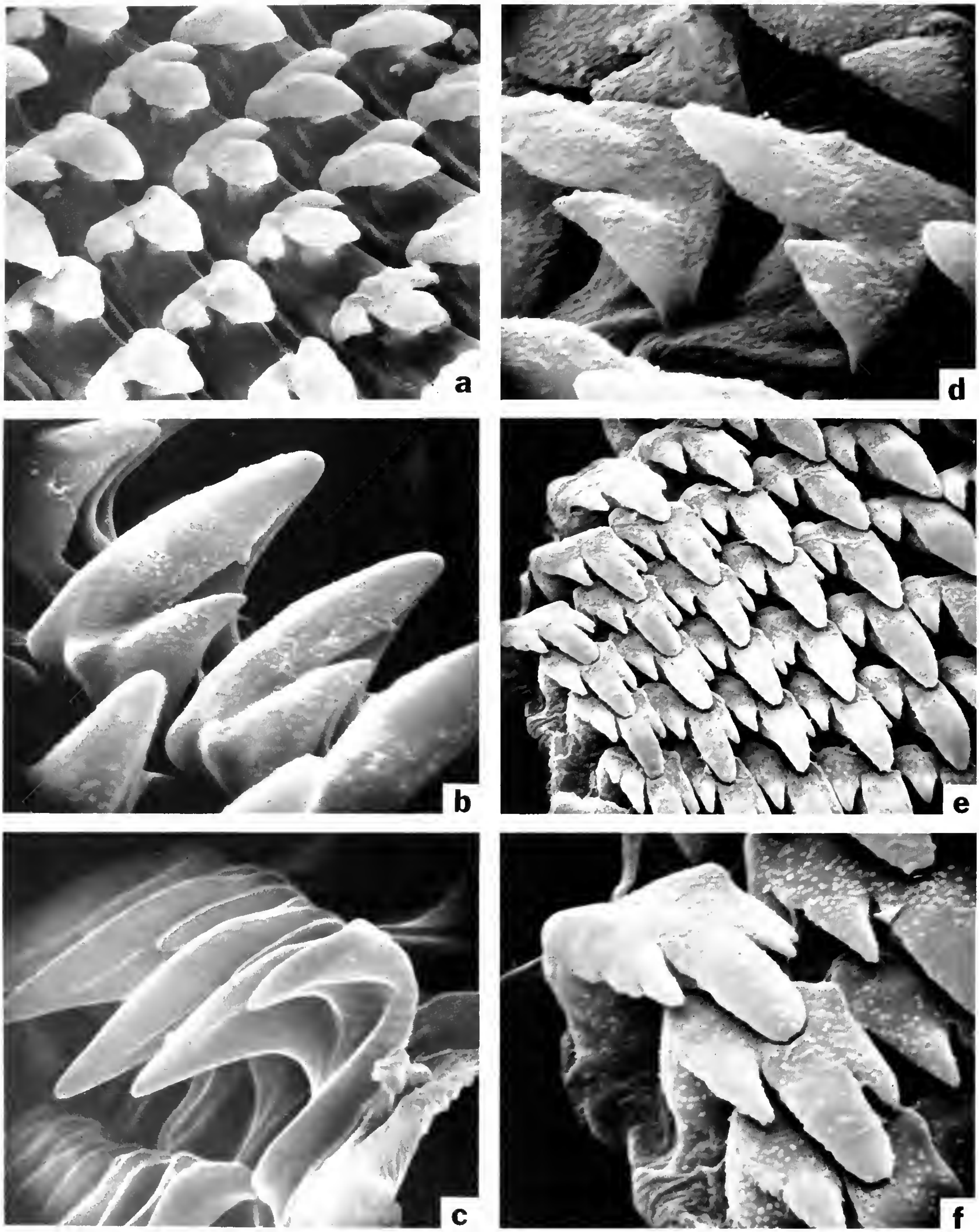

FIG. 51. Radular teeth of *Libera fratercula rarotongensis*. Station R15, east of Avarua, Rarotonga, Cook Islands. FMNH 152744: **a**, central and early laterals viewed from low posterior angle at 1,850×; **b**, anterior view of early laterals at 4,225×; **c**, inside view of right laterals at 5,150×; **d**, outside view of right laterals at 5,375× showing interrow support; **e**, lateromarginal transition viewed from left posterior at 2,150×; **f**, detail of marginal teeth at 5,325×.

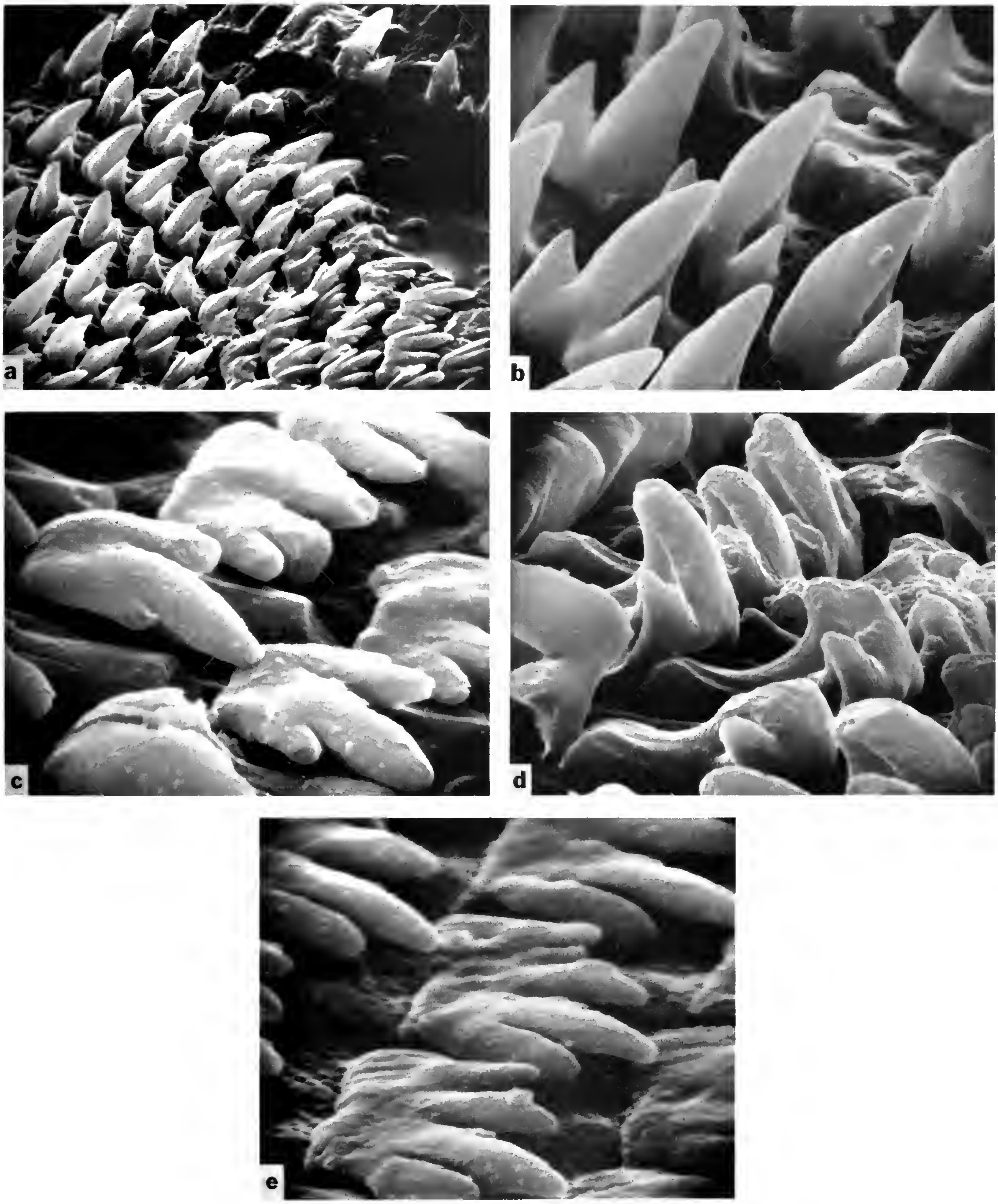

FIG. 52. Radular teeth of *Taipidon petricola decora*. North side of Vaituha Valley, 600 ft. elevation, Eiao, Marquesas. BMNH: **a**, partial row of teeth viewed from anterior front at 1,275×; **b**, central and first lateral teeth viewed from anterior side at 3,075×; **c**, worn mid-marginal teeth from right side of radula at 5,350×; **d**, worn lateral teeth from right side of radula at 3,435×; **e**, late marginal teeth at 5,215×.

projects forward under the kidney base, indenting rather deeply the inner surface of the kidney. The position of the hindgut has been described previously.

Variations in esophagus length correlate exactly with pallial cavity length. Variations in stomach length are a factor of how many whorls of the shell are actually occupied by the soft parts as adults (pp. 94-95), plus changes in the cross-sectional areas of the whorls. With elongation of the soft parts and narrowing of the whorls, the stomach will be longer. Shortening of the soft parts and increase in the cross-sectional whorl area will shorten the stomach. Extreme contraction of the animal when the stomach is empty will give the illusion of a shorter stomach, since the severely compacted soft parts will collapse the early section of the stomach to permit maximum withdrawal.

Only in the radula and jaw are there significant changes in size and structure. Almost all of this work was done prior to the late 1960's general availability of the scanning electron microscope. Hence the data presented here is far less satisfactory than could be accomplished with the same material today. Because the radula is extremely tiny and the individual teeth are in the 6-16 μ size range, optical observation was quite difficult. It was not possible to observe outer marginal teeth in the vast majority of species due to mounting problems. More than in any other group of snails that I've studied, the marginal teeth of the radula fold under or fragment off during handling. With the size of the central tooth ranging from 4 × 6μ in *Taipidon centadentata* to 13 × 16 μ in *Ruatara oparica reductidenta,* observations on other than the point of transition to marginal teeth (indicated by endoconal appearance and tooth-size reduction) and basic cusp patterns were not possible. Recently I have been able to study the radular teeth of *Thaumatodon spirrhymatum* and *Priceconcha tuvuthaensis* (Solem, 1973d), *Libera fratercula rarotongensis* (fig. 51), *Taipidon petricola decora* (fig. 52), *Endodonta fricki* (fig. 53), and *Thaumatodon hystricelloides* (fig. 54) using the scanning electron microscope. This has added considerable information.

The basic pattern is that of a tricuspid central tooth (figs. 51a; 52b) with the two ectocones quite small compared with the mesocone, and the mesocone itself often slightly shorter than the mesocone on the flanking first lateral teeth. On either side are generally five to six bicuspid laterals (figs. 51b, c) in which the ectocone is slightly less than half to only one-third the mesoconal length. There is no trace of an endocone, except in teratological rows (fig. 54b). The transition to marginal teeth generally occurs over a three-tooth spread, involving size reduction of the tooth, shortening of the basal plate, appearance of an endocone, partial reduction in size of the mesocone, and increase in relative ectoconal prominence. The marginal teeth, which usually were lost in preparation, tend to more or less multicusped ectocone, smaller size, widened form, and shortened length. Since the transition from lateral to marginal teeth occurs over several teeth, observers may count them differently. Cooke (1928) reported four laterals in *Endodonta lamellosa,* five in *E. marsupialis,* and seven or nine in *E. fricki,* with, respectively, 16-19, 17-20, and 12-14 marginals. These differ from my observations slightly. In the few cases

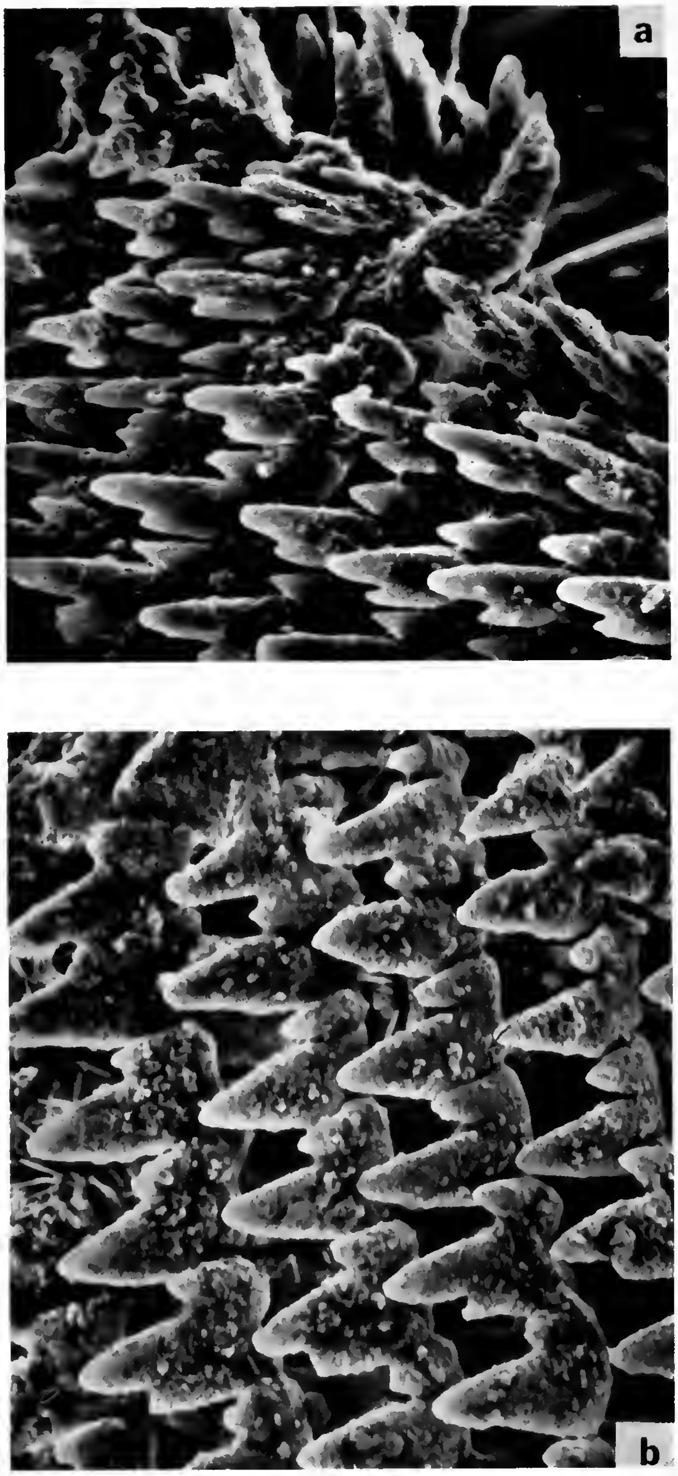

FIG. 53. Radular teeth of *Endodonta fricki* (Pfeiffer). Makalea, Waianae Mts., Oahu, Hawaii. FMNH 53042: **a**, early marginal teeth at 1,090×; **b**, lateral teeth from left side of radula at 1,200× (note deformed row with endocone at lower area). Extracted from a dried specimen and incompletely cleaned.

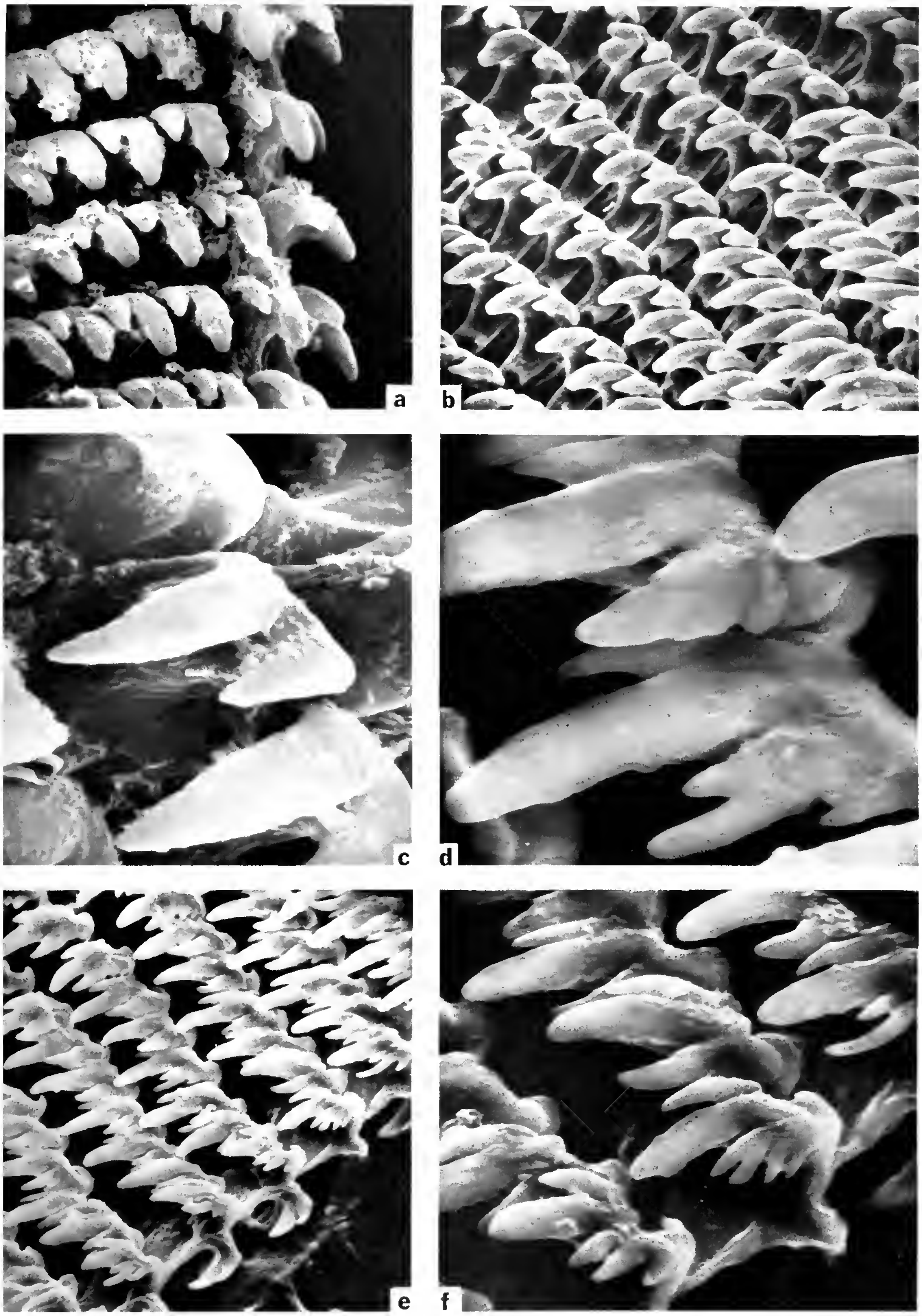

FIG. 54. Radular teeth of *Thaumatodon hystricelloides* (Mousson). Station 19, Lake Lanuto'o, Upolu, Western Samoa. FMNH 153130: **a**, worn laterals from left side of radula at 1,795×; **b**, lateromarginal transition zone from right side of radula showing a deformed longitudinal row (upper left) at 1,265×; **c**, early unworn laterals from right posterior at 5,975×; **d**, early marginals from same area of radula at 6,325×; **e**, late marginals from right side of radula at 1,240×; **f**, late marginals in detail at 3,175×. Figures *b, d, e, f* courtesy of Engis Equipment Company demonstration of a Cambridge scanning electron microscope.

where complete or nearly complete marginal fields were mounted successfully, there were 9-13 marginals, the number increasing to as many as 20 in *Endodonta marsupialis,* for example. The number of laterals increased to seven to eight in the three *Thaumatodon, Nesophila tiara, Planudonta subplanula, Taipidon fragila,* and *T. varidentata. Cookeconcha hystricellus, C. hystrix,* and *Planudonta concava* had 9-10 laterals; *Cookeconcha jugosus* and *Taipidon semimarsupialis* had 11-14 laterals; and in *Taipidon centadentata* there were 22-23 laterals. The increase in laterals in *T. semimarsupialis* was accompanied by an increase in marginals to 16-17 and a decrease in size of the teeth, as measured by the central tooth, to only 4 × 6 μ, compared with the 8 × 10 μ in most other *Taipidon.* This change in number of lateral teeth is not size correlated, but is phyletically limited to *Cookeconcha* and the *Taipidon-Planudonta* sequence.

The number of tooth rows ranged from 80 to 115 in the few species for which this could be tallied. The total number of radular teeth varied from perhaps a low of 2,700 in many *Opanara* to a maximum of 8,100 in *T. semimarsupialis.* Most of the species have about 3,000-4,000 in denticles. This is far below the typical pattern seen in zonitoid taxa such as the Pacific Island Microcystinae, Helicarioninae, Euconulinae, and Trochomorphidae, where only 8 of 169 taxa for which data are available in H. B. Baker (1938b, 1940, 1941) had radular tooth counts of under 6,000. Mean tooth counts for these family level taxa were, respectively, 14,900, 28,500, 13,450, and 11,750 teeth per radula. In the New Zealand typical Charopidae, using data from Suter (1913), total tooth numbers average only 3,175, while the modified "flammulinids" average 5,676, although ranging from 2,300 to 9,380 teeth. The possible significance of this is discussed below (pp. 104-105).

The approximate size of the central tooth was measured for each species using an optical micrometer and a Leitz Ortholux microscope with phase-contrast illumination. In *Cookeconcha* and *Orangia,* for example, the teeth were narrow and elongated, measuring, respectively, 6-8 × 14 μ and 6-8 × 10-13 μ. The largest teeth were seen in *Endodonta* (13 μ square) and *Ruatara* (13 × 14-16 μ). The smallest were in *Opanara fosbergi* (5 × 8 μ) and *Taipidon centadentata* (4 × 6 μ). None of these variations show obvious shell-size correlation. Phyletic lineages are not involved as *Cookeconcha* has elongate denticles and those of its descendent genus *Endodonta* are virtually square. On Rapa, *Orangia* has elongated denticles; those of *Ruatara* are very large and squarish; and *Opanara* has variable-sized denticles.

Optical study of the Rapan species suggested yet another pattern of variation. In *Opanara, Ruatara,* and *Orangia,* by the fourth lateral there is a marked inward curve of the mesocone. By the eighth or ninth tooth from the center, there is a distinct endocone and the mesocone is like that of the typical species. Previously it was much larger. After the sixth or seventh tooth, the size decreases rapidly to typical multicuspid marginals. In *Rhysoconcha,* the marginals appear to be the same size as in the other taxa, but the central (6 × 8 μ) and laterals appear noticeably smaller than in most other Rapan species. Unfortunately, their size was so small and the mounts so poor that I am uncertain as to the exact cusp structure in comparison with the larger species. The decrease in size for mid-radular teeth in *Rhysoconcha,* elongation in *Orangia,* variability in *Opanara,* and large square shape in *Ruatara* possibly indicate specialization in feeding or substrate factors. The above material had been mounted for optical study and returned before I had access to a scanning electron microscope. It was not practical to reopen this phase of the study.

Scanning electron microscope observations have been made on six species of Endodontidae (Solem, 1973d; this paper), plus 39 species of Charopidae and Punctidae from Australia, New Zealand, New Caledonia, and Lord Howe Island. Data about the Endodontidae are summarized first.

As is typical of pulmonate radulae, the central and lateral teeth show an interlocking device between longitudinal teeth rows. The stressed cusp will receive support from the basal plate in the next anterior row. The existence of this inter-row support mechanism was first reported in a variety of taxa (Solem, 1972a) and the pattern of change in the Charopidae reviewed subsequently (Solem, 1973a, pp. 166-167). The basal plate of the central tooth in the Endodontidae, as exemplified by *Libera fratercula,* has a raised lateral ridge on each side of the basal plate (fig. 51a). In the early laterals (figs. 51c, d) the flared lateral ridge is restricted to the ectoconal (outer) side of the tooth and functions to prevent lateral shifting of the teeth under stress. The endoconal (inner) side (fig. 51a, upper right) of the laterals has virtually no trace of the support ridge. Exactly the same pattern is seen in *Taipidon* (fig. 52d), *Thaumatodon* (fig. 54b; Solem, 1973d, figs. 6, 7), and *Priceconcha* (Solem, 1973d, figs. 13, 14).

The marginal teeth are characterized by basal plates that are greatly reduced in length (but not width), development of a medium to prominent endocone, reduced mesocone, and often split ectocone. The transitional area from laterals to marginals (figs. 51e; 52a; 54b; Solem, 1973d, fig. 8) is short. Apparently there are significant differences in the pattern of marginal tooth structure, but because of their small size and the nature of these differences, only the few species studied with the SEM can be discussed. In *Taipidon* (figs. 52c, e) the cusp sits very low on the basal plate, all cusps become narrow and elongated, while the ectocone tends to become bicuspid. In *Libera* (figs. 51e, f) the early marginal teeth sit much higher on the basal plate, the ectocone tends more to fragment, and the mesocone is not nearly so narrow.

Thaumatodon hystricelloides (figs. 54d, e, f) has a very long and dagger-shaped mesocone, a slender and much shorter endocone, and initially a simple ectocone that becomes highly fragmented on outer teeth (f). The cusps of this species are elevated very high above the extremely short basal plate. Only the first few marginals were seen in *T. spirrhymatum* (Solem, 1973d, fig. 15), but these agree with the other *Thaumatodon.* In *Priceconcha tuvuthaensis* (Solem, 1973d, figs. 8, 9) there is quite a different pattern of ectoconal splitting on the marginals. Instead of roughly coequal splitting of the ectocone, lateral knob-like buds appear. The differences lie in the elevation of the cusps above the basal plate, the method of splitting for the ectocone, and the pattern of cusps on the marginals. While these can be studied with the SEM in angled view, they are below the level of optical examination.

In summary, the Endodontidae have a relatively uniform pattern of tricuspid central, bicuspid laterals that number five to eight, only rarely increasing in number, and somewhat more numerous tricuspid to multicuspid marginal teeth. Tooth size and shape varies within lineages, with changes in tooth numbers basically occurring only in *Cookeconcha* and the Marquesan *Taipidon-Planudonta* lineage. The latter group shows the greatest amount of radular change, with *Planudonta concava, Taipidon semimarsupialis,* and *T. centadentata* showing progressively increased tooth number, but progressively decreased tooth size (table LV). The changes are not size correlated, since the teeth of *Nesophila tiara,* whose mean shell diameter of 11.29 mm. is vastly larger than the shell of *Cookeconcha jugosus* (5.01 mm.) or *C. hystricellus* (4.98 mm.), show no increase either in size or actual numbers.

The typical radula found in the Charopidae presents a number of obvious differences. In the vast majority of species there is a tricuspid central tooth that is markedly smaller than the flanking laterals, which normally are tricuspid with equal-sized endocone and ectocone. Generally, all laterals have a narrow mesocone and large side cusps, but a few taxa show significant modifications (based on unpublished SEM observations). The New Zealand *Allodiscus dimorphus* (Pfeiffer, 1853) has bicuspid laterals, but typically multicuspid marginals; the New Zealand *Thalassohelix propinqua* (Hutton, 1883) has bicuspid laterals and unicuspid marginals; the New Zealand *Serpho kiwi* (Gray, 1843) has a unicuspid central, bicuspid laterals, and early marginals that approach the helicarionid marginal structure; while on Lord Howe Island the succineiform *Mystivagor mastersi* (Brazier, 1876) (Solem, 1973a, fig. 6) has a peculiar anterior supporting flare developed and *Pseudocharopa lidgbirdi* (Etheridge, 1889) has unicuspid marginals. Apparently all of these modified taxa are partly-to-completely arboreal in habitat, which probably explains the selective pressure behind the modifications. The marginals in the Chaopidae vary widely in shape and form, much more than in the Endodontidae.

Consideration of this variation is deferred. Standing in extreme contrast to both radular types are the denticles in the Punctidae. They have a unique pattern of very tiny lateromarginal undifferentiated teeth in which there is a narrow, bicuspid tooth with slender basal plate and evenly curved anterior that rises to the cusps, which point essentially directly forward and have extremely tiny accessory cusps on each side of the tooth and then between the two main cusps. This peculiar pattern was detected by H. B. Baker many years ago (Pilsbry, 1948, p. 642, fig. 349,

TABLE LV. - RADULAR TOOTH SIZE AND NUMBERS IN NESOPHILA, COOKECONCHA, TAIPIDON, AND PLANUDONTA

Species	Tooth numbers Laterals	 Marginals	Central tooth size in microns
Cookeconcha			
hystricellus	9-10	10-11	8 X 13-14
jugosus	14	8+++	6 X 14
Nesophila			
tiara	8	8+++	9-10 X 14
Taipidon			
p. petricola	6	?	7-8 X 8
varidentata	7	13	8 X 10
fragila	7-8	9-10	8 X 10-11
semimarsupialis	13-15	10-13	6-8 X 8
centadentata	22-23	16-17	4 X 6
Planudonta			
subplanula	8	10	6 X 8-10
concava	10-11	7+++	8 X 10

d), but is much more easily interpreted with scanning electron microscope observations.

In typically unmodified endodontoid taxa, inspection of the radular lateral teeth is quite sufficient to establish family affinities. They are bicuspid in the Endodontidae, bicuspid but very differently curved and with accessory microcusps in the Punctidae, and tricuspid in the Charopidae. This presents one of the clearest diagnostic features in terrestrial species, but is subject to at least partial convergence in the arboreal Charopidae.

TABLE LVI. - SHELL SIZE AND JAW STRUCTURE IN THE ENDODONTIDAE

State	Number of taxa	Shell diameter in mm.
Separated square plates	1	2.93
Separated elongated plates	16	3.74±0.19 (2.54-5.79)
Central plates partly fused	9	5.75±0.50 (4.23-8.99)
All plates fused	1	11.29

Jaw structure in the Endodontidae varies with size (table LVI). Typically (fig. 125g), the jaw consists of many separate, elongated chitinous plates. This is the pattern found in *Opanara, Australdonta, Thaumatodon,* most *Aaadonta, Planudonta concava, Taipidon varidentata,* and *T. fragila.* One species, *Aaadonta fuscozonata,* has the plates nearly square in shape. In a number of species, all *Cookeconcha, Endodonta, Nesodiscus, Planudonta subplanula, Taipidon centadentata,* and *T. semimarsupialis,* the central plates of the jaw are at least partly fused, although the plates on either side are clearly separated from each other and retain the typical elongated shape. Finally, in *Nesophila tiara* the jaw plates are completely fused together. The correlation of increasing jaw plate fusion with increasing size is obvious (table LVI). In the Charopidae there is a basically similar pattern of separated and elongated plates, with partial fusion occurring first in the center of the jaw, while in the Punctidae only the pattern of small, clearly separated plates has been observed. Presumably, this correlates with the small size of most punctids.

Variations in the jaw structure, stomach length, esophageal length, and possibly the number of marginal teeth correlate with size and whorl count factors. Radular cusp size and shape variations cannot be studied effectively by optical viewing, but only a few taxa could be examined with the scanning electron microscope.

Free muscle system

In all the dissected species, the right ommatophoral retractor passed through the penioviducal angle, while the right rhinophoral retractor passed outside the angle. Fusion of the tentacular retractors, buccal retractors and tail fan to form the columellar retractor occurs at slightly different relative positions, correlating mainly with the length of the pallial cavity. The pattern of free muscle fusions detailed for *Endodonta fricki* and *Nesophila tiara* are typical. For most taxa, only obvious differences from this pattern have been annotated in the text. The origin of the columellar retractor muscle has been discussed above.

Nervous system

In both *Thaumatodon hystricelloides* and *Libera fratercula fratercula* the penis is enervated from the right cerebral ganglion. The ganglia in the dissected Endodontidae are proportionately much smaller than those in such families as the Tornatellinidae and are much more heavily encased in sheets of connective tissue. Because of the limited material and reduced prominence of the structures, no attempt was made to study details of the nervous system.

External body features

Throughout the Endodontidae, the body color is a pale yellow white, with the eye spots and early portion of the ommatophoral retractors providing the only touch of darker color. This contrasts immediately with those Charopidae living in arboreal or semi-arboreal habitats. The tentacles, head, neck, and often the tail of these species have scattered to heavy greyish pigmentation, although the ground strata species have the same yellow-white body color seen in the Endodontidae.

The foot in the Endodontidae is universally long and slender, bluntly rounded posteriorly and truncated anteriorly, without longitudinal or transverse grooving. There is a prominent pedal and noticeably weaker suprapedal groove (FS) on the sides of the foot that unite above the tail, but there is no development of a caudal foss or caudal horn (fig. 163a). The slime network is weakly defined. Without exception the gonopore is a short vertical slit located below the right ommatophore and both above and slightly behind the right rhinophore. The mantle collar (fig. 163b) is without developed lobes or exterior protrusions, although several species show an extension of glandular materials onto the pallial cavity roof (pp. 84-85).

In the Pacific Island Charopidae the above descriptions apply, but in the extralimital taxa there are major variations. Several New Caledonian taxa, for example, develop a "pseudo-operculum" on the tail (Solem, *unpublished*), and in many arboreal and semi-arboreal taxa from New Zealand there is a weak to very prominent caudal horn developed (see Climo, 1969a for references and pp. 105-106 of this monograph for a review of the controversy concerning the systematic value of this feature).

Patterns of elongation

As outlined below (pp. 113-114), one of the repetitive trends within the Endodontidae is for whorl count and size increase to the "*Nesodiscus*" and "brood chamber" levels of specialization. While this involves some elongation of the soft parts, a much more typical pattern is for the animal to withdraw in part from the upper whorl of the shells. In groups such as the land prosobranch family Pomatiasidae, the pulmonate Urocoptidae, and such subulinids as *Rumina decollata* (Linné), the early whorls will be evacuated by the animal which seals off the upper whorls by a thick calcareous plug. The early whorls usually break off. This reduces shell length highly effectively with cylindrical coiling patterns, but is not an option open to planulate or heliciform taxa. Where these species show a great increase in whorl count over "typical" taxa, such as in the trochomorphid *Coxia m. macgregori* (Cox, 1870), almost half of the 10¾ whorls of the shell are above the apex of the soft parts (fig. 55a). In *Libera fratercula* (fig. 55b), a seven-whorled shell may have only the lower 3¼ whorls occupied by the animal. As outlined elsewhere (Solem, 1969b), the upper whorls are filled with calcium carbonate by the snail and thus provide a source of shell calcium for the young that hatch in the brood chamber, then eat their way out through the shell apex. So far as is known, this is the only species in the Endodontidae to fill in the apical whorls with calcium, but in most of the species a part to all of at least the nuclear whorls are not occupied by the adult animal. Because only a few species were available with shell and soft parts still together, I can present no statistical data concerning the variations in withdrawal from the upper whorls.

Coxia macgregori was chosen for comparison because it shows the greatest whorl count of any aulacopod land snail species available to me with soft parts. A member of the limacacean family Trochomorphidae, it obviously differs in having a typically sigmurethrous ureter (KD) and in numerous genital and radular features, but it is comparable in terms of elongation patterns. The pallial cavity is about 1⅜ whorls long, the stomach occupies seven-eighths whorl after a space for the albumen gland and intestinal loops, the ovotestis (G) is strung along almost five-eights whorl, and the digestive gland extends 2¾ whorls above the ovotestis apex. The upper 5⅛ whorls of the shell are "empty space." In *Libera* the pallial cavity extends about seven-eighths whorl, followed by a short gap for the albumen gland and intestinal loops, with the stomach occupying a full one-half whorl, the ovotestis a little less than one-half whorl, and the digestive tissue extending nearly 1¼ more whorls. A total of slightly over 3¼ whorls in the seven-whorl shell is "adult occupied" in *Libera,* compared with the 5¾ of 10⅞ whorls in *Coxia.* The details of organ lengths are different, but the general pattern of withdrawal from apical whorls is equivalent.

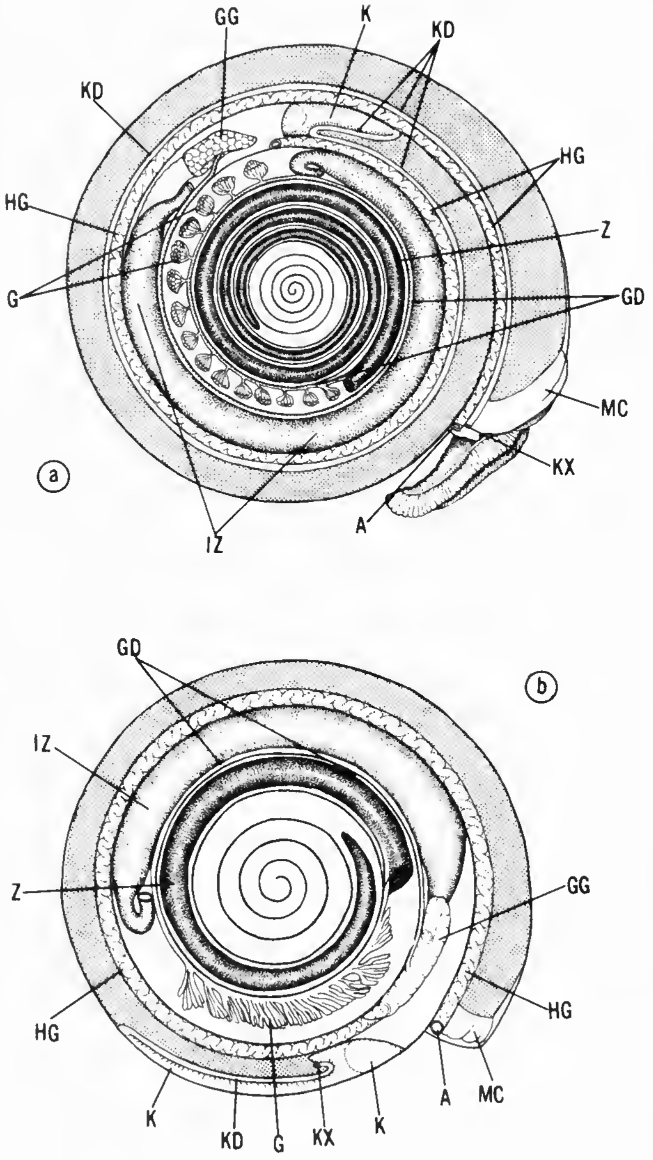

FIG. 55. Animal length and shell whorl count in elongated taxa: **a**, *Coxia;* **b**, *Libera f. fratercula.* Identified structures are: A - anus; G - ovotestis; GD - hermaphroditic duct; GG - albumen gland; HG - hindgut; IZ - stomach; K - kidney; KD - ureter; KX - ureteric pore; MC - mantle collar; Z - digestive gland.

This is one way of partly coping with increased visceral hump length. Yet another way is through differential elongation of organs. The counterpart of visceral hump elongation in many whorled shells is visceral hump shortening in "semi-slugs," where organs must be compacted, rather than elongated. In both situations the change seems to occur in morphological zones that encompass all the organ systems that pass through the zone. If the pallial cavity is elongated, for example, the pallial gonoducts will lengthen, whereas if the head and neck are elongated (or compacted) it is the terminal genitalia whose proportions will be shifted.

The most frequent example of this alteration in the genitalia of the Endodontidae, and the easiest to quantify, is the change in relative lengths of the free oviduct and prostate. For 43 taxa it was possible to score this feature, with 10 taxa (three *Cookeconcha,* two *Orangia, Nesophila tiara, Taipidon centadentata, T. varidentata, Thaumatodon hystricelloides,* and *T. euaensis*) having the free oviduct distinctly shorter than the prostate, 14 taxa (two *Ruatara, Opanara altiapica,* three *Taipidon,* two *Planudonta, Libera cookeana,* four *Aaadonta,* and *Thaumatodon spirrhymatum*) having them about the same length,

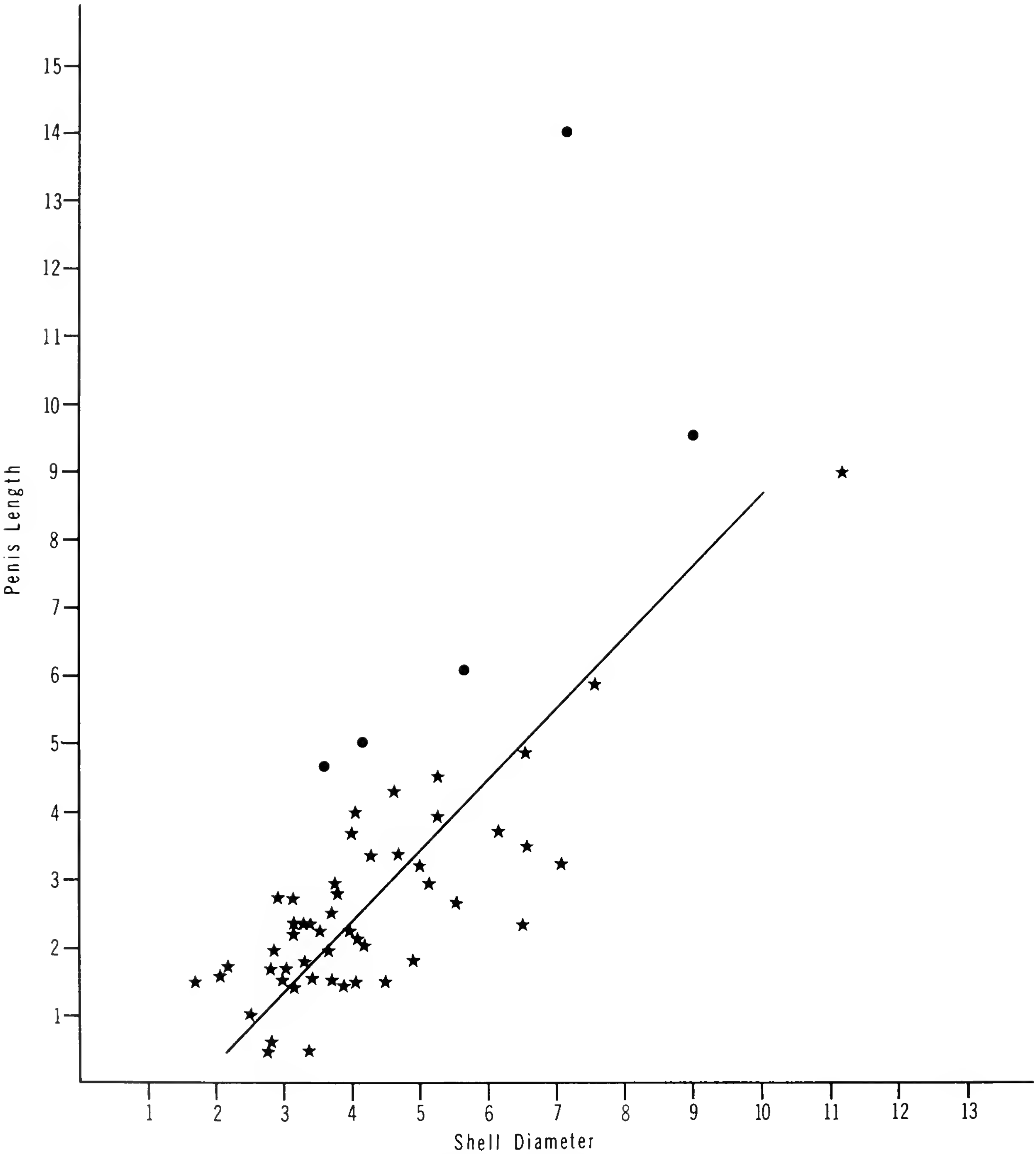

FIG. 56. Penis length and shell diameter in the Endodontidae. Those species with columellar muscle origin of the penial retractor are indicated by "dots," those with diaphragm origin by "stars."

and 19 taxa (one *Minidonta*, three *Opanara*, one *Rhysoconcha*, *Orangia maituatensis*, two *Australdonta*, *Taipidon fragila*, *Nesodiscus fictus*, two *Endodonta*, five *Libera*, *Aaadonta fuscozonata*, and *Priceconcha*) having the free oviduct much longer than the prostate. Species with these three states do not differ significantly as groups in either shell size or whorl count. The small *Minidonta* and *Rhysoconcha*, for example, which have about five whorls, have the long free oviduct, and yet *Orangia cookei* has a short free oviduct. If there is a shift within a genus or between derivative genera from short to equal, or equal to long, then there is a significant (half whorl or more) increase in whorl count.

TABLE LVII. - PATTERNS OF AULACOPOD RADULAR DENTITION

Family taxon	Total teeth	$\bar{X}$ rows	Number of - Lateral teeth	Marginal teeth
Endodontidae (6, 8, 37, 22)	3,550 (2,850-4,095)	98.4	7.2 (5-23)	11.2 (7-19)
Charopidae (15, 15, 58, 58)	3,767 (2,100-9,380)	102.7	7.1 (3-18)	14.5 (6-32)
Microcystinae (111, 127, 129, 143)	11,750 (3,850-31,800)	98.3	8.0 (2-13)	48.3 (24-175)
Euconulinae (17, 19, 18, 20)	12,875 (4,550-36,900)	96.0	8.4 (1-12)	54.7 (19-137)
Helicarioninae (13, 14, 16, 17)	26,800 (3,900-63,000)	107.1	16.9 (5-38)	103.1 (30-252)
Trochomorphinae (28, 28, 31, 31)	14,150 (4,700-25,600)	124.5	10.1 (5-17)	43.8 (19-70)

TABLE LVIII. - MAJOR DIFFERENCES BETWEEN ENDODONTIDAE AND CHAROPIDAE

Character	State in - Endodontidae	Charopidae
Ovotestis	many follicles in line along duct; angled to shell axis	few follicles in usually one or two clumps; curved around axis
Prostate-uterus	separate ducts	fused with a common lumen
Epiphallus	usually absent, penis chamber derived	usually present, vas deferens derived
Verge or vergic papilla	absent	often present
Terminal female organs	simple tubes	usually internal complex structures
Kidney	weakly bilobed	strongly bilobed
Secondary ureter	absent	present
Radular laterals	bicuspid	almost always tricuspid
Shell apical sculpture	radials usually dominant, microspirals "squiggly"	spirals usually dominant in Pacific Island taxa
Apertural denticles	present; microdenticles uniformly triangular	absent in most, when present microdenticles variable
Shell sculpture formation	mostly in calcareous layers	mostly in periostracal layers

TABLE LIX. - MINOR DIFFERENCES BETWEEN ENDODONTIDAE AND CHAROPIDAE

Character	State in -	
	Endodontidae	Charopidae
Talon head	elongately oval	globose
Albumen gland	longer, rarely indented by intestine, alveoli smaller	shorter, usually indented by intestine, alveoli larger
Prostate	alveoli larger, shorter, in rows	alveoli longer, slenderer, irregular spacing
Uterus	less sharply differentiated	sharply differentiated
Penis pilasters	two longitudinal	highly variable, but not two longitudinal
Penial retractor insertion	penis apex or side	penis-epiphallus junction, epiphallus, or penis with vas deferens piercing muscle
Spermathecal insertion	variable	free oviduct
Mantle glands onto pallial roof	often	rarely
Radular central	slightly smaller than 1st lateral	much smaller than 1st lateral

This is a simple space problem solution. The relatively featureless free oviduct and vas deferens sections of the genitalia tend to lengthen more than do the prostate and uterus, which are more complex in structure.

The penis, with its retractor muscle, generally extends from the atrium to the pallial cavity apex. Variations in the proportions between penis length and penial retractor muscle length were not studied. Since the penis length was recorded, it is possible to plot it against shell diameter for either the dissected individuals or the mean diameter for that species. The results are presented in Figure 56; those species in which the penial retractor muscle origin has shifted to the columellar muscle are indicated by "dots," while those with diaphragm origin are indicated by "stars." The greater penial length obtainable with the shift to the columellar muscle origin is obvious. Particularly since the penis can vary in length because of interactions with sympatric congeners (p. 82), the close correlation between shell diameter and penis length is quite remarkable. Their correlation coefficient is 0.82 when the columellar insertion taxa are excluded, and 0.74 even if they are included. Thus the departure of penis length from the plotted regression line in Figure 56 could be used as a quick estimate to see whether species interactions were involved as a selective factor in the penis length of an endodontid, when compared with others in its genus. The taxa furthest from the regression line to the right are the two *Nesodiscus*. Why they should have such a relatively short penis is unknown.

Summary of anatomical variation

The Endodontidae have a basically conservative body plan that offers a number of contrasts to the structures seen in the Charopidae. These differences are summarized in Tables LVIII and LIX as part of the family level classification discussion. Many features of the anatomy in the Endodontidae — penis length, degree of jaw fusion, stomach length, esophageal length, length of hermaphroditic duct, proportionate lengths of free oviduct and prostate — vary in direct relationship to whorl count and body size. Changes in organ position and shapes in the pallial complex relate to shell barriers and shell shape features as space accommodations, while partial coiling of the hermaphroditic duct may serve as an indicator of whorl count reduction from the condition found in the immediate ancestors.

Other features, particularly involving the penis pilaster pattern, seem to be involved in species recognition among sympatric congeners and have great utility to the taxonomist in sorting out "sibling species." Both penis length and possibly the length of the talon shaft also may be involved in species recognition interactions. Very limited data suggests that possibly the size and shape of radular central and lateral teeth may be involved in niche specialization, but the work needed to test this hypothesis could not be undertaken.

There are comparatively few clear progressive trends in anatomical variation or addition of new structures, which stands in very marked contrast to the situation in the Charopidae. There is a change in pilaster shape from low and rounded to high and lamellate. Several taxa show a tendency toward adding glandular tissue between the penis head and penial retractor muscle, thus giving a potential for "epiphallic" secretions. One group, the *Thaumatodon-Aaadonta* complex, has the penial retractor shifted to the side of the penis, a much altered entrance of the vas deferens, and thus an equivalent to a "penial epiphallus" has developed. In *Taipidon* and *Planudonta,* the only Marquesan endodontids, there is addition of a pustulate zone on the penis interior that has no equivalent in other genera. In two separate areas, involving the Hawaiian *Cookeconcha* and the two Marquesan genera, there is an expansion in radular tooth numbers.

Other features, such as the origin of the penial retractor muscle (diaphragm or columellar muscle) and spermathecal insertion (on penis, atrium, or free oviduct), vary without direct size correlation and the changes occurred in several lineages. The shift of the penial retractor muscle to the columellar muscle does permit a definite increase in penis length, but there is no indication of any size "trigger" to this shift. Probably it occurred as a rare mutation, with the resultant opportunity for penial enlargement providing the size-release mechanism.

HABITAT RANGE AND EXTINCTION

With few exceptions, data on the observed niche for endodontids are monotonous. Found under stones, in talus slopes, in or under rotting logs, in leaf litter in heavy forest — all summarize the classic pattern for litter-and-leaf-mould forest dwellers. Essentially all localities involve primary forest situations. The endodontids were ground stratum inhabitants of "primary forests" on the Pacific Islands.

There are only a handful of exceptions. Pilsbry and Vanatta (1906, p. 783) reported that species of *Cookeconcha* "live on dead stumps and logs, and under the bark of dead trees, but also among fallen leaves." They also have been found in heavy moss on large boulders and at low levels on tree trunks (Solem, *personal observation*). *Libera b. bursatella* was taken in the axils of *Freycinetia* at 4,700-5,500 ft. elevation on Mt. Aorai, Tahiti. The Lau Archipelago *Priceconcha tuvuthaensis* Solem (1973d, p. 24) was taken on tree trunks up to 10 ft. above ground level. *Libera fratercula* lives in coastal forests on several islands of the Cook group and has become adapted to living under coral rock in the narrow shore zone of storm-tossed boulders (pp. 418-419). Material of *Rhysoconcha* was collected by members of the Mangarevan Expedition from coffee plantations, native forest, and mixed vegetation areas in the Maitua region on Rapa. The resulting apparently hybrid populations of *Rhysoconcha* from ecotonal stations present a highly interesting phenomenon (pp. 264-265).

The *Cookeconcha* and *Libera bursatella* exceptions are in zones where the rainfall exceeds 175-200 in. annually, so that water conservation selective pressure would be minimal. Why *L. fratercula* exists successfully in a shore zone that is subject to at least short periodic droughts is unknown. The general pattern of the endodontids being restricted to the ground level of primary forests is clear. This contrasts greatly with the Charopidae, where a large number of species are arboreal or semi-arboreal. This difference probably can be explained by the difference in excretion regimes. The Charopidae possess a water-conserving secondary ureter, while the Endodontidae do not. They must periodically use part of the pallial water reservoir to evacuate excreted matter, and thus are more tightly tied to the high humidity levels of the primary forest ground stratum. In Australia, New Zealand, New Caledonia, Viti Levu, Upolu, and Tahiti, I have found charopids in non-primary forest and even on the fringes of plantations, but except for the records of *Libera fratercula* and *Rhysoconcha,* no endodontids have been taken from disturbed primary forest or secondary vegetation zones. This could relate to the change in litter composition and/or humidity levels when the forest is opened up to sunlight drying, or a subtle alteration in food source. In Hawaii, on both Oahu and Kauai, traces of endodontids were found only in isolated high mountain patches of native plants, while on the island of Upolu, Price and I took material of *Thaumatodon hystricelloides* (Mousson) only at relatively high elevations in heavy forest that had not been invaded by introduced ants (see Wilson and Taylor, 1967 for an account of introduced Polynesian ants). In the 1860's, *T. hystricelloides* was common in lowland forests, but today it is restricted in its distribution. This correlates with the presence or absence of introduced ants, particularly the rapacious *Pheidole megacephala*.

On both Oahu and Upolu, I have observed the concordance between the presence of swarming ants and the absence of many endemic snails and insects. This was documented in detail by Zimmerman (1948, pp. 172-177) for Hawaii. The possibility that this exists in relation to the endodontid fauna of Rapa, for example, has considerable evidence in its favor. Wilson and Taylor (1967, p. 6, table 2), record eight species of introduced ants from Rapa. From September 6, 1963 through December 15, 1963, J. L. Gates Clarke of the National Museum of Natural History collected insects and some land snails on Rapa (Clarke, 1971, pp. 1-26). Through the kindness of Dr. Joseph Rosewater, it was possible to examine this material. Endemic tornatellinids and zonitids were represented, but there were no endodontids. Subsequently, Dr. Harald Rehder of the National Museum of Natural History visited Rapa to collect marine mollusks. He is also an experienced land snail collector and, at my request, made a special trip to the Maitua area and searched, without success, for endodontids. Clarke (1971, p. 10, fig. 12) illustrated yet another disturbing factor in the ecology, the presence of goats on even some of the very steepest slopes. The ability of goats to seriously alter ground strata environments is legendary.

The reason for the apparent endodontid absence wherever ants are common probably relates not to adult predation, since the apertural barriers of endodontids would presumably be effective against ant predation, but to egg or juvenile predation. The habit of egg deposition in the shell umbilicus common to endodontids would provide no protection against the ant mouth parts. Hence establishment of a foraging ant colony in an area could easily prevent successful reproduction of endodontids through continued loss of eggs from the umbilical cavities, even though conceivably the adults might not be bothered.

Between the visits to Rapa of the Mangarevan Expedition of the Bishop Museum in 1934 and Clarke's visit in 1963, "noticeable reduction of forest" occurred (Clarke, 1971, p. 9). The combination of reduction in forest cover, high-altitude disturbance by goats, and activities of ants easily could combine to produce great reduction, if not near total extinction of the endodontid fauna on Rapa. The Mangarevan endodontids had been wiped out by habitat alteration prior to 1934, and it may well be that the Rapan radiation has joined the ranks of the extinct.

The material of *Priceconcha* (Solem, 1973d, p. 24, fig. 19, *a*) was heavily parasitized and this could indicate yet another factor limiting the current western distribution of the Endodontidae. No other endodontid or charopid specimens were seen with any trace of parasites.

Habitat disturbance, introduced predatory ants, and possibly parasites acting separately or in combination would effectively explain the rapid extinction of the endodontid fauna. Because of structural limitations in the pallial complex, they basically were restricted to ground strata in primary forests and thus were among the first taxa destroyed or displaced by human disturbance or the addition of ground-litter predators. Their low diversity in Western Samoa (only *Thaumatodon* on Upolu is known) may well stem from the presence of endemic ants in Samoa (Wilson and Taylor, 1967), but not on the Cook, Society, Austral, Marquesan, or Hawaiian Islands, where endodontids were quite abundant.

PHYLOGENY AND CLASSIFICATION

Before discussing the variation patterns found within the Endodontidae, proposing a phylogeny, and deriving a classification scheme from the proposed phylogeny, it is necessary to place the endodontoid snails within a broader context. The higher classification and phylogenetic relationships of gastropods still are controversial. Elsewhere I (Solem, 1974; In press B) have discussed the possible origin of snails and reviewed the higher level classification of land snails. These papers present several changes from the summary given in Solem (1959a, pp. 32-36), which was based on the classic accounts by Pilsbry (1900a, b) and H. B. Baker (1955).

Phylogenetic Position of the Endodontoid Snails

I concur with Fretter and Graham (1962, p. 612) that the euthyneurous condition in the Opisthobranchia and Pulmonata are derived independently. A basic classification into the Subclasses Prosobranchia, Opisthobranchia, and Pulmonata thus reflects phylogeny far better than the split into Subclass Streptoneura (=Prosobranchia) and Euthyneura (=Opisthobranchia and Pulmonata) used by Taylor and Sohl (1962). Elsewhere I have reviewed the evidence that the Pulmonata are a grade containing three superorders, the Basommatophora, Systellommatophora, and the Stylommatophora (Solem, In press B). These groups are "pulmonate" in the same sense that the monotremes, marsupials, and eutherians are "mammalian." It is thus quite possible that the "Pulmonata" is polyphyletic, but in the same way that the "Mammalia" is polyphyletic.

Within the Stylommatophora, authors either list 12 superfamilies (Thiele, 1931, pp. 492-734) or recognize a series of higher categories, based on the divisions proposed and amplified by Pilsbry (1900a, b, 1918, 1948) and H. B. Baker (1955, 1963). Modification of the latter scheme (Solem, In press B) has been based on work suggested by the present study that led in turn to re-evaluating the basic trends along land snails. This work deliberately parallels the type of analysis done by Romer, Simpson, and others concerning the vertebrates. This methodology involves attempting to delineate the basic patterns of ecological advances made within a large taxonomic unit, attempting to identify the physiological factors or the structures (preadaptations) that permitted crossing ecological thresholds, and then identify the adaptations that permitted consolidating this gain through successful adaptive radiations. In the absence of any direct evidence from fossils, determining convergence in structures through analysis of ontogenetic changes is a powerful tool, since the same structure, if developed in different ways, does not suggest close phyletic relationship but rather equivalent life styles. This can be applied more successfully to snails than many groups, since the shell grows by edge accretion, leaving a frozen record of life stages visible even when the animal is fully adult.

The basic problem of land life for a snail is water conservation. The land-dwelling prosobranchs have an open pallial cavity, are active only under conditions of very high humidity, and depend for water conservation on sealing themselves behind the operculum when retracted. The pulmonates have bonded the mantle cavity to the body, retaining a pallial cavity that is open to the exterior through the pneumostome. This greatly reduces water loss, and, in addition, permits the pallial cavity to hold a significantly large reserve supply of extrasomatic water (Blinn, 1964). In marine mollusks and land prosobranchs the kidney opens near the posterior of the pallial cavity. In the marine and fresh-water species, water currents sweep the excreted matter out of the cavity, but in land prosobranchs this option is not available. Pallial water or a "squirt" of excreted water must be used, at least occasionally, to flush out excreted matter.

In the Basommatophora (Delhaye and Bouillon, 1972a) the land-dwelling Ellobiidae have a simple kidney with no ureter, while the fresh-water dwellers have an anterior nephridial pouch that is involved in osmoregulation. The whole kidney is elongated and extends well toward the anterior edge of the pallial cavity. In groups such as the Planorbidae (F. C. Baker, 1945, pls. 44-47) there is a reflexed anterior termination that has been called a ureter.

In the Stylommatophora there are fundamentally different structural patterns that have been used, first by Pilsbry (1900a, b), to delineate several orders. The basic configurations of the pallial complex in the ordinal groups as outlined by Pilsbry (1918, 1948) and H. B. Baker (1955, 1963) were summarized in an earlier paper of mine (Solem, 1959a, pp. 32-35, fig. 1). There are only three basic configurations among the five orders. The kidney in the Orthurethra resembles that of the Basommatophora in that it extends far forward toward the pneumostome, tapering gradually, and ending in an anterior ureteric pore that opens inside a reflexed ridge that extends partly posteriorly (Pilsbry, 1900a, pl. XVII, fig. 3). In the Mesurethra, the kidney is shortened and triangular and remains at the pallial cavity posterior; there is no strong anterior extension of the kidney and the ureteric pore is a simple opening at the anterior kidney tip. This condition is found in the Cerionidae, Clausiliidae, Strophocheilidae, and Dorcasiidae, but not the Corillidae (Solem, 1966a, pp. 94-95) which originally were included in the Mesurethra. The Sigmurethra have a ureter starting at or near the anterior tip of the kidney, following its upper margin back to the posterior of the kidney, then reflexing forward along the hindgut as either an open groove (most Holopodopes) or closed tube that is heavily vascularized (most Aulacopoda and Holopoda). The initial backward extending part is called the "primary ureter" and the section along the hindgut the "secondary ureter." Delhaye and Bouillon (1972b) reported that the orthurethran kidney differs significantly in histological structure from that of the Sigmurethra, and they propose that the Sigmurethra were derived from the Mesurethra by addition of the ureter to the mesurethran kidney. Rather than the Sigmurethra being descendants of the "more primitive" Orthurethra, these taxa are parallel experiments probably derived independently from the "Urpulmonata," whatever group that may be.

The above summarizes the basic structural patterns seen in the stylommatophoran pallial complex. On the basis of both gross morphology and histology, the orthurethran kidney is very different from that of the mesurethran and sigmurethran lineages. The derivation of sigmurethran type from the mesurethran situation has an appealing simplicity, but requires further investigation because of complicating variations in several groups. The two ordinal groups with variations from these basic patterns are the Tracheopulmonata (Family Athoracophoridae) and Heterurethra (Family Succineidae). The former are slugs with the visceral hump organs compressed completely into the foot cavity. Their multi-looped ureter is a secondary modification to the visceral hump reduction. The heterurethrous pallial configuration was suggested by H. B. Baker (1955) as the probable ancestral condition to the Sigmurethra. Elsewhere I (Solem, 1969b; In press B) have reviewed the relationships of the Succineidae and suggested that they are modified Sigmurethra rather than being primitive. Bouillon and Delhaye (1970) reported that the basic structure of the kidney and ureter in the Succineidae and Sigmurethra were the same, but subsequently (Delhaye and Bouillon, 1972b, p. 141) concluded that because the opening from the kidney into the ureter differs in the Sigmurethra and Heterurethra, they are not related. Generally, they live under quite different water regimes, the Heterurethra in semi-aquatic and the Sigmurethra in terrestrial, often water shortage conditions. The addition of a sphincter to the kidney pore in the Sigmurethra, or its secondary loss in the Heterurthra, if my interpretation of their relationships is correct, is not a major difference.

I consider it highly significant, in terms of judging relative phyletic position, that all land-slug taxa have sigmurethrous ureters. There is great water conservation potential in the closed, complete ureter that opens to the exterior at the pneumostome. This permits keeping the pallial water supply for replacing water evaporated from the extended head and foot. The ureter can function to resorb water from the excretory products, and no pallial water need be used to flush out the excretory products. The evolution of a "pseudosigmurethrous" pallial structure in some enids (Solem, 1964) is another point suggesting the fundamental importance of the pallial structures to progressive land-snail evolution.

With this background information, the pallial complex in the Endodontidae can be compared with the basic patterns. It is closest to the sigmurethrous condition, but in having only a primary ureter, with no trace of a secondary ureteric groove or tube, it represents a significantly different structure. A possibly parallel situation is seen in the Australian Caryodidae, where the primary ureter opens posteriorly, without there being any rectal kidney lobe, much less the slight reflexion of the ureter seen in the Endodontidae. The similarity is undoubtedly convergent, since the endodontid and caryodid ureters are very different in internal structure (Solem, *unpublished*). Whether the ureter in the Endodontidae is a forerunner of that seen in the Charopidae and typical Sigmurethra, or an independent experiment is uncertain. Certainly this represents a major difference in structure. The orthurethrous kidney is too different to be viewed as a potential ancestor to the endodontid condition. In terms of pallial complex configuration, the Endodontidae are less advanced than the rest of the Sigmurethra, but more advanced than the Mesurethran taxa. There is no evidence at all that the Mesurethra are ancestral to the endodontoid group.

In respect to other organ systems, the trends of variation are either less clearly delineated, or else simply have not been analyzed in sufficient detail to permit firm phyletic statements. To summarize the limited data presented elsewhere (Solem, In press B), in general, it would be correct to say that taxa with no spermatophore formation (=no differentiated epiphallus), no accessory dart sacs or mucus glands, no vergic structure, and separated pallial gonoducts (prostate and uterus completely separate tubes) are more "primitive" (=generalized) than those with a hard spermatophore, dart sacs and/or mucus glands, a verge, and united pallial gonoducts. These criteria are based on the assumptions that: 1) hermaphroditism in snails was achieved by combining separate male and female systems. Union of ovary and testis into an ovotestis was followed by subsequent union of progressively lower portions of the pallial gonoducts (Solem, 1972b, pp. 108-112); 2) transfer of sperm by snails in a "protective package" is (subject to secondary modification) more advanced than transfer of sperm loose in fluid (for mollusks, not mammals). The "advanced" conditions have been arrived at independently in each of several lineages, judged by analysis of structures in groups with different types of such accessory structures. The helicarionid, helicid, and helminthoglyptid dart sacs, for example, are very different in structure, although performing identical functions. Union of the prostate and uterus into a "spermoviduct" can be traced as separate developments in at least helicid, helicarionid, endodontoid, partulid, pupillid, and ellobiid stocks (Solem, 1972b).

H. B. Baker (1955, 1956, 1962a) recognized three major groups among the Sigmurethra. The Aulacopoda and Holopoda, established by Pilsbry (1896), differ in foot structure, pedal groove presence or absence, basic radular features, and shell characteristics. The Holopodopes contains mainly elongated herbivorous and specialized carnivorous taxa that show numerous differences from the other groups. The Holopoda are universally accepted as being more advanced and, in most characters, are derivable from the Mesurethra. Relationships of the Holopodopes to the other groups are uncertain.

The endodontoid snails have the basic foot and radular structures of the Aulacopoda. While the Charopidae have a sigmurethrous ureter, differentiated epiphallus, usually a verge, and fused pallial gonoducts, the Endodontidae lack a secondary ureter, only rarely have any indication of an epiphallus, lack a verge, and have separated pallial gonoducts. Thus the Endodontidae have aulacopod features, but in the few pallial and genital structures where it is possible to make any positive statements concerning primitive *versus* derived characters, in every case the Endodontidae show the primitive condition. Because of basic differences in structure, it is not possible to derive the Sigmurethra from the Orthurethra. The large and specialized Mesurethra show many genital features that are more advanced than the structures seen in the Endodontidae. We are thus left with an inability to focus on any group of living land snails as possessing a greater number of generalized structures than the Endodontidae. Questions concerning potential derivation of the other endodontoid families from the Endodontidae are deferred until the second monograph. Family groupings for the more advanced endodontoids also will be considered elsewhere, except for the many comparisons with the Pacific Island Charopidae.

The basic division within the Aulacopoda was recognized by Pilsbry (1896, p. 110), who characterized the superfamilies later named Limacacea (H. B. Baker, 1941, p. 206) and Arionacea (H. B. Baker, 1955, p. 109). The cited "key character" was the structure of the radular marginal teeth, but the smooth and shiny, often colorful "limacoid" shell, frequent development of highly elaborate accessory genital structures, and strong development of mantle collar lobes and extensions in the Limacacea, stand in great contrast to the dull, heavily sculptured, frequently flammulated shell and comparatively rare development of accessory genital structures or mantle extensions in the "endodontoid" Arionacea. Preliminary work (Solem, *unpublished*) suggests that some of the Austrozelandic arionaceans (=advanced Charopidae) may be partly transitional in some characters to the shell-bearing limacaceans. The general "Gondwanaland" dominance of the arionaceans and "Laurasian" dominance of the limacaceans probably have influenced the general acceptance of the Limacacea as the derived taxon. This view very probably is correct, but presentation of the evidence must be postponed.

Although the basic difference between the Arionacea and Limacacea is usually cited as the shape of the marginal teeth — narrow, lengthened basal plates with unicuspid, multicuspid, or bicuspid teeth in the Limacacea and short, wide, often squarish basal plates with unicuspid or several cusped teeth in the Arionacea — there also are differences in the sheer number of teeth. The data are spotty, particularly since few row counts were made during this study and my observations on the number of marginal teeth in the Endodontidae and Charopidae are quite incomplete. Nonetheless, the basic trend is clear.

Data have been compiled from this report for the Endodontidae. Many tooth counts, but few row counts, are available for the New Zealand Charopidae (listed as Phenocohelicidae, Endodontidae, and *Otoconcha*) from Suter (1913, pp. 620-732). Massive information on the Pacific Island limacacean radulae was presented by H. B. Baker (1938b, 1940, 1941). A rough estimate of the total teeth on each radula was calculated by multiplying the individual row count by the number of rows on the radula. Counts of lateral teeth and marginal teeth in a half row for each species were averaged for major taxonomic units. These data are summarized in Table LVII. The numbers under the taxon name refer to the number of observations included in each column to the right. The classification of the limacacean groups is slightly altered from H. B. Baker, in that the Trochomorphidae is listed as a full family; and the Helicarioninae includes the Sesarinae of H. B. Baker (1941, pp. 238-263) as was suggested earlier (Solem, 1966a, pp. 22-24).

The low total tooth count on the radulae in the Endodontidae and Charopidae stands in great contrast to the situation in the limacacean groups. The figure for the Endodontidae omits the two *Taipidon* with grossly enlarged tooth counts. They are quite atypical for the family. Their inclusion in such a small sample would distort the results. The slightly higher marginal tooth count for the New Zealand Charopidae reflects the inclusion of the several "flammulinids" with altered marginal teeth. These are altered not only in tooth number, but also in form and cusp structure to the point that Suter (1894a, p. 62) had stated that "the radula is more or less pseudo-zonitoid" in these genera.

The Microcystinae and Euconulinae, which are the most generalized and smallest sized members of their respective families, have added only one lateral tooth, but tripled to quadrupled the number of marginal teeth. This change in both number and tooth form of the marginals suggests a major shift in feeding. By use of critical point drying techniques followed by SEM observation with the radular ribbon in a normal position (see Runham, 1969, fig. 1, for an example of this technique) much information could be gathered on the differences in functioning. This could be the key to understanding the adaptive shift from the arionoids to the limacoids.

While the Euconulinae and Microcystinae are comparable in adult size to the Endodontidae and Charopidae, the Pacific Island Helicarioninae (*Orpiella, Dendrotrochus, Ryssota, Epiglypta, Helicarion*) are 10-55 mm. in shell diameter, and thus much larger in size. Similarly, the Trochomorphidae are mostly 8-20 mm. in shell diameter, again substantially exceeding the endodontoids in size. Hence the increased number of tooth rows in both taxa, and greatly increased tooth numbers in the Helicarioninae can be partly the result of simple size increase. This only accentuates the basic pattern in which the limacaceans are seen to differ mainly through the multiplication and change in form of the marginal teeth on the radula. A comparative study of the more generalized limacaceans and the Austrozelandic charopids with "pseudo-zonitoid" teeth might yield considerable data on the inter-relationships of these superfamilies.

In summary of the above discussion, the endodontoid snails are a group that are "comfortably sigmurethran" (Charopidae) to "protosigmurethran" (Endodontidae). They comprise the least specialized complex of the Aulacopoda. This group parallels the Holopoda, but is not as probable an ancestor to the Holopoda as would be the Mesurethra. While several family groups may be derived from the endodontoid complex (including the Limacacea), no extant group of land snails can be pointed out as possibly representing the stem group for the endodontoid complex. The statement that the "Endodontidae probably are the most primitive living sigmurethrans" (Solem, 1959a, p. 77), which was based more on intuition than evidence, has not been altered by more than a decade of patient poking into endodontoid guts. What has been altered is the concept of family units and definitions expressed in the same paper. A review of family units precedes discussion of phylogeny within the Endodontidae.

Family Classification of the Endodontoids

The following family level names are available for endodontoid snails. They are listed in order of nomenclatural priority.

Punctinae Morse (1864, p. 27)
Patulinae Tryon (1866, p. 243)
Charopidae Hutton (1884b, p. 199)
Phenacohelicidae Suter (1892a, p. 270)
Otoconchinae Cockerell (1893, pp. 188, 205)
Endodontidae Pilsbry, 1895 (Pilsbry, 1893-1895, p. xxviii)
Flammulinidae Crosse (1894, p. 210)
Thysanotinae Godwin-Austen, 1907 (Godwin-Austen, 1889-1914, p. 189)
Laominae Suter (1913, p. 732)
Goniodiscinae Wagner (1927, p. 305)
Helicodiscinae Pilsbry *in* H. B. Baker (1927, pp. 226, 230)
Rotadiscinae H. B. Baker (1927, pp. 226, 228)
Stenopylinae Thiele (1931, p. 569)
Amphidoxinae Thiele (1931, p. 575)
Discinae Thiele (1931, p. 578)
Dipnelicidae Iredale (1937b, pp. 22-23)
Paralaomidae Iredale (1941a, p. 263)
Hedleyoconchidae Iredale (1942, pp. 34-35)
Pseudocharopidae Iredale (1944, p. 312)

The Iredale taxa are virtually *nomina nuda*, and consideration of the extralimital units Thysanotinae, Goniodiscinae, Discinae, Helicodiscinae, Rotadiscinae, Amphidoxinae, and Stenopylinae is deferred. Of the remaining taxa, the name Patulinae is ignored for the following reasons. The describer (Tryon, 1866, p. 242) noted that the Patulinae was "not proposed with any intention but to facilitate the determination of species." Although used as a family name by Moellendorff (1890, p. 221; 1900, p. 109), it has been ignored by other authors of that period and by subsequent students, until listed with disapproval by H. B. Baker (1956, pp. 134, 138). It is now equivalent in modern context to the Goniodiscinae and Discinae, since the genus *Patula*, after a very long and checkered career, has settled as a subjective synonym of *Discus*. May both *Patula* and Patulinae rest in peace.

Morse (1864, p. 27) established the Punctinae on the basis of having a jaw composed of 16 distinct plates, and minute radular teeth that he thought resembled those of *Carychium*, an ellobiid, under optical study. There are shell, radular, and genital features which combine to separate the Punctidae as a family unit (Solem, *unpublished*). The Laominae of Suter (1913) is not separable from the Punctidae, as has been recognized by Pilsbry (1893-1895), Thiele (1931), and Climo (1969a).

The first use of the name Charopidae (Hutton, 1884b, p. 199) was based on the heliciform shell and development of a caudal mucus gland. The latter feature, which not only is very characteristic of arboreal snails in general, but is highly variable in degree of development at a very low taxonomic level, was the subject of more than a decade of controversy concerning endodontoid classification. In a series of papers Pilsbry (1892a, pp. 54-55; 1892b, pp. 68-69;

1893a, pp. 401-402; 1893b), Hedley (1893a, p. 163), and Ihering (1893, p. 121) downgraded the importance of this character, although Crosse (1894, pp. 210, 219) and Moellendorff (1895, pp. 157-158; 1899; 1900, p. 109) gave primary importance to the caudal mucus pore. Suter (1892a, p. 270) had proposed the family unit Phenacohelicidae, citing the "caudal gland" as a significant feature, but subsequently (Suter, 1894a, p. 62) agreed with Pilsbry and stated "I do not attach very great importance to the presence or absence of the caudal gland, as we really do not know its true significance; but in the mollusks classed under *Flammulina* the jaw is always stegognath, the radula is more or less pseudo-zonitoid, and, besides, a mucous tail-gland is always present; whilst in *Endodonta* and *Charopa* the jaw is only striated, the radula is much more helicoid, and there is no caudal gland." Suter was using *Endodonta* in a very broad context, and not in the restricted sense of this study.

Early attempts at classifying the Australian and the New Zealand endodontoids were made sequentially in terms of writing, but not in publishing, by Pilsbry (1892a, pp. 54-55), Hedley (1893a, b), Pilsbry (1892b, pp. 68-69), Hedley and Suter (1893, pp. 633-660), and Pilsbry (1893a, pp. 401-402). Pilsbry summarized his views (Pilsbry, 1893-1895, pp. 6-54) in an annotated check list, which included his (Pilsbry, 1893a, pp. 401-404) placing *Laoma* and *Punctum* into a "Group Polyplacognatha" and the remaining into "Group Haplogona" of the Family Endodontidae. The latter name must date from February 2, 1895, the publication date for the introductory pages in that volume.

In his monumental survey of New Zealand mollusks, Suter (1913) defined the Phenacohelicidae (p. 621) as with a mucus pore and the Endodontidae (p. 684) as lacking a pore. He divided the latter family into two subfamilies, the Endodontinae with tricuspid lateral teeth and a thin striated jaw, while the Laominae have bicuspid lateral teeth and a jaw of separate plates. Suter (1913, pp. 619-621) also included a peculiar slug-like animal, *Otoconcha dimidiata* (Pfeiffer, 1853), as a limacid slug, although Cockerell (1893, pp. 188, 205) had placed it in a subfamily, Otoconchinae, without giving any description. Subsequently, H. B. Baker (1938a) stated "I am inclined to regard it as constituting an aberrant subfamily of the Endodontidae, but, with almost equal reason, it might be considered as another primitive member of the Arionidae or be erected into a separate family, the Otoconchidae, until intermediate forms are found." Climo (1969a, 1971a) has used Otoconchinae as a subfamily unit and provided much important anatomical data on its relatives.

Iredale (1913, p. 375; 1915a, p. 479) continued attacking the mucus pore (along with all other anatomical features). Gabriel (1930, pp. 72, 78, 84), in a major paper, proposed the family units Endodontidae, Flammulinidae, and Laomidae for Austalian taxa. Iredale (1937a) adopted this system, without acknowledgment, only substituting the name Charopidae for Endodontidae and (Iredale, 1937b, p. 26) adopting Stenopylinae (Thiele, 1931) as a full family unit. Subsequent efforts by Iredale added four undescribed family names, but made no meaningful changes in classification of the Pacific taxa.

Climo (1969a, 1970, 1971a, b) has proposed using a single family, Punctidae, with four subfamilies, Charopinae, Phenacohelicinae, Punctinae, and Otoconchinae. The two latter are based on the now traditional jaw and radular features (Punctinae) and inevitable consequences of visceral hump reduction (Otoconchinae). To distinguish between the Charopinae and Phenacohelicinae, Climo relied on the presence (Charopinae) or absence (Phenacohelicinae) of an epiphallus. In many taxa with reduced visceral humps, the vas deferens-derived epiphallus will be compacted forward into the penis sheath (Solem, *unpublished*). Other dissections suggest that the epiphallus in different groups of Australian and New Zealand taxa may be independently derived. In laying to final rest the mucus gland arguments, Climo has performed a notable service, but I do not agree with his criteria for family classification.

Only one extralimital paper requires consideration. H. B. Baker (1927, pp. 226-235) reviewed the anatomy and classification of some North and Central American endodontoids. His division into the subfamilies Punctinae, Rotadiscinae, and Helicodiscinae was based on changes in pallial cavity configuration and length of the secondary ureter. The pattern of pallial cavity change from *Helicodiscus* (H. B. Baker, 1927, pl. 18, fig. 42) and *Radioconus* (pl. 17, fig. 30), to *Chanomphalus* (pl. 20, fig. 52), to *Radiodiscus* (pl. 17, fig. 24), to *Punctum* (pl. 16, fig. 12), to *Rotadiscus* (pl. 16, fig. 17) would present a virtually continuous transitional series from the pattern found in the Endodontidae to that seen in the Charopidae of the Pacific Islands. In addition, *Rotadiscus* (pl. 16, figs, 13, 19) shows apparently only partial fusion of the prostate and uterus, while the other genera have fused pallial gonoducts. It is premature to try to propose a worldwide classification for this group, since most of the African, South American, Australian, New Caledonian, and Lord Howe Island taxa have not been dissected. The genitalia of the species studied by H. B. Baker (1927) do have typically "charopid" features, so that the pallial configurations sequence does not negate the validity of family level separation.

I propose here a three-family classification of the Pacific Basin taxa, into Punctidae, Endodontidae, and Charopidae. The Punctidae have the bicuspid lateromarginal teeth with accessory cusps mentioned above (p. 93) and several differentiating anatomical features that will be discussed elsewhere. The Endodontidae and Charopidae, as represented on the Pacific Islands, differ in a number of major (table LVIII) and minor (table LIX) anatomical features. There are no known extralimital representatives of the Endodontidae, but the Charopidae have their primary abundance elsewhere. I include in the Charopidae such taxa as the Phenacohelicinae and Otoconchinae in the sense of Climo (1969a, 1971a), Flammulinidae in the sense of Gabriel (1930) and Iredale (1937a and following), Hedleyoconchidae, and Pseudocharopidae. The question of subfamily divisions within the Charopidae is deferred until more data are available on Australian and New Caledonian taxa. The relationships of northern hemisphere discids and Neotropical taxa are not discussed at this time.

Suter (1913) based family units on the mucus gland; H. B. Baker (1927) based subfamilies on the pallial complex, Thiele (1931) divided the Endodontidae into eight subfamilies on shell and radular features, Zilch (1959-1960, pp. 203-230) essentially copied Thiele's classification, except for ranking Otoconchidae as a distinct family, and Climo (1969a) used the presence or absence of an epiphallus for subfamily units. In proposing an increase in rank for units in the classification, as well as altering both the number and composition of these units, I must answer the question as to equivalence with other family units in the Aulacopoda. The characters of major phyletic significance used to separate the Endodontidae from the Charopidae are the absence of the secondary ureter, the complete separation of the prostate and uterus, the very simple structure of the terminal genitalia, and the difference in the ovotestis structure. The other features mentioned in Tables LVIII and LIX are useful, but carry less phyletic weight. The shell structure differences, particularly in the mode of sculpture formation, may have equally significant weight, but need further investigation.

The nearest equivalent situation would be the division of the Pacific Island limacaceans into Helicarionidae and Zonitidae by H. B. Baker (1941, p. 205). His definitions involve divergent patterns of specialization, such as development of dart apparatus on the female (Helicarionidae) or male (Zonitidae) sides of the terminal genitalia, without listing any equivalent major structural gaps between family units. One of the important changes used here is present within the Helicarionidae. The Microcystinae, the more primitive group that is dominant on the Pacific Islands, has the prostate separated from the uterus, while in the other subfamilies they are united into a "spermoviduct." But no equivalent of the other major changes exists in the Limacacea. All the limacaceans have a typical sigmurethrous pallial complex. There is great specialization of the genitalia including epiphallus formation and (except in the Microcystinae) spermatophore formation with frequent development of accessory genital structure.

On the basis of degree of difference, the phyletic gap between the Endodontidae and Charopidae is wider than the gaps between family units of the Limacacea.

Much descriptive and some anatomical information on extralimital Charopidae can be located in faunistic studies. The reports on the molluscan faunas of the Kermadecs (Iredale, 1913, 1915b), Papua (Iredale, 1941c; Solem, 1970a), Lord Howe Island (Iredale, 1944), Norfolk Island (Iredale, 1945), New Caledonia (Solem, 1961), New Zealand (Suter, 1913; Powell, 1957), and the Australian check list (Iredale, 1937a, b, c) provide summaries of the literatures. The incredible nomenclatural nightmare of Iredale (1933) unfortunately cannot be ignored completely, while his subsequent papers on the faunas of New South Wales (Iredale, 1941a, b), and Western Australia (Iredale, 1939) also must be used. The few Philippine Islands (Solem, 1957) and Indonesian (Solem, 1958, 1959b) endodontoids also have been summarized. Connolly (1939) reviewed the South African taxa, and a brief survey of the St. Helena taxa is included in Solem (In press A). Data on Neotropical taxa are very widely scattered.

PHYLOGENY WITHIN THE ENDODONTIDAE

Perhaps the key problem in phylogenetic analysis today is the question of how to weight characters in determining phylogeny. Opinions vary from the classical pheneticists who stated that every character is of equal weight, to the classical typologists who picked out single characters on which to base decisions. In between are the vast majority of systematists. The present study is more pragmatic than philosophical, although based on the tiered approach to character analysis developed in Solem (In press B). I assume that the major changes involved in progressive evolution require shifts in ecological roles accompanied by morphological alterations. Adaptative radiations within such a new zone will involve change at a different level, while the interactions between sympatric species will produce yet a third level of evolutionary change. While the basis of change is genetic, as a practical matter most systematic work must be with morphology, expressed as either a direct or pleiotropic effect of a genetic shift. Biochemical criteria, physiological factors, behavior patterns, and molecular data would follow similar patterns.

In relation to this study, I consider that the changes from Endodontidae to Charopidae (strictly terrestrial to semi-arboreal, wider tolerance of disturbed conditions, changed pallial structures, advanced genital structures) are representative of progressive evolution. No such changes were detected within the Endodontidae, but there are some minor adaptative shifts and numerous instances of sympatric species interactions (see pp. 80-81, tables LII - LIV). Because I have not been able to pinpoint an ancestor group for the Endodontidae, reference to a more primitive outgroup for determination of generalized character states has not been possible. Instead I have used a short set of pragmatic guidelines. These are based in part on the distributional fact that the Pacific Island endodontoids occur on tiny specks of land that are widely separated from each other. This has the practical effect of making a systematist investigate with great care situations where a species, found on one of the Palau group, for example, has characters that appear very similar to or identical with characters found otherwise only in a Marquesan species. Continental areas have, in many parts of the world, been subject to multiple migrations, invasions, extinctions, and recolonizations because of Pleistocene phenomena. It is intellectually far more satisfying (and comfortable) to accept disjunct similar species on continental areas as representing distributional relicts of common ancestry than to assume that the Palau and Marquesan species had common ancestry.

The basic criteria used in judging change in character states in regard to individual structures or complex patterns of growth are:

1) If formed in exactly the same way they are presumed to have common ancestry;

2) If formed in different ways, although performing the same function or showing the same end growth pattern, they are independently derived;

3) Greater complexity may be suggestive of a derived condition, but if the less complex conditions are noncoherent with each other, while the more complex condition has detailed structural consistency, then secondary simplification is postulated.

In regard to distributional factors, I have assumed that:

4) Widely distributed character complexes that have structural consistency probably are ancestral to sporadically distributed different states of these complexes that lack structural consistency.

5) Character states of limited geographic occurrence should be analyzed in terms of development from or into states of wide geographic distribution.

6) Character states must be interpreted also in reference to conditions existing among sympatric or probably sympatric taxa.

7) Character states occurring in only one geographic area may be either generalized or derived in comparison with widely distributed states, with interpretation resting on correlated changes with other characters that can be interpreted more objectively.

Examples of the ways in which these criteria have been applied during this study are:

1) and 2) The apertural barriers in the Endodontidae have the same type of microdenticulations on their upper surface and therefore the barriers are assumed to be of common origin, while the barriers in the Charopidae show different types of structure and superior microdenticulations, strongly suggesting multiple origins (Solem, 1973b, p. 305). The brood chamber growth pattern in the Endodontidae occurs in several different geographic areas. In each situation the method of secondarily narrowing the umbilicus is different, suggesting multiple origin of the growth pattern (pp. 27-30).

3) Reduction of the apertural barriers results in a very simple ridgelike structure, particularly when compared with the detailed structures found on the larger barriers. As shown above (pp. 57,62), the patterns of reduced barriers are much more varied than are the patterns of fully developed barriers. Reduced shell sculpture (pp. 47-50) correlates with increased shell size and the patterns of reductions have greater variability than do the basic complex sculpture.

4) The pattern of the penis with two low pilasters, the vas deferens entering below the apex, and penial retractor muscle inserting on the penis apex is widely distributed, while the additions of epiphallic tissue to the penis apex and changes in the pilaster patterns occur sporadically.

5) and 7) The presence of a glandular zone inside the penes of Marquesan Endodontidae has no counterpart elsewhere in the family, and, if eliminated, the penis structure would still be specialized in terms of the family pattern. Hence this is interpreted as an additive, specialized structure.

6) The variations in penis size and pilaster patterns (tables LII, LIII, LIV) are largest when sympatry of congeners is involved. Hence aberrant structural patterns in the penis complex are viewed first as suggesting "species recognition" interactions between populations. Comparisons must be made with sympatric or at least same-island taxa before predicting whether the variation represents a general adaptational trend or essentially local character displacement to aid species recognition.

All of the above guidelines are based on the attempt to understand the ontogenetic development of structures and to place them within the framework of species-level interactions. This approach is more applicable to mollusks than to arthropods or vertebrates, since the ontogenetic pattern of shell growth is available in each adult specimen, while obviously lacking in the adult arthropod or vertebrate. Both the key to and difficulty of this approach involve the necessity to interpret not just the final structure, but to analyze its components and ontogeny as an aid toward deciding its significance in phylogenetic analysis.

TABLE LX. - SHELL PARAMETERS OF THE ENDODONTIDAE

	Minimum	1st Quartile	Median	3rd Quartile	Maximum
Height	0.92	1.58	1.98	2.57	7.26
Diameter	1.68	3.01	3.77	4.85	12.26
H/D ratio	0.344	0.466	0.531	0.589	0.789
Whorls	3-5/8	5-1/8	5-1/2+	6-3/8-	8+
D/U ratio[1]	1.68	3.14	3.94	5.61	closed
Ribs[2]	19	63.6	80.0	104.4	250
Ribs/mm.	1.41	5.0	7.6	11.1	40.4

[1] Excluding brood chamber taxa

[2] Excluding those without countable ribbing on body whorl

Portrait of a generalized endodontid

Although the most basic trends in the Endodontidae are toward increased size accompanied by structural alterations, there is evidence that at least one genus, *Rhysoconcha,* is secondarily dwarfed (pp. 255-256). It should not be assumed automatically that the smallest species in size represent the most generalized taxa. A reduction in adult whorl count also can effectively produce smaller adult size without requiring major structural alterations.

Table LX summarizes the distribution of several shell parameters in the Endodontidae. Allowing for the tendency toward larger size that often is the pattern in most taxa, and utilizing data from the discussion given above on variation in structures, the "generalized endodontid" structure can be described rather simply. The shell would be about 3.0-3.5 mm. in diameter, with 5¼ - 5½ whorls, the height being slightly less than half the shell diameter, and the widely open umbilicus would be contained about 3.5 times in the diameter. There would be a prominent sculpture, numbering perhaps 65-90 ribs on the body whorl, spaced six to eight per millimeter of shell periphery, and with four to eight microradials between each pair of major ribs. The apex and spire would be slightly to moderately elevated, reaching up to half the body whorl width in terms of actual protrusion. The body whorl itself would be rounded or laterally flattened. Inside the aperture there would be 2 to 3 parietal barriers extending three-sixteenths to one-quarter whorl posteriorly, 1 columellar barrier, and 4 palatal barriers at or near the lip edge that extended one-eighth to three-sixteenths whorl posteriorly. All the barriers would be slightly to moderately widened above on the posterior half to two-thirds, and capped on the expanded portions with triangular microdenticulations that point toward the outside of the aperture. The anterior portion of each barrier would gradually descend to a sharper truncation in many palatals and an anterior threadlike portion in the lower parietals. The net effect of these barriers would be to grossly narrow the apertural opening, except for a slightly widened zone in the upper palatal area to permit effective withdrawal of the head and foot.

In the anatomy, only the few variable features need to be outlined, since the structural plan is relatively uniform. The pallial cavity would extend about three-quarters whorl, with the kidney weakly bilobed, and probably there would be no mantle gland extension onto the pallial roof. The genitalia would have the penial retractor muscle inserting directly on the head of the penis and originating from the diaphragm. Inside the penis would be two low and rounded, longitudinal pilasters, with the vas deferens opening just below their point of apical union. The spermathecal insertion is uncertain, and other features of the genital system seem to vary more in size correlated features than anything else. The radula would have about 100 rows of teeth, with a tricuspid central, five or six bicuspid laterals, and perhaps 10-12 marginals with split cusps. The jaw would be composed of separate, elongated plates held together by a thin membrane.

Converting the above description into an ancestor of the present endodontids probably would involve only a reduction in shell diameter and whorl count, with correlated changes in ribbing, D/U ratio, and pallial length.

Identifiable major trends

Smaller shell size can be reached by the *Rhysoconcha* strategy of secondary size reduction without major reduction in whorl count, or by the pattern that may exist in the smallest *Minidonta, Cookeconcha,* and *Mautodontha* where greatly reduced whorl counts are common. By far the most prevalent trend is for increase in shell size, most often by simple continued addition of more whorls to the shell. Associated with this increased size are a tendency for loss of shell sculpture, fusion of the jaw plates, often a more elevated spire as the decoiling growth continues, sometimes lengthening and size reduction of the

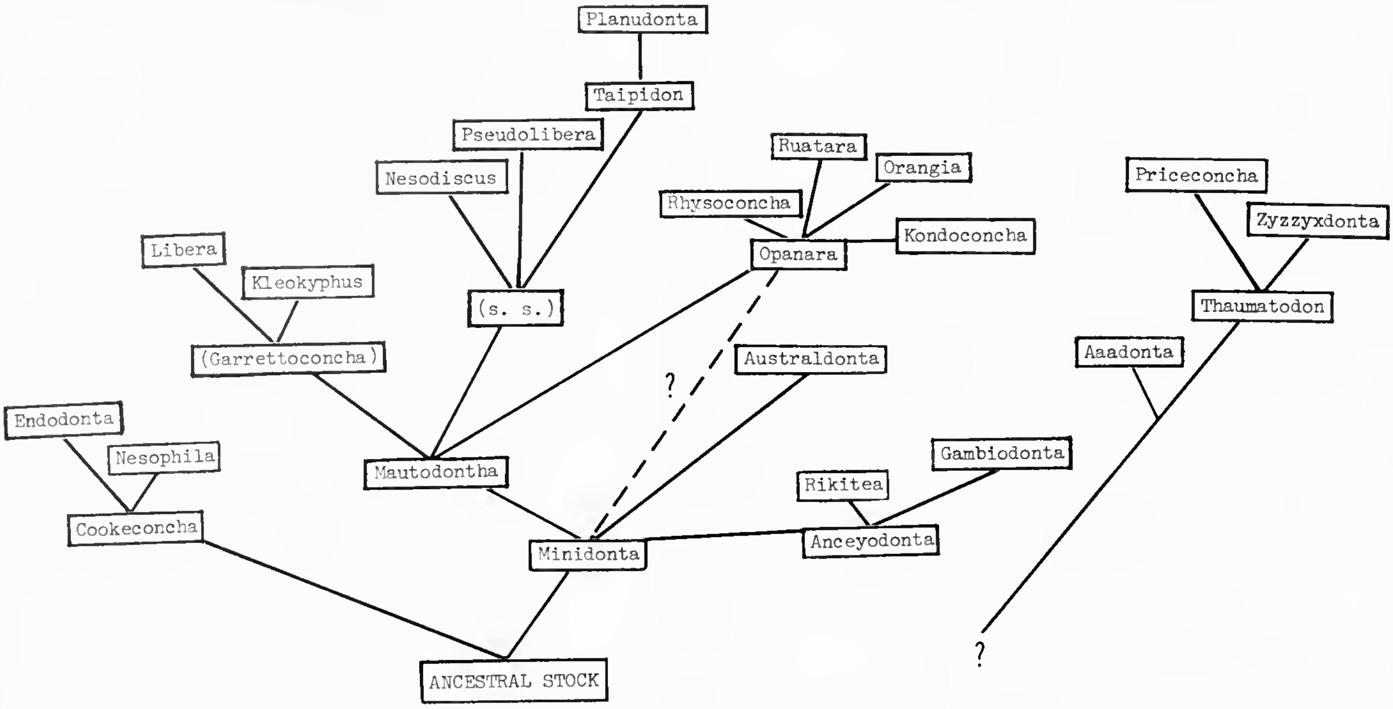

FIG. 57. Phyletic diagram of the Endodontidae showing hypothesized origins of extant taxa.

apertural barriers, and various minor lengthening trends as outlined in discussions of the characters above.

Such simple continued incremental growth in whorl numbers also will tend toward a very widely open umbilicus and proportionately higher shell that may reduce the ability of the animal to crawl into narrow crevices. The widely open umbilicus particularly may have led to a functional problem with egg retention. In some *Nesodiscus* (p. 345) eggs deposited in the widely open umbilicus are covered by a solid sheet of mucus to form an encapsulated situation, but in at least five groups (p. 28) there has been secondary narrowing of the umbilicus to form a "brood chamber" in which the eggs are deposited. Inevitably, widening of the umbilicus had to precede the secondary narrowing (fig. 189), and it is the differences in the way that the narrowing is achieved that indicate separate origin of this growth pattern. These then are two basic trends in shell variation – size increase through whorl accretion leading to first a very widely open shell umbilicus and a tendency toward secondary narrowing of the umbilical cavity to form a brood chamber.

Anatomical variations are, in general, correlated with minor features of shell variation. Only a few seem to be independent of the trends in shell structure. Ignoring the "species recognition" changes in genital structure, the one really striking alteration is in the pattern of the penis-vas deferens-epiphallus relationship. This is geographically limited. Many Rapan and most Marquesan taxa show an added zone of glandular tissue to the penis apex (fig. 46), while the Palau Island *Aaadonta,* Fijian *Priceconcha, Zyzzyxdonta,* and *Thaumatodon* have a quite different entrance of the vas deferens and altered attachment of the penial retractor, that, in effect, forms a penial epiphallic section. Other local changes in anatomical structure that can be called trends are the addition of a pustulate zone within the penis of Marquesan taxa, and the tendency for increase in radular tooth numbers for some Hawaiian and Marquesan taxa.

While many features of the shell sculpture and apertural barriers were shown above to be partly size correlated, others vary more within a phyletic unit on a geographic basis. The obvious change in barrier microdenticulation from a continuous surface in most genera to the "beaded" structures seen in the *Aaadonta-Thaumatodon* group correlates with the penial epiphallus grouping, and represents a major change in structure. As an example of retaining a marked pattern of variation through major shell size and shape shifts, the very characteristic apertural barriers of *Anceyodonta* also are seen in the Mangarevan *Minidonta* and *Gambiodonta.* All the Mangarevan taxa also have the tendency to develop microdenticulated trace barriers (figs. 71c; 89d, f; 187).

Phylogenetic conclusions

The Pacific Island Endodontidae are characterized by a repetitive set of conchological specializations that have produced frequent convergences in appearance, plus a few anatomical trends that do not correlate with the basic conchological trends. If more taxa had been available for dissection, particularly from areas such as Mangareva and the Society Islands, the number of identified anatomical trends undoubtedly would have increased. My ideas concerning the phylogeny of the Endodontidae are summarized in Figures 57 and 58. The first is a typical phyletic tree

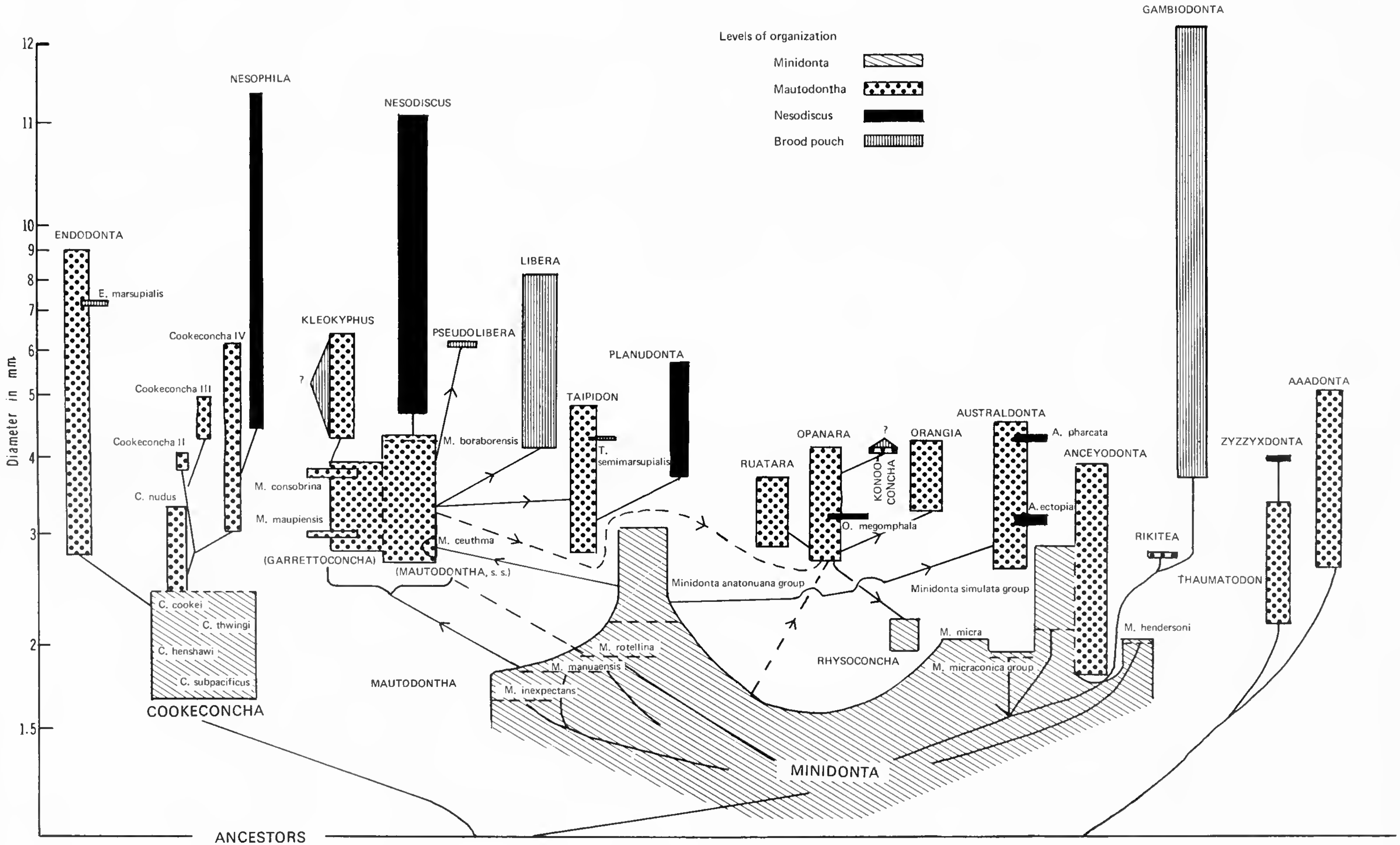

FIG. 58. Levels of specialization in the Endodontidae, size range within genera, and hypothesized directions of evolutionary change. The size range is based on mean shell diameter in mm. *Libera* is incorrectly placed as coming from *Mautodontha, s. s.,* rather than *Garrettoconcha,* and *Priceconcha* (described in Solem, 1973d), which should be an added *Nesodiscus*-level taxon placed where the "*Zyzzyxdonta*" label now resides, is omitted.

diagram, while the second introduces additional data concerning degree of relationships and patterns of specialization. Detailed arguments concerning intergeneric relationships are developed in the systematic review and are not repeated here.

The first conclusion, shown in Figure 57, is that *Cookeconcha* and *Minidonta,* although now showing divergent patterns of structure, shared a direct common ancestor and formed the stem groups for subsequent evolution. That they are truly primitive in all features is unlikely, since the unusual umbilical decoiling pattern of many *Minidonta* (figs. 62c, f; 63b; 69c, f) and the bifid parietal of many *Cookeconcha* represent highly atypical situations within the context of the family. Nevertheless, their patterns of distribution and most structural features place them perhaps nearest to the potential ancestral group of any extant taxa. The Hawaiian radiation into *Nesophila* and *Endodonta* is derived from *Cookeconcha.* Undoubtedly more generic level taxa will be delineated when the Hawaiian fauna has been reviewed in detail.

Mautodontha, Australdonta, and *Anceyodonta* represent separate specializations from the *Minidonta* complex, each subsequently giving rise to other taxa. The Society, Cook, and Tuamotu island *Libera, Kleokyphus, Nesodiscus,* and *Pseudolibera* represent local developments from subgenera of *Mautodontha.* The Marquesan *Taipidon* also is derivable from very generalized *Mautodontha*, but shows a variety of specializations, one of which led to the endemic *Planudonta.* All available data suggest that the Rapa Island radiation is monophyletic, with *Opanara* representing the generalized condition from which *Rhysoconcha, Ruatara, Orangia,* and *Kondoconcha* were independently derived. *Opanara* more probably was derived from a *Mautodontha*-type ancestor, but could have evolved from a *Minidonta*-level ancestor of large size. On Mangareva in the Gambier Islands, *Rikitea* and *Gambiodonta* represent local derivates either directly from the *Minidonta* stock or from *Anceyodonta.*

As outlined in the zoogeography section (pp. 488-492), the *Thaumatodon-Aaadonta* complex has a very different pattern of distribution from that shown by the other taxa. It also shows significant changes in structure. I regard it as being a more recent element in the Pacific Island fauna, one that evolved from endodontids formerly in the Indonesia-New Guinea-Australia axis that are now extinct, their place having been taken by the Charopidae. While *Thaumatodon* and its derivatives share a distant common ancestry with the other species groups, this complex probably is not derived from any of the extant Pacific Island taxa, but rather from extralimital groups. Although the structures found in the *Thaumatodon-Aaadonta* complex can be derived from those found in the *Mautodontha*-level taxa, the discordance in distribution type is so large and the morphological gap so abrupt that the hypothesis of an independent origin followed by secondary colonization seems far more probable to me.

A different approach is taken in Figure 58 which indicates four levels of conchological specialization that are in great part size correlated, presents additional data about interrelationships of species groups, summarizes size range within genera, and also includes data on probable directions of evolution within the group. One error resulting from lay-out problems and one omission need to be mentioned. *Libera* probably is derived from a *Garrettoconcha*-type ancestor rather than *Mautodontha, s. s.,* and *Priceconcha* should have been shown as coming from the *Thaumatodon* stem as a "*Nesodiscus* level" taxon right under the "*Zyzzyxdonta*" label. Inclusion of the recently described *Priceconcha* would have required redoing the entire chart.

A brief outline of the characteristics for each of the four specialization levels follows. In increasing order of specialization, they are the *Minidonta, Mautodontha, Nesodiscus,* and brood-chamber levels.

Three genera are included on the *Minidonta* level. These include the genus *Rhysoconcha* by secondary derivation, the most generalized species group of *Cookeconcha* (excluding *C. nudus*), and *Minidonta* itself. As summarized in Table LXI, these species show an average H/D ratio, but fall into the lower quartile in both diameter and whorl count (cf. table LX). The umbilicus is slightly narrower than average, relating to both the low whorl count and the peculiar pattern of umbilical decoiling seen in some *Minidonta.* All of these taxa retain a prominent shell sculpture, and the vast majority (16 of 21) have the aperture moderately to strongly constricted by the barriers. *Minidonta* and the most generalized *Cookeconcha* closely approach each other in overall structure, but there are numerous characters in which they contrast, as discussed under *Cookeconcha subpacificus* on pp. 211-212. The other Hawaiian genera are derivable from the generalized *Cookeconcha,* while the species groups within *Minidonta* serve as effective stem groups for many other taxa. *Minidonta* grades almost imperceptibly into the Mangarevan *Anceyodonta* (pp. 179-181), while *Australdonta* can be derived from the *M. anatonuana* complex. The Rapan radiation could be descended from either *Minidonta* or, more probably, the *Mautodontha* complex, as indicated by the dotted lines. *Mautodontha* is, in itself, a stem group for a wide variety of taxa. Estimating the exact relationships between the more specialized *Mautodontha*-level taxa and the species groups clustered as *Minidonta* is hampered by the virtual lack of any anatomical data for species in either *Minidonta* or *Mautodontha.* A simpler classification would result if the geographical species groups of *Minidonta* were associated with their geographical derivatives, to form linear genera. I have not done so, since the morphologic gap between the derived genera and the *Minidonta*-species groups that are logical ancestors to them usually is greater than

TABLE LXI. - SHELL PARAMETERS FOR LEVELS OF ORGANIZATION

	Minidonta	Mautodontha	Nesodiscus	Brood chamber
Number of taxa	21	114	17	29
Diameter	2.25 ±0.095 (1.68-3.26)	3.75 ±0.098 (1.87-8.99)	5.90 ±0.538 (3.75-11.29)	5.39 ±0.277 (4.23-12.26)
H/D ratio	0.545 ±0.010 (0.445-0.625)	0.528 ±0.009 (0.344-0.789)	0.449 ±0.016 (0.346-0.560)	0.597 ±0.012 (0.480-0.702)
Whorls	4.83 ±0.12 (3-5/8 - 5-1/2+)	5.49 ±0.06 (4-8)	6.40 ±0.19 (4-7/8 - 7-3/8)	6.78 ±0.11 (5-3/8 - 8+)
D/U ratio	4.87 ±0.39 (2.66-10.1)	--	2.24 ±0.10 (1.68-3.14)	--

the gaps between the species groups clustered within *Minidonta.*

The *Mautodontha* level of organization contains the bulk of the species and genera. They show the median pattern in size, H/D ratio, and whorl count (tables LX, LXI). Since species with closed umbilici fall into this grouping, the mean D/U ratio was not calculated. Currently, the stem genus, *Mautodontha,* is virtually geographically isolated from *Minidonta,* except for the joint occurrence on Raivavae in the Austral Islands caused by the inclusion of *Mautodontha ceuthma* in that genus. This means that I consider *Mautodontha* to be potentially a grade, rather than a clade. With the lack of anatomical data and limited material available, I have included *M. ceuthma* in *Mautodontha* rather than with the derivative *Australdonta.* Discussions of the derivation patterns for *Kleokyphus, Nesodiscus, Pseudolibera, Libera, Taipidon,* and *Australdonta* are discussed under the respective genera. Several groups show general trends toward, or include species that actually have reached, the more specialized levels. For example, *Taipidon semimarsupialis* has a definite brood chamber, although no other member of the genus comes close to attaining this level of specialization. In contrast, while only *Endodonta marsupialis* has secondary umbilical narrowing, most of the other taxa have a U-shaped, deep umbilicus and are perfectly "pre-adapted" to a narrowing trend. *Kleokyphus* from Makatea and *Kondoconcha* from Rapa also are close to this specialization pattern. Yet another taxon, *Thaumatodon euaensis,* also shows umbilical narrowing, but never had enough umbilical expansion to justify calling this a brood chamber development. *Australdonta pharcata, A. ectopia, Opanara m. megomphala,* and *O. m. tepiahuensis* are *Mautodontha*-level taxa that show or approach the *Nesodiscus* pattern of specialization.

The *Nesodiscus*-level genera, *Nesophila, Nesodiscus, Planudonta,* and *Priceconcha* are quite strongly characterized. There is a gross reduction in sculptural prominence (less in *Planudonta*), usually great-to-complete reduction in the apertural barriers, a sharp increase in diameter (table LXI) accompanied by an extremely widely open umbilicus, a whorl count mostly in the upper quartile, but also a lower quartile H/D ratio. These species have increased their whorl count in regular fashion, but with umbilical widening not followed by a change in growth vectors to produce either a brood chamber or a very high spire. The trends to sculpture reduction and loss or reduction of the apertural barriers are quite consistent and contrast with the pattern in the brood-chamber taxa, where sculpture reduction is much less frequent and the size reduction in the parietal barriers far less accentuated. The method of sculpture reduction also differs. In the *Nesodiscus* level this occurs first by multiplication of rib numbers and crowding, followed by their loss (except in *Planudonta*). In brood-chamber taxa rib loss occurs by gradual size reduction in the major ribs, rather than multiplication, then loss. In calculating the averages for the *Nesodiscus* level, I omitted the *Australdonta* and *Opanara* species listed above, since they agree only with part of the character complex. One additional genus requires comment. The very poorly known Mangarevan taxon *Rikitea* has the shape and growth pattern of the *Nesodiscus* specialization, but differs quite obviously in retaining a very large parietal barrier and prominent radial ribbing. The two *Australdonta* (fig. 137) come much closer to reaching "*Nesodiscus* status."

The brood-chamber taxa, *Libera, Gambiodonta, Pseudolibera, Endodonta marsupialis,* and *Taipidon semimarsupialis,* show a continued increase in whorl count, an H/D ratio in the upper quartile, and a lower diameter than the *Nesodiscus*-level taxa. These are functional requirements of this level, since secondary narrowing of the brood chamber necessitates shifting growth vectors to increase the shell height and lessen the diameter. Their retention of strong sculpture and prominent apertural barriers, in contrast to the *Nesodiscus* series, suggests that these represent parallel rather than sequential stages. While umbilical widening in the *Nesodiscus* pattern is a mandatory prelude to secondary narrowing and brood chamber formation, the derivation of *Nesodiscus* from a species very similar to *Mautodontha boraborensis* is discussed below (p. 345) and the derivation of *Libera* from the subgenus *Garrettoconcha* (p. 165) hints at the contrasting patterns. Whether the sculpture reduction, barrier reduction and continued umbilical widening of the *Nesodiscus* are genetically linked in a formal sense or became linked in a channeled development pattern is unknown. It is probable, however, that no *Nesodiscus*-level taxon would alter its pattern to shift into the U-shaped and then narrowed umbilicus seen in brood-chamber taxa. In contrast, the tendency of many *Mautodontha*-level taxa to form U-shaped umbilici while retaining heavy sculpture and prominent barriers suggests that there is more than chance to these divergent patterns.

Most detailed discussion of phylogeny in the systematic review is based on geographic lineages, since the patterns in variation of the apertural barriers and anatomy that are not size correlated clearly link together the taxa from each island group. For example, in the Hawaiian genera there are the common patterns of bifidity in the barriers, shift in radular tooth shape, and standard penis structure; the Mangarevan taxa have a characteristic tooth structure that encompasses all material except the peculiar *Rikitea;* the Marquesan genera have the altered penis structure; and the *Thaumatodon-Aaadonta* complex has not only the altered penis but also the very striking change in barrier expanded surfaces. The convergences in the shell size, shape, and sculpture that mostly correlate with size factors are extensive enough that they swamp the few factors used to establish phyletic affinity if all are tossed into a phenetic program.

During the middle portion of this study, I was able to have data on the shell variables put through both the "minimum steps" and Sharrock-Felsenstein "combinatorial" programs for computing phylogenies. Forty-seven meristic or structural features were coded and directional changes from the postulated "generalized" condition indicated. The computer programs available for use at that time required data on every species for each character used, which effectively eliminated using any anatomical data, and could handle only 25 taxa at a time. The characters used were the shell features discussed above (pp. 19-72). The only difference was that my analysis of the ways in which the same state could be achieved independently had not been carried nearly as far, nor were character correlations as fully understood. As would be expected, the programs separated out highly differentiated taxa, such as distinguishing between *Thaumatodon, Aaa-*

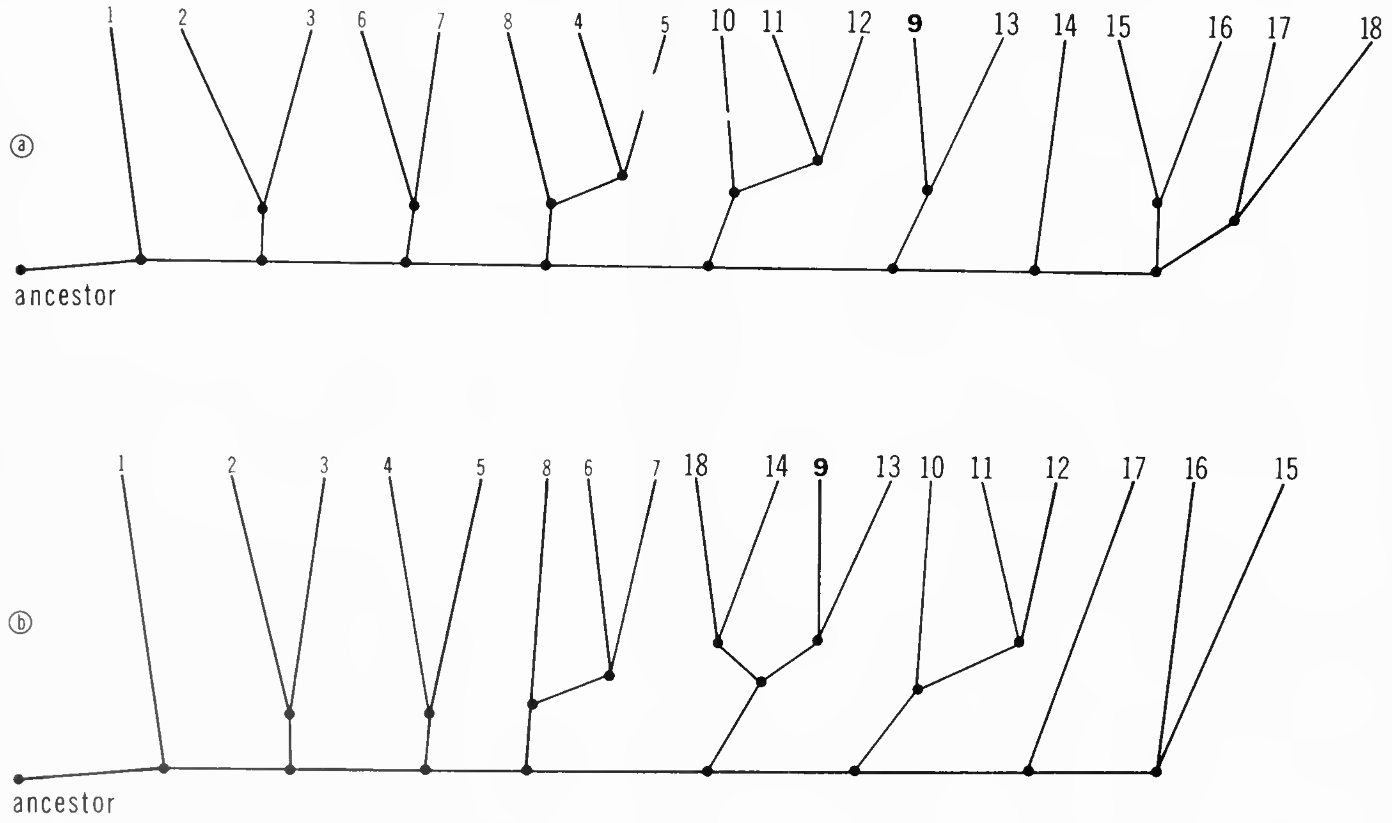

FIG. 59. Computer generated phylogeny, "combinatorial" method, of *Thaumatodon, Zyzzyxdonta,* and *Aaadonta.* Derivation from left to right in sequence. Extant species are: 1) *Thaumatodon multilamellata;* 2) *T. decemplicata;* 3) *T. laddi;* 4) *T. subdaedalea;* 5) *T. corrugata;* 6) *T. hystricelloides;* 7) *T. vavauensis;* 8) *T. euaensis;* 9) *Zyzzyxdonta alata;* 10) *Aaadonta pelewana;* 11) *A. f. fuscozonata;* 12) *A. f. depressa;* 13) *A. kinlochi;* 14) *A. irregularis;* 15) *A. c. komakanensis;* 16) *A. c. babelthuapi;* 17) *A. c. constricta;* 18) *A. angaurana.* Small numbers are *Thaumatodon;* large numbers *Aaadonta;* bold face *Zyzzyxdonta. a* and *b* represent different computer runs.

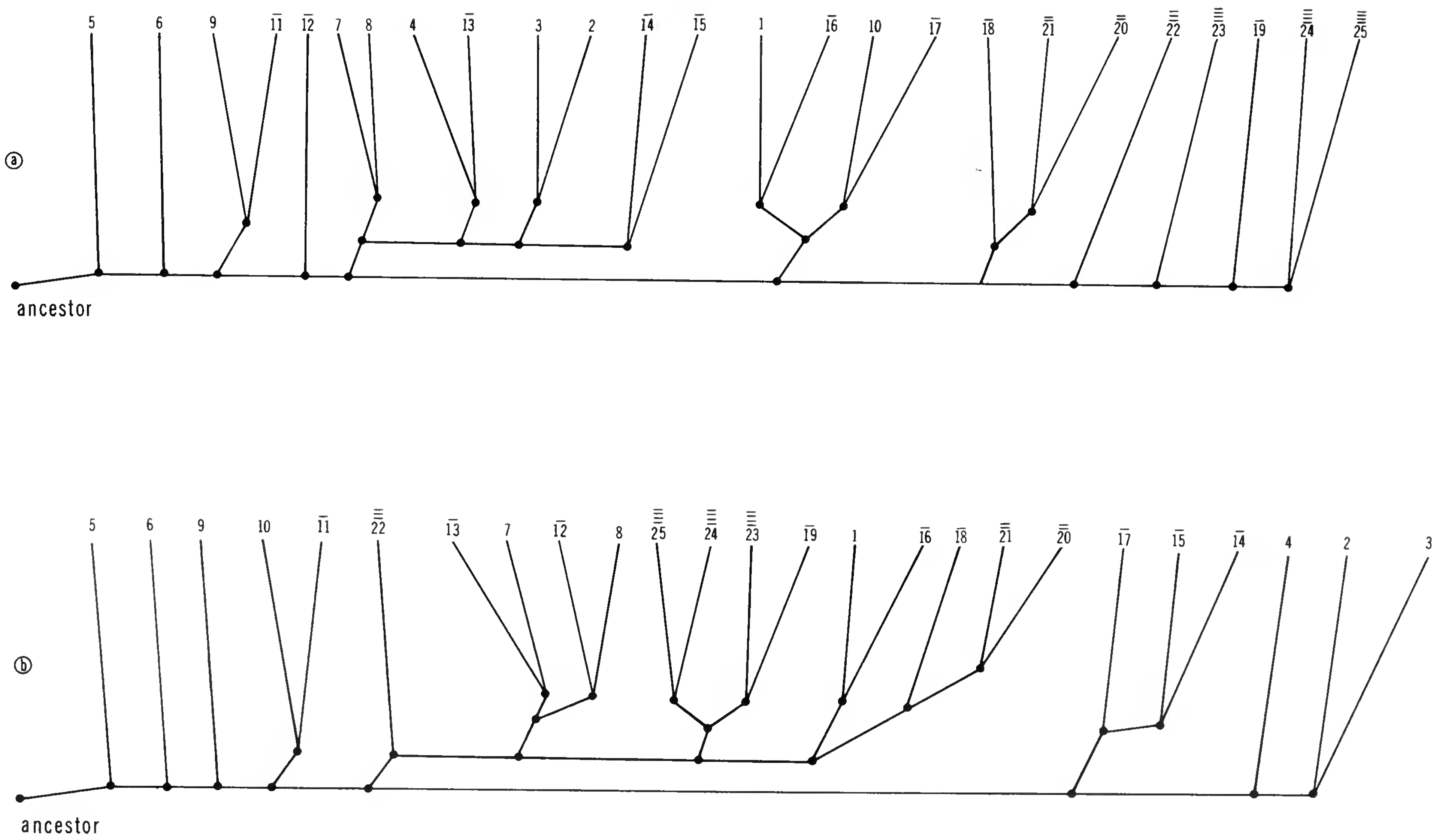

FIG. 60. Computer generated phylogeny, "combinatorial" method, of *Taipidon* and generalized Rapan taxa. Derivation from left to right in sequence. Extant species are: 1) *Taipidon petricola;* 2) *T. woapoensis;* 3) *T. analogica;* 4) *T. marquesana;* 5) *T. octolamellata;* 6) *T. anceyana;* 7) *T. semimarsupialis;* 8) *T. centadentata;* 9) *T. varidentata;* 10) *T. fragila;* 11) *Opanara depasoapicata;* 12) *O. megomphala;* 13) *O. duplicidentata;* 14) *O. areaensis;* 15) *O. a. densa;* 16) *O. caliculata* and *O. altiapica* averaged; 17) *O. bitridentata;* 18) *O. fosbergi;* 19) *O. perahuensis;* 20) *Rhysoconcha atanuiensis;* 21) *R. variumbilicuta; 22) Kondoconcha othnius;* 23) *Orangia cookei;* 24) *Orangia sporadica;* 25) *Orangia maituatensis.* No bar over number is *Taipidon;* one bar is *Opanara;* two bars, *Rhysoconcha;* three bars, *Kondoconcha;* four bars *Orangia.* **a** and **b** represent different computer runs.

donta, and *Zyzzyxdonta* (fig. 59), but when presented with somewhat similar taxa from different islands, such as *Orangia, Opanara,* and *Rhysoconcha* from Rapa, plus *Taipidon* from the Marquesas (fig. 60), or *Minidonta, Mautodontha,* and *Cookeconcha subpacificus* (fig. 61), the results were less satisfactory.

The differentiated taxa run (fig. 59) had *Zyzzyxdonta* (species 9) from Fiji associated with *Aaadonta kinlochi* (species 13) from Palau. Both species are low-spired, carinated, and show quite different proportions from typical members of either genus. Different computer runs (fig. 59a, b) give different results. *A. angaurana* (species 18) could be associated with either *A. c. constricta* (species 17 in fig. 59a) or *A. irregularis* (species 14 in fig. 59b). Both runs mixed up the *Thaumatodon* geographically, grouping Fiji (3) and Ellice (2), Samoa (6) and Tonga (7) in Figure 59a, and partly in Figure 59b. Both runs segregated the races of *Aaadonta constricta* and recognized *A. pelewana* and *A. fuscozonata* as a monophyletic assemblage.

The *Taipidon* and generalized Rapa Island taxa (fig. 60a, b) included only situations where the genera are very well differentiated by anatomical criteria. The shells show a wide variety of convergences. In the absence of anatomical data it would be unreasonable to expect that the computer would avoid confusing convergence with phyletic affinity. It did not. Linking *Opanara megomphala* (species 12) with *Taipidon centadentata* (species 8 in fig. 60b) is quite logical on overall appearance, provided no anatomical data is available.

The extensive mixing of geographic and generic groups in the *Minidonta-Mautodontha* run (fig. 61) requires no commentary. What is intriguing in this phylogeny is the placement of *Cookeconcha subpacificus* (species 1) in basal position, the grouping of *Kleokyphus* (species 24, 25) as highly specialized taxa, and the two peculiar Aitutaki species (13, 23) as highly derived taxa sharing many similarities.

Shell data alone, particularly when convergent variations are not carefully screened out, are quite inadequate to permit obtaining "good phylogenies" in the Endodontidae by computer analysis. The fault lies not with the computer, but with the subtle and repetitive nature of the variations. The island distributions were an incalculably great aid to this study. If a continental pattern had been involved, I doubt very much that I would have been able to recognize patterns so clearly. The results of both the conventional and computer studies do emphasize the need to understand the functional significance of character variation and to weight the variations accordingly. The computer is an invaluable tool in sorting taxa, suggesting possible relationships, emphasizing convergences, and forcing one to examine and analyze far more data than previously. But it is no substitute for the more conventional approaches used here.

The above discussion completes the tentative review of endodontid phylogeny. As a final and totally subjective comment, there are geographical "styles" of variation. While the Mangarevan and Society Islands differentiations into more specialized levels are "mature" in character, the Marquesan experiments into brood chamber and *Nesodiscus* level seem tentative and "juvenile." The end results were achieved in *Taipidon semimarsupialis* and *Planudonta,* respectively, but in far less polished ways than is shown by the other groups. The Hawaiian taxa show almost an exuberant pattern of minor experimentations, which is equalled by *Thaumatodon* and its derivatives in the Lau Archipelago of Fiji. In contrast, the divergence of *Aaadonta* in Palau shows only minor variations on a theme, while on Rapa there has been variation more in anatomy than shell structure. Quite possibly this is a function of island age and time of colonization, but such zoogeographic topics are deferred.

FOSSIL ENDODONTOID LAND SNAILS

In favorable circumstances, fossils can yield data that are crucial to interpreting phylogeny and estimating rates of evolution. Unfortunately, the fossil endodontoid land snails (Ladd, 1958, 1968; Ladd et al., 1967, 1970) add details rather than providing major input. At present there are six taxa known, two charopids, *"Ptychodon" eniwetokensis* Ladd (1958) and *"P." davidi* Ladd (1968), two endodontids that are reviewed below (*Minidonta inexpectans,* p. 132, and *Cookeconcha subpacificus,* p. 212), and two undescribed species from the core drillings on Midway.

These range in age from Lower Miocene to Late Pleistocene or Recent. They are discussed in order of decreasing age. The oldest species, *Cookeconcha subpacificus* from the Lower Miocene of Bikini Atoll at 1,807-1,818 ft. is based on a fragmentary specimen that agrees most closely with the *Cookeconcha henshawi* group (p. 213). None of the preserved features on this shell are inconsistent with extending *Cookeconcha* back to the Lower Miocene and from the present Hawaiian range to include the Marshall Islands. *"Ptychodon" eniwetokensis,* from the Upper Miocene of Eniwetok at 820-831 ft., also is based on a fragmentary example, but the available features place it in a relatively advanced genus (undescribed) of the Charopidae. The Eniwetok fossil agrees more with extant congeneric taxa from Niue and Vaitupu in the Ellice Islands than with the species from Fiji and Tonga. The latter are more specialized in structure. The three more generalized taxa thus form a rough fringing pattern of distribution within the genus. The range extension from Vaitupu to Eniwetok is not very significant in terms of geography, although placing the fringe distribution in an Upper Miocene context has some importance. The Pliocene to Pleistocene *Minidonta inexpectans* from Bikini at the 447-453 ft. level is very close to the recent Samoan *Minidonta manuaensis* (pp. 130-132). Together with *Minidonta*

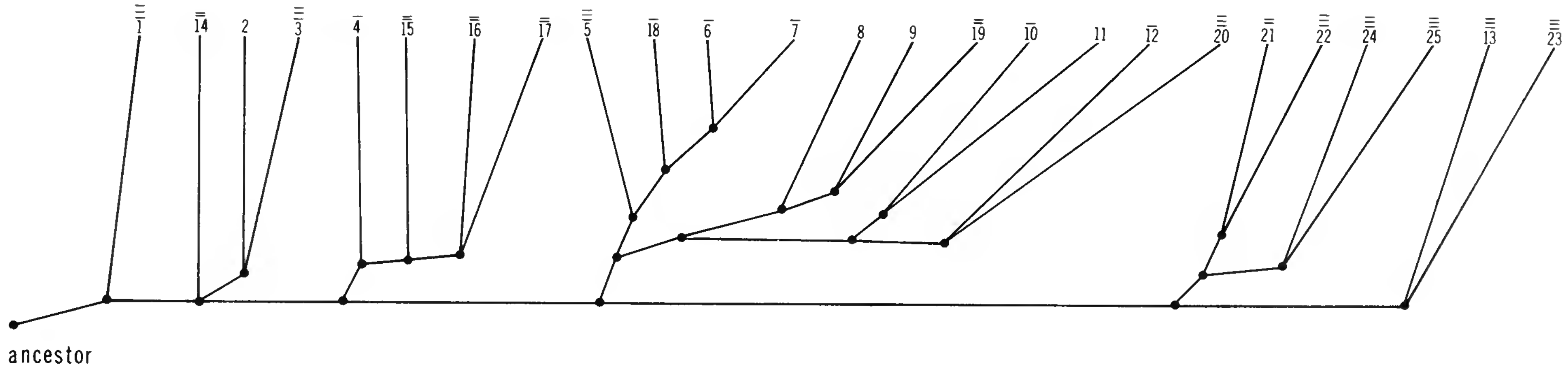

FIG. 61. Computer generated phylogeny, "combinatorial" method, of *Minidonta, Mautodontha, Kleokyphus,* and *Cookeconcha subpacificus.* Derivation from left to right in sequence. Extant species are: 1) *Cookeconcha subpacificus;* 2) *Minidonta micra;* 3) *M. hendersoni;* 4) *M. micraconica* and *M. gravacosta* averaged; 5) *M. manuaensis* and *M. inexpectans* averaged; 6) *M. sulcata;* 7) *M. haplaenopla;* 8) *M. taunensis* and *M. taravensis* averaged; 9) *M. extraria;* 10) *M. anatonuana;* 11) *M. simulata;* 12) *M. planulata;* 13) *M. rotellina;* 14) *Mautodontha aoraiensis;* 15) *M. consimilis;* 16) *M. zimmermani;* 17) *M. zebrina;* 18) *M. ceuthma;* 19) *M. punctiperforata;* 20) *M. rarotongensis;* 21) *M. boraborensis;* 22) *M. daedalea;* 23) *M. imperforata;* 24) *Kleokyphus callimus;* 25) *K. hypsus.* Numbers are coded geographically: no bar is Mangareva; one bar is Austral Islands; two bars, Society Islands; three bars other areas.

micra from Mangareva and *M. hendersoni* from Henderson Island, they form the most generalized group of *Minidonta* and also show a fringing distribution pattern to the other *Minidonta.* The range extension of *Minidonta* from its current western limits of American Samoa to Bikini is a major geographic extension. Several specimens of this species were available and the concurrence with *M. manuaensis* is very strong.

The two morphotypes from Midway Atoll, found in the upper levels of both cores, are Pleistocene in age (Ladd et al., 1970, p. A16). One specimen is clearly a *Cookeconcha* and eight specimens belong to a distinct genus that is intermediate between the characters of *Cookeconcha* and *Endodonta.* The above comments are based on personal examination of this material. The existence of a varied endodontid fauna on Midway when it was an elevated island is not unexpected. The probability that one form is generically distinct should not be given any great importance, since the generic limits used for Hawaiian species in this report are not intended to be definitive. Undescribed species of endodontids from the other Hawaiian Islands also show intermediate conditions between *Endodonta* and *Cookeconcha.*

"Ptychodon" davidi (Ladd, 1968) belongs to a charopid genus (undescribed) that is represented by two species from Fiji, two from the Bismarcks, and a single species that has been found in West Irian, Misool, Biak, Aru Islands, Timor, and Ambon. The Funafuti Atoll Pleistocene to Recent fossil, from the 166-170 ft. level, is only very weakly differentiated from one of the extant Fijian species.

The fossils thus take extant generalized and specialized genera back to the Miocene, demonstrate the presence of endodontids and charopids in the Marshall Islands when they were high islands, and suggest that the range of both *Minidonta* and *Cookeconcha* have shrunk because of extinction as the former high islands of the Marshall chain became low atolls. Evidence that Bikini and Eniwetok formerly were high islands with upland forest is presented by Leopold (1969). More detailed consideration of the distributional and historical data is deferred until the second monograph.

PREVIOUS GENERIC CLASSIFICATIONS

The general similarity in shells of the endodontoid taxa, based on their prominent radial ribbing, often flammulated color pattern, and simple helicoid form led most early authors to group known forms into almost a Linnean genus (see *Eyryomphala* in Beck, 1837, pp. 8-9). Albers (1850, pp. 64-65, 89) grouped most species under *Patula,* although describing *Endodonta,* while H. Adams and A. Adams (1854-1858, pp. 113-114) placed the Holarctic species in *Discus* and the various Pacific Basin taxa into *Pitys* (which is now restricted to an endemic Rapan tornatellinid, see Cooke and Kondo, 1960). The second edition of Albers (1860, pp. 59-63, 82, 85-91, 100), edited by von Martens, established most of the classic divisions. *Amphidoxa* and *Stephanoda* were proposed for the Juan Fernandez and South American species; *Charopa* and *Thalassia* for New Zealand and Australian species; *Endodonta* continued to be used for the Pacific Island species with apertural barriers; while *Patula* and *Discus* were grouped with *Trochomorpha* as barrierless taxa.

The first catalogue of Pacific Island land snails (Pease, 1871a, pp. 474-475) used *Endodonta* for large, carinated species with apertural barriers, and *Pitys* for small species, with and without barriers. This was a period of great descriptive activity in terms of species (table III), but great conservatism in terms of generic units. Garrett (1881) proposed *Libera* for brood-chamber taxa, used *Patula* for taxa with only one barrier or no barriers, and later (Garrett, 1884) used a heirarchy based on barriers and shell shape. His system was:

Barriers in aperture
  Periphery carinated — *Endodonta*
  Periphery rounded — *Pitys*
  Umbilical brood chamber — *Libera*
No barriers in aperture — *Patula*

Tryon (1887, pp. 59-72) used *Endodonta* and *Libera* as "sections" of his broadly defined genus *Helix.*

Pilsbry (1893-1895, pp. 6-54) summarized the endodontoids in a critical checklist, recognizing as full genera in the Endodontidae *Punctum, Laoma, Flammulina, Endodonta, Phasis, Amphidoxa, Pyramidula,* and *Pararhytida.* All of the Pacific Island taxa were distributed among various subgenera and sections of *Endodonta.* This was a compilation needed to complete his checklist and revision of the helicoid taxa, but included virtually no original observations. His rationale for division of *Endodonta,* ignoring those taxa erroneously included, was:

Barriers in aperture
  Umbilical brood chamber — Subgenus *Libera*
  No umbilical brood chamber
    St. Helena Island — Section *Helenoconcha* Pilsbry, 1892
    New Zealand — Polynesia
      Periphery keeled — Section *Endodonta*
      Periphery rounded
        Palatal wall without barriers — Section *Nesophila* Pilsbry, 1893
        Palatal wall with barriers
          New Zealand — Section *Ptychodon* Ancey, 1889
          Polynesia — Section *Thaumatodon* Pilsbry, 1893
No barriers in aperture — Subgenus *Charopa* and various New Zealand taxa

Pilsbry (1893-1895, p. 21) recognized the pattern of tooth loss, but commented "The distinction between *Charopa* and *Endodonta* is of little value, on account of the degeneration of the teeth (=barriers) in some forms of the latter, producing species which technically fall under the former group." Except for nomenclatural changes, his system was only an extension of that proposed by Garrett (1884), although Pilsbry did recognize higher level dichotomies (pp. 105-106). This is one of the very few examples where Pilsbry summarized a group without making fundamental modifications in the classifications.

Subsequently, Thiele (1931, pp. 569-575) recognized 25 genera in the Subfamily Endodontinae. I retain parts of only four genera in the restricted Endodontidae. Most others belong to the Charopidae. *Ptychodon* was used by Thiele for taxa with a rounded periphery and barriers (including *Nesophila* and *Thaumatodon* as sections), *Endodonta* for carinated shells with apertural barriers from the Hawaiian Islands, and *Libera* (under a substitute name *Garrettina*) for brood-chamber taxa. He proposed a new genus, *Nesodiscus,* for *N. fabrefactus* (Pease, 1864), the only completely barrier-free endodontid, which also is very unusual in its shape, has an extremely wide umbilicus, and a total lack of shell sculpture. Zilch (1959-1960, pp. 211-216) essentially copied Thiele's classification.

Up to now, the classification scheme consisted of using the barrier and periphery pigeonholes proposed by Garrett (1881, 1884). In the absence of anatomical data and critical analysis of the shell structures, no meaningful alternative option was available. It does mean that only five generic names are available for use. In order of priority they are: *Endodonta* Albers (1850), *Libera* Garrett (1881), *Thaumatodon* Pilsbry (1893), *Nesophila* Pilsbry (1893), and *Nesodiscus* Thiele (1931).

PROPOSED GENERIC CLASSIFICATION

Most classifications are a compromise between user utility, making identification simpler, and an attempt to express the postulated lines of phylogeny. Given the same phylogenetic scheme, particularly if it is at all complex, equally competent systematists will derive slightly to grossly different schemes of classification. The question is partly whether to recognize broadly drawn or narrowly defined genera. Any classification usually is influenced by the inherent conservatism of systematists. If a genus has been proposed and used for a period of time, there is great inertia against making a change in its status. Because of the few available names and obvious artificiality of the extant classification, this problem did not exist for the Endodontidae and Pacific Island Charopidae. Mostly the problem is that classifications present neat dichotomies, while evolution is messy.

A major concern has been to try and establish comparability of generic units, to make "generic level differentiation" represent a roughly equivalent degree of change throughout the family. This is, of course, virtually impossible to attain, since there will be differences in the phylogenetic and morphologic gaps between species clusters. As in distinguishing species, it is possible to establish minimum distance, but it was not feasible to establish a set of mathematical criteria to delimit a range of difference levels between species clusters. In some cases data were lacking. In reviewing the Hawaiian fauna, I deliberately used far broader generic units than elsewhere in this monograph, simply because the Hawaiian fauna was surveyed cursively, although material for a critical revision is available in the Bishop Museum. Refinement of the Hawaiian endodontid classification and phylogeny is left to others.

My actual criteria have depended on the clusters concerned. They also involve the degree of morphologic gap between clusters as they relate to the four levels of specialization and/or anatomical changes. In many situations clear phylogenetic gaps exist, but there are situations in which a virtually continuous series exists between end points that show "generic level differences" (*Minidonta* and *Anceyodonta*). In other situations, a single species might have specializations of a different level of organization, but retains so many features common to the stem complex that retention within that genus seems preferable. In a real sense, the classification proposed is thus a continuous series of compromises between phyletic lines, degree of morphologic gaps, overall similarity, importance assigned to structural differences within each unit, and, perhaps most important, what I consider to be the current evolutionary stages and potentials of the species clusters.

A few examples will serve to illustrate the way in which these criteria were applied. The brood-chamber taxa *Libera, Gambiodonta,* and *Pseudolibera* show major size and structural differences from taxa that apparently are ancestral. No confusion of these derived genera with *Mautodontha, Minidonta,* and *Mautodontha* or *Kleokyphus,* respectively, is possible. The former show a clearly defined and substantial "degree of difference." In the Society Islands, *Mautodontha boraborensis* (Garrett, 1884) shows the trends needed to advance from *Mautodontha* into *Nesodiscus,* but (p. 153) retains enough *Mautodontha* characteristics to fit more comfortably into that genus. Logically it could be classified in either. On the Marquesan Islands, *Taipidon* and *Planudonta* share anatomical features that are not found elsewhere in the family (p. 315). They obviously shared common ancestry, with *Planudonta* being derivable from *Taipidon* by undergoing "*Nesodiscus* specializations." The increased whorl count, widened umbilicus, and dramatically reduced size of the apertural barriers in *Planudonta* when compared with *Taipidon* are typical "*Nesodiscus* specializations." They result in a wide enough "morphologic gap" to warrant generic separation, even though there is no sculpture reduction. In contrast, *Taipidon semimarsupialis* has achieved brood-chamber formation in a rather crude way (in terms of complexity of morphological changes). In virtually every character except whorl number and a very inelegant secondary umbilical narrowing, *T. semimarsupialis* is a *Taipidon*.

The Rapan taxa illustrate classification problems within a specialization level. *Rhysoconcha* differs in its secondary size reduction; *Ruatara* shows a major change in penial structure, whorl count, and growth pattern; *Kondoconcha* differs in several features from the basic *Opanara* pattern; and *Orangia* shows more conchological than anatomical changes. The average pattern within each genus is clearly different from that found within the others, and there is very little evidence of intergradation. The differences between these genera are of the same order of magnitude as are those between *Australdonta, Mautodontha, Taipidon, Kleokyphus,* and *Anceyodonta,* other genera at the *Mautodontha* level of specialization.

Cookeconcha and *Minidonta* approach each other rather closely, although retaining patterns of difference, but *Minidonta* and *Anceyodonta* blend almost insensibly on Mangareva. While typical *Anceyodonta* is a quite well characterized genus on the *Mautodontha* level, the fusion between the less specialized species and *Minidonta* only shows that evolution was in progress. Description of *Anceyodonta* and making an arbitrary (p. 179) dividing line between it and *Minidonta* focuses on the advanced *Anceyodonta* far more effectively than would inclusion of all species in *Minidonta* or the use of subgenus.

Division of the *Thaumatodon* complex into genera, by contrast, presented few problems. *Thaumatodon* has the most typically endodontid shell structure, although the *T. hystricelloides* complex shows significant variations. *Aaadonta* differs in penial pilaster pattern, but most strikingly in shell-sculpture reduction and shell shape. *Priceconcha* is modified in habitat (tree trunk), shell form (*Nesodiscus* pattern), and sculpture, while *Zyzzyxdonta* has major shape and sculpture alterations. The differences are more obvious, but perhaps no more significant than are those seen in the Rapan radiation.

TABLE LXII. - FREQUENCY DISTRIBUTION OF SPECIES/GENUS IN PACIFIC ISLAND ENDODONTOIDS

Species level taxa in genus	Number of genera in: Endodontidae	Punctidae and Charopidae
1	5	10
2	2	4
3-5	4	4
6-9	4	2
10-15	6	-
16-19	3	-
over 50	-	1
Total species level taxa in family	185	98

Such differences in "phyletic distance" are inevitable when a two-dimensional static system attempts to circumscribe evolutionary progress at a single time moment. The attempt to make generic units comparable through establishing a minimum phyletic distance as warranting generic recognition, leaves the maximal phyletic distance unspecified and totally ignores the question of how many species are in each genus. For the Pacific Island taxa, the number of species per genus frequency is tallied in Table LXII. The high number of monotypic genera in the Charopidae and presence of a single highly speciose genus in that family contrasts with a more even distribution in the Endodontidae. This reflects different patterns of evolution in the two families and will be considered in the zoogeographic portion of the second monograph.

SYSTEMATIC REVIEW

FAMILY ENDODONTIDAE

Small to large endodontoids at least primitively with prominent radial sculpture on both apex and lower whorls, sculpture often becoming reduced or lost in larger species. Microsculpture of radial riblets and primitively of microspiral "squiggly" cords that are lower than the microradials, with most sculpture formed by calcareous layers under a periostracal template, except for periostracal setae and rib peak extensions. Whorls in adults 3½-9, coiled with varying degrees of spiral protrusion or depression, umbilicus generally widely open, regularly decoiling and used as an egg deposition site. In many taxa whorl count increased and umbilical cavity secondarily narrowed to form a nearly enclosed brood chamber for the eggs. Color generally flammulated with alternating irregular reddish and yellow brown markings. Aperture of shell primitively with high and complex barriers on all walls, posterior elevated portions of barriers expanded and capped with triangular microdenticulations that point toward the apertural opening. Barriers reduced in many taxa, absent only in one. Foot of animal undivided, prominent pedal and suprapedal grooves present that unite above tail, but without caudal horn or enlarged mucus pore. Radula with tricuspid central, primitively 5 to 6 bicuspid laterals, and 8-14 short, broad marginals usually with split ectocones, tooth numbers increased in a few taxa. Rest of digestive tract without unusual features. Pallial complex with kidney reaching hindgut and having a weak rectal lobe, primary ureter well developed and slightly reflexed at posterior, but opening directly into pallial cavity without trace of groove or channel to pneumostome. Mantle collar without lobes or shell laps. Genitalia with following diagnostic features: ovotestis with multiple palmately clavate clumps angled to shell axis; hermaphroditic duct normally without coiling; talon with elongately oval head on a variable lengthened shaft; prostate and uterus completely separate tubes, alveoli of prostate large and thick, usually arranged in rows opening into duct; vas deferens normally opening through a simple pore subapically on penis, in one lineage with altered opening into a penial epiphallus; penis primitively with two longitudinal pilasters, variously modified under conditions of sympatry and with minor added structures in some lineages, but never with a verge or vergic papilla; free oviduct a simple tube that may or may not unite with spermathecal shaft before atrium; spermatheca with ovate head lying above pallial cavity apex, shaft inserting onto free oviduct, atrium, or base of penis; penial retractor muscle originating from columellar retractor or diaphragm, inserting variously on penis head or side; penis enervated from right cerebral ganglion.

Of the genera that have been dissected, the compact group of *Thaumatodon, Aaadonta, Priceconcha,* and *Zyzzyxdonta* is the most distinctive. The degree of difference, however, is not great enough to warrant subfamily recognition, or possibly even "tribal" or any equivalent intermediate status. Since the subfamily divisions in the Charopidae still remain undefined, I defer assigning any formal rank to this group of genera. I simply wish to emphasize again that they are the most strongly differentiated endodontid taxa in terms of phyletic position.

The order in which genera are discussed in any monograph must be an unsatisfactory compromise between goals of phyletic order, structural similarity, user convenience, and faunistic unity. The sequence adopted here arbitrarily places the specialized *Thaumatodon-Aaadonta* complex last, while ordering the remaining genera roughly as to their level of specialization. Since some genera span two levels, this introduces immediate distortion. Geographic and phyletic unity has been partly sacrificed for clustering morphologically similar taxa together. The first five genera include the basic *Minidonta* and *Cookeconcha,* plus three relatively generalized derivatives from *Minidonta*—the Mangarevan *Anceyodonta,* the basically Cook and Society Island *Mautodontha,* and the Makatea Island endemic *Kleokyphus.* Since *Cookeconcha* contains many altered species, it and the relatively specialized *Kleokyphus* are placed after the others. The monophyletic Rapan radiation—*Opanara, Rhysoconcha, Ruatara, Orangia,* and *Kondoconcha*—follow, except for the latter which is grouped with the conchologically similar *Endodonta* for ease in comparison. *Australdonta* and *Taipidon* are equivalent derivatives and somewhat similar to *Orangia.* Hence these three genera are clustered together.

Planudonta is a local derivative of *Taipidon,* and together with *Rikitea, Nesodiscus,* and *Nesophila,* form a distinctive level of specialization. *Kondoconcha* and *Endodonta* are pre-"brood chamber" specializations, and thus precede *Pseudolibera, Libera,* and *Gambiodonta.*

Thaumatodon, Priceconcha, and *Zyzzyxdonta,* which form a monophyletic series from Polynesia and its western fringes, precede *Aaadonta,* the only Micronesian endodontid group.

The function of keys is to facilitate identifications. Because of extensive convergence in shell features, and the probable future unavailability of preserved soft parts, any phyletic key would be unusable. Any artificial key to genera would involve so many multiple entries as to be unwieldy. As a functional compromise, keys are presented only to genera from limited geographic areas. Since the shells will continue to be confused, these keys include couplets sorting out charopid taxa from the endodontids where applicable.

Keys to the charopid genera and species must be deferred until the second monograph, however, since virtually all of the generic names are new.

Under each species, the following format has been adopted. First, a diagnosis summarizes the observed range of variation in high-information shell features for all material studied. This is followed by a short paragraph of comparative remarks that summarizes "key character" differences from those taxa with which it is most likely to be confused. A description of the nomenclatural type specimen follows, which includes the only data presented on color patterns. Information on the holotype location, geographic range, paratypes, and list of material studied precedes a usually short discussion on local variation or morphological deviants observed within that species or subspecies. When available, description of anatomical features completes the treatment of the species.

Presentation of both a diagnosis and a description is done with reluctance, but out of necessity. Particularly for taxa from areas such as the Palau, Society, Austral, Gambier, and Marquesan Islands, the species limits presented here often include populations showing noticeable differences. While currently limited material has led me to propose including them under a single name, I will not be in the least surprised if a number of these prove to be compound taxa. Too much detailed work in the last few decades has revealed the complexity of island speciation patterns and the narrowness of morphological differences for me to think otherwise. A "lumper" by both philosophy and training, I have preferred to err on making species limits too broad rather than to subdivide on incomplete evidence. But this does impose on me an obligation to establish unequivocally what is intended as the name-bearing part of the morphologic range. The designation of specified stations does this in part, but both the illustration (usually) of the "holotype" and presentation of a type description will greatly simplify future work.

Illustrations usually include only a side and bottom view of the shell (since the coiling pattern varies only slightly), sometimes a detailed view of the aperture, and whatever part of the soft anatomy could be depicted. In a few cases, unusual shell variants are illustrated. For most Hawaiian taxa no shells have been depicted. Through use of the keys and illustrations species can be identified readily, but usually averaged measurements will be needed.

Discussion of variational trends within genera and relationships between species have been combined at the beginning of each genus to save space and avoid repetition.

LIST OF THE TAXA

Genus *Minidonta*, new genus

Minidonta manuaensis, new species — American Samoa: Manua Group, Olosega and Ta'u
Minidonta inexpectans (Ladd, 1958) — Marshall Islands: Bikini (fossil)
Minidonta micra, new species (Solem & Cooke) — Gambier Islands: Mangareva
Minidonta hendersoni, new species (Cooke & Solem) — Henderson Island
Minidonta micraconica, new species — Austral Islands: Raivavae
Minidonta gravacosta, new species — Austral Islands: Raivavae
Minidonta rotellina (Pease, 1870) — Cook Islands: Aitutaki
Minidonta anatonuana, new species — Austral Islands: Raivavae
Minidonta sulcata, new species — Austral Islands: Raivavae
Minidonta haplaenopla, new species — Austral Islands: Rurutu
Minidonta planulata, new species — Austral Islands: Raivavae
Minidonta taunensis, new species — Gambier Islands: Mangareva
Minidonta taravensis, new species (Solem & Cooke) — Gambier Islands: Mangareva
Minidonta simulata, new species (Solem & Cooke) — Gambier Islands: Mangareva
Minidonta extraria, new species (Cooke & Solem) — Gambier Islands: Mangareva

Genus *Mautodontha*, new genus

Mautodontha (*M.*) *boraborensis* (Garrett, 1884) — Society Islands: Borabora, 800-900 ft. elevation
Mautodontha (*M.*) *daedalea* (Gould, 1846) — Tuamotu Islands: Makatea, Anaa and Niau
Mautodontha (*M.*) *ceuthma*, new species — Austral Islands: Raivavae, Mt. Taraia
Mautodontha (*M.*) *zimmermani*, new species — Society Islands: Tahiti, Mt. Aorai, 3,500-6,300 ft. elevation
Mautodontha (*M.*) *zebrina* (Garrett, 1874) — Cook Islands: Rarotonga
Mautodontha (*M.*) *aoraiensis*, new species — Society Islands: Tahiti, Mt. Aorai, 4,700-5,500 ft. elevation
Mautodontha (*Garrettoconcha*) *consobrina* (Garrett, 1884) — Society Islands: Huahine
Mautodontha (*Garrettoconcha*) *saintjohni*, new species — Society Islands: Borabora, 800 ft. elevation
Mautodontha (*Garrettoconcha*) *maupiensis* (Garrett, 1872) — Society Islands: Maupiti
Mautodontha (*Garrettoconcha*) *punctiperforata* (Garrett, 1884) — Society Islands: Moorea
Mautodontha (*Garrettoconcha*) *imperforata* (Pease, 1870) — Cook Islands: Aitutaki
Mautodontha (*Garrettoconcha*) *parvidens* (Pease, 1861) — Society Islands: Tahiti, Moorea, and Huahine
Mautodontha (*Garrettoconcha*) *subtilis* (Garrett, 1884) — Society Islands: Huahine
Mautodontha (*Garrettoconcha*) *rarotongensis* (Pease, 1870) — Cook Islands: Atiu
Mautodontha (*Garrettoconcha*) *consimilis* (Pease, 1868) — Society Islands: Raiatea
Mautodontha (*Garrettoconcha*) *acuticosta* (Garrett, 1884) — Society Islands: Raiatea
Mautodontha (*Garrettoconcha*) *unilamellata* (Garrett, 1874) — Cook Islands: Rarotonga

Genus *Anceyodonta*, new genus

Anceyodonta ganhutuensis, new species (Cooke & Solem) — Gambier Islands: Mangareva
Anceyodonta subconica, new species (Solem & Cooke) — Gambier Islands: Mangareva
Anceyodonta constricta, new species (Cooke & Solem) — Gambier Islands: Mangareva
Anceyodonta andersoni, new species (Cooke & Solem) — Gambier Islands: Mangareva
Anceyodonta alternata, new species (Cooke & Solem) — Gambier Islands: Mangareva
Anceyodonta difficilis, new species — Gambier Islands: Mangareva
Anceyodonta soror, new species — Gambier Islands: Mangareva
Anceyodonta sexlamellata (Pfeiffer, 1845) — Gambier Islands: Mangareva

Anceyodonta densicostata, new species (Cooke & Solem) – Gambier Islands: Mangareva
Anceyodonta obesa, new species – Gambier Islands: Mangareva
Anceyodonta labiosa, new species – Gambier Islands: Mangareva
Anceyodonta hamyana (Ancey, 1889) – Gambier Islands: Mangareva

Genus *Cookeconcha,* new genus

Cookeconcha subpacificus (Ladd, 1958) – Marshall Islands: Bikini (fossil)
Cookeconcha henshawi (Ancey, 1904) – Hawaiian Islands: Hawaii, Hamakua slope of Mauna Kea
Cookeconcha cookei (Cockerell, 1933) – Hawaiian Islands: Oahu, Mt. Tantalus
Cookeconcha thwingi (Ancey, 1904) – Hawaiian Islands: Hawaii, Kona coast
Cookeconcha nudus (Ancey, 1899) – Hawaiian Islands: Hawaii
Cookeconcha contortus (Ferussac, 1824) – Hawaiian Islands: Oahu, Waianae Mts.
Cookeconcha ringens (Sykes, 1896) – Hawaiian Islands: Lanai and Molokai
Cookeconcha elisae (Ancey, 1889) – Unknown, probably Hawaiian Islands
Cookeconcha luctiferus (Pilsbry & Vanatta, 1905) – Hawaiian Islands: Molokai
Cookeconcha hystricellus (Pfeiffer, 1859) – Hawaiian Islands: Oahu, Waianae Mts.
Cookeconcha stellulus (Gould, 1844) – Hawaiian Islands: Maui
Cookeconcha paucicostatus (Pease, 1870) – Hawaiian Islands: Kauai
Cookeconcha paucilamellatus (Ancey, 1904) – Hawaiian Islands: Hawaii
Cookeconcha thaanumi (Pilsbry & Vanatta, 1905) – Hawaiian Islands: Maui, Hawaii, and Molokai
Cookeconcha hystrix (Pfeiffer, 1846) – Hawaiian Islands: Oahu
Cookeconcha decussatulus (Pease, 1866) – Hawaiian Islands: Maui and Molokai
Cookeconcha lanaiensis (Sykes, 1896) – Hawaiian Islands: Lanai, Hawaii and Kauai
Cookeconcha jugosus (Mighels, 1845) – Hawaiian Islands: Kauai

Genus *Kleokyphus,* new genus

Kleokyphus callimus, new species – Tuamotu Islands: Makatea
Kleokyphus hypsus, new species – Tuamotu Islands: Makatea

Genus *Opanara,* new genus

Opanara depasoapicata, new species – Austral Islands: Rapa, Mt. Perahu at 1,200-1,500 ft. elevation
Opanara bitridentata, new species – Austral Islands: Rapa, Mt. Perahu at 1,500-1,850 ft. elevation
Opanara duplicidentata, new species – Austral Islands: Rapa, Mt. Perahu at 1,200-1,500 ft. elevation
Opanara areaensis areaensis, new species and subspecies – Austral Islands: Rapa
Opanara areaensis densa, new subspecies – Austral Islands: Rapa, 800 ft. elevation
Opanara areaensis microtorma, new subspecies – Austral Islands: Rapa, Mt. Perahu, 1,300-1,500 ft. elevation
Opanara caliculata, new species – Austral Islands: Rapa, Mt. Perahu, 1,800-1,900 ft. elevation
Opanara altiapica, new species – Austral Islands: Rapa, Mt. Mangaoa, 1,000-1,100 ft. elevation
Opanara megomphala megomphala, new species and subspecies – Austral Islands: Rapa, 800 ft. elevation, N. W. of Tautautu, Maitua, 500 ft. elevation
Opanara megomphala tepiahuensis, new subspecies – Austral Islands: Rapa, Mt. Tepiahu, 550 ft. elevation
Opanara fosbergi, new species – Austral Islands: Rapa, Mt. Perahu, 1,500-1,900 ft. elevation
Opanara perahuensis, new species – Austral Islands: Rapa, Mt. Perahu, 1,800-1,900 ft. elevation

Genus *Rhysoconcha,* new genus

Rhysoconcha variumbilicata, new species – Austral Islands: Rapa, Mt. Mangaoa, 800-900 ft. elevation
Rhysoconcha atanuiensis, new species – Austral Islands: Rapa

Genus *Ruatara,* new genus

Ruatara koarana, new species – Austral Islands: Rapa, Oromange, Mt. Koara, 800 ft. elevation
Ruatara oparica oparica (Anton, 1839) – Austral Islands: Rapa, Mt. Tanga
Ruatara oparica normalis, new subspecies – Austral Islands: Rapa
Ruatara oparica reductidenta, new subsqecies – Austral Islands: Rapa

Genus *Orangia,* new genus

Orangia cookei cookei, new species and subspecies – Austral Islands: Rapa
Orangia cookei montana, new subspecies – Austral Islands: Rapa, Mt. Perahu at 1,200-1,800 ft. elevation
Orangia cookei tautautuensis, new subspecies – Austral Islands: Rapa, Mt. Tautautu, 750 ft. elevation
Orangia maituatensis, new species – Austral Islands: Rapa
Orangia sporadica, new species – Austral Islands: Rapa

Genus *Australdonta,* new genus

Australdonta pseudplanulata, new species – Austral Islands: Rurutu
Australdonta rimatarana, new species – Austral Islands: Rimatara
Australdonta degagei (Garrett, 1879) – Cook Islands: Mauke. Austral Islands: Rurutu and Rimatara
Australdonta tapina, new species – Austral Islands: Rurutu
Australdonta yoshii, new species – Austral Islands: Rurutu
Australdonta magnasulcata, new species – Austral Islands: Rurutu
Australdonta radiella radiella (Pfeiffer, 1846) – Austral Islands: Tubuai
Australdonta radiella rurutuensis (Garrett, 1879) – Austral Islands: Rurutu
Australdonta raivavaeana, new species – Austral Islands: Raivavae
Australdonta tubuaiana, new species – Austral Islands: Tubuai
Australdonta pharcata, new species – Austral Islands: Tubuai
Australdonta ectopia, new species – Austral Islands: Raivavae

Genus *Taipidon,* new genus

Taipidon petricola petricola, new species and subspecies – Marquesas Islands: Hatutu
Taipidon petricola decora, new subspecies – Marquesas Islands: Eiao
Taipidon octolamellata (Garrett, 1887) – Marquesas Islands: Hivaoa
Taipidon uaapoensis (Garrett, 1887) – Marquesas Islands: Uapou
Taipidon marquesana (Garrett, 1887) – Marquesas Islands: Nukuhiva
Taipidon anceyana (Garrett, 1887) – Marquesas Islands: Hivaoa
Taipidon analogica (Pease, 1870) – Marquesas Islands (no exact locality known)
Taipidon semimarsupialis, new species – Marquesas Islands: Nukuhiva, Mt. Ooumu
Taipidon centadentata, new species – Marquesas Islands: Nukuhiva, Mt. Ooumu
Taipidon varidentata, new species – Marquesas Islands: Hivaoa
Taipidon fragila, new species – Marquesas Islands: Hivaoa

Genus *Planudonta,* new genus

Planudonta subplanula, new species – Marquesas Islands: Nukuhiva
Planudonta intermedia, new species – Marquesas Islands: Nukuhiva, Mt. Ooumu
Planudonta concava, new species – Marquesas Islands: Nukuhiva, Mt. Ooumu
Planudonta matauuna, new species – Marquesas Islands: Hivaoa

Genus *Rikitea,* new genus

Rikitea insolens, new species (Cooke & Solem) – Gambier Islands: Mangareva

Genus *Nesodiscus* Thiele, 1931

Nesodiscus taneae (Garrett, 1872) – Society Islands: Maupiti and Borabora
Nesodiscus huaheinensis (Pfeiffer, 1853) – Society Islands: Huahine
Nesodiscus obolus (Gould, 1846) – Society Islands: Huahine and Raiatea
Nesodiscus cretaceus (Garrett, 1884) – Society Islands: Borabora at 600 ft. elevation
Nesodiscus fictus (Pease, 1864) – Society Islands: Tahaa
Nesodiscus fabrefactus (Pease, 1864) – Society Islands: Raiatea and Tahaa
Nesodiscus fabrefactus var. *piceus* (Garrett, 1884) – Society Islands: Raiatea
Nesodiscus magnificus, new species – Society Islands: Borabora, 800 ft. elevation

Genus *Nesophila* Pilsbry, 1893

Nesophila tiara (Mighels, 1845) – Hawaiian Islands: Kauai
Nesophila baldwini (Ancey, 1889) – Hawaiian Islands: Kauai
Nesophila distans (Pease, 1866) – Hawaiian Islands : Kauai
Nesophila capillata (Pease, 1866) – Hawaiian Islands: Kauai

Genus *Kondoconcha,* new genus

Kondoconcha othnius, new species – Austral Islands: Rapa

Genus *Endodonta* Albers, 1850

Endodonta ekahanuiensis, new species – Hawaiian Islands: Oahu, Waianae Mts., Ekahanui Gulch
Endodonta binaria (Pfeiffer, 1856) – Hawaiian Islands: Kauai
Endodonta apiculata (Ancey, 1889) – Hawaiian Islands: Kauai
Endodonta rugata (Pease, 1866) – Hawaiian Islands: Maui
Endodonta laminata (Pease, 1866) – Hawaiian Islands: Kauai
Endodonta kamehameha (Pilsbry & Vanatta, 1906) – Hawaiian Islands: Molokai
Endodonta concentrata (Pilsbry & Vanatta, 1906) – Hawaiian Islands: Lanai
Endodonta lamellosa (Ferussac, 1824) – Hawaiian Islands: Oahu, Koolau Mts.
Endodonta marsupialis (Pilsbry & Vanatta, 1906) – Hawaiian Islands: Oahu, Koolau Mts., Mt. Tantalus
Endodonta fricki (Pfeiffer, 1858) – Hawaiian Islands: Oahu, Waianae Mts.

Genus *Pseudolibera,* new genus

Pseudolibera lillianae, new species (Cooke & Solem) – Tuamotu Islands: Makatea

Genus *Libera* Garrett, 1881

Libera micrasoma, new species – Society Islands: Tahiti, Mt. Aorai, 5,600-6,300 ft. elevation
Libera bursatella bursatella (Gould, 1846) – Society Islands: Tahiti, Mt. Aorai, 4,700-7,300 ft. elevation
Libera bursatella orofenensis, new subspecies – Society Islands: Tahiti, Mt. Orofena, 4,000-6,600 ft. elevation
Libera cookeana, new species – Society Islands: Tahiti, Mt. Aorai, 4,700-6,300 ft. elevation
Libera gregaria Garrett, 1884 – Society Islands: Moorea, southwest
Libera recedens Garrett, 1884 – Society Islands: Moorea, west side
Libera dubiosa (Ancey, 1889) – Society Islands: Moorea, north and east sides
Libera spuria (Ancey, 1889) – Society Islands: probably Tahiti
Libera garrettiana, new species – Society Islands: Tahiti, northwestern part
Libera umbilicata, new species – Society Islands: Tahiti, Mt. Orofena, 4,500 ft. elevation
Libera retunsa (Pease, 1864) – Society Islands: Tahiti, south side
Libera streptaxon (Reeve, 1852) – Society Islands: probably Tahiti
Libera heynemanni (Pfeiffer, 1862) – Society Islands: probably Tahiti
Libera incognata, new species – Society Islands: probably Tahiti
Libera jacquinoti (Pfeiffer, 1850) – Locality unknown
Libera fratercula fratercula (Pease, 1867) – Cook Islands: Aitutaki, Atiu, Mauke, Mangaia Islands and satellite islets of Rarotonga
Libera fratercula rarotongensis, new subspecies – Cook Islands: Rarotonga
Libera subcavernula (Tryon, 1887) – Cook Islands: Rarotonga, mountain ravines
Libera tumuloides (Garrett, 1872) – Cook Islands: Rarotonga, one inland locality

Genus *Gambiodonta,* new genus

Gambiodonta agakauitaiana, new species (Solem & Cooke) – Gambier Islands: Mangareva
Gambiodonta pilsbryi pilsbryi, new species (Cooke & Solem) – Gambier Islands: Mangareva
Gambiodonta pilsbryi aukenensis, new subspecies (Cooke & Solem) – Gambier Islands: Mangareva
Gambiodonta mangarevana, new species (Solem & Cooke) – Gambier Islands: Mangareva
Gambiodonta mirabilis, new species (Cooke & Solem) – Gambier Islands: Mangareva
Gambiodonta tumida, new species (Cooke & Solem) – Gambier Islands: Mangareva
Gambiodonta grandis, new species (Cooke & Solem) – Gambier Islands: Mangareva

Genus *Thaumatodon* Pilsbry, 1893

Thaumatodon multilamellata (Garrett, 1872) – Cook Islands: Rarotonga
Thaumatodon decemplicata (Mousson, 1873) – Ellice Islands: Nukufetau and Vaitupu
Thaumatodon hystricelloides (Mousson, 1865) – Samoan Islands: Upolu
Thaumatodon euaensis, new species – Tonga Islands: Eua
Thaumatodon vavauensis, new species – Tonga Islands: Vavau
Thaumatodon subdaedalea (Mousson, 1870) – Fiji Islands: Lau Archipelago, Kimbombo, Mango, Vanua Mbalavu
Thaumatodon corrugata, new species – Fiji Islands: Lau Archipelago, Mango
Thaumatodon laddi, new species – Fiji Islands: Lau Archipelago, Wangava
Thaumatodon spirrhymatum Solem, 1973 – Fiji Islands: Lau Archipelago, Thithia

Genus *Priceconcha* Solem, 1973

Priceconcha tuvuthaensis Solem, 1973 – Fiji Islands: Lau Archipelago, Tuvutha

Genus *Zyzzyxdonta,* new genus

Zyzzyxdonta alata, new species – Fiji Islands: Lau Archipelago, Yangasa Cluster, Navutu-I-Loma

Genus *Aaadonta,* new genus

Aaadonta constricta constricta (Semper, 1874) – Palau Islands: Peleliu
Aaadonta constricta babelthuapi, new subspecies – Palau Islands: Babelthuap, Ngemelis
Aaadonta constricta komakanensis, new subspecies – Palau Islands: Koror
Aaadonta fuscozonata fuscozonata (Beddome, 1889) – Palau Islands: Koror
Aaadonta fuscozonata depressa, new subspecies – Palau Islands: Peleliu
Aaadonta pelewana, new species – Palau Islands: (exact locality unknown)
Aaadonta irregularis (Semper, 1874) – Palau Islands: Peleliu
Aaadonta angaurana, new species – Palau Islands: Angaur
Aaadonta kinlochi, new species – Palau Islands: Angaur

GEOGRAPHIC KEYS TO THE GENERA

The following keys are based on the observed range of variation for adult specimens. They often will not work for juveniles or badly damaged shells. For user convenience, only shell features are incorporated.

Effective use of the keys to both genera and species requires making standard measurements (fig. 5) and calculating basic ratios. Where only one species in a genus occurs in an island group, that species is listed by name. Otherwise the generic key or discussion is cross referenced.

Since the Caroline, Mariana, and main Fijian Islands only have charopids, and no endodontids, keys to these areas are omitted from Part I. The geographic groupings, in order of presentation, are:

Austral Islands, except Rapa
Cook Islands
Ellice Islands
Hawaiian Islands
Lau Archipelago, Fiji
Mangareva, Gambier Islands
Marquesas Islands
Marshall Islands
Palau Islands
Rapa Island
Samoan Islands
Society Islands
Tonga
Tuamotu Islands, including Henderson

AUSTRAL ISLANDS, EXCEPT RAPA

1. Shell minute, diameter less than 1.8 mm.; at most 1 deeply recessed parietal barrier, usually no barriers visible..................2
Shell small to large, diameter 1.8-5.3 mm.; usually many barriers, if only 1 parietal, then diameter over 4.2 mm.............3
2. Apical sculpture of radial ribs; umbilicus very widely open; body whorl deflected; diameter over 1.2 mm. *Discocharopa* (see Part II)
Apical sculpture of spiral cords; umbilicus narrower; body whorl not deflected; diameter less than 1.1 mm. *Punctum* (see Part II)
3. Periphery angulated or keeled 4
Periphery rounded 5
4. Secondary spiral grooves visible at 80×; or shell diameter over 3.5 mm. ....*Australdonta* (p. 289)
No secondary spiral grooves visible at 80×; diameter less than 3.2 mm..*Mautodontha ceuthma* (p. 158)
5. Secondary spiral grooving visible at 80×; whorl count average over 5½..........................*Australdonta degagei* (Garrett) (p. 298)
No secondary spiral grooving visible at 80×; whorl count generally averages less than 5¼ ....*Minidonta* (p. 126)

COOK ISLANDS

1. Apical sculpture of spiral cords; no apertural barriers. Charopidae (see Part II)
Apical sculpture of radial ribs; at least 1 apertural barrier..........2
2. Umbilicus secondarily narrowed to form a brood chamber in adults..*Libera* (p. 390)
Umbilicus not secondarily narrowed to form a brood chamber in adults..3
3. Apertural barriers numerous, expanded portion of palatals with large points or hooks (figs. 192d, e). *Thaumatodon multilamellata* (Garrett) (p. 448)
Apertural barriers numerous or reduced, with at most minute serrations above..4
4. Shell diameter less than 2.4 mm.; sculpture very fine and crowded; umbilicus open. *Minidonta rotellina* (Pease) (p. 139)
Shell diameter more than 2.7 mm.; sculpture only very fine and crowded if umbilicus closed......................*Mautodontha* (p. 151)

ELLICE ISLANDS

1. Apical sculpture of spiral cords ....Charopidae (see Part II)
Apical sculpture of radial ribs. *Thaumatodon decemplicata* (Mousson) (p. 451)

HAWAIIAN ISLANDS

1. Periphery of shell sharply carinated; apertural barriers usually large and prominent; sculpture often greatly reduced. *Endodonta* (p. 371)
Periphery of shell rounded or bikeeled; apertural barriers large in small (under 3 mm.) species, often reduced or absent in larger; sculpture usually prominent..2
2. Parietal wall with 1-2 barriers or ridges, often with palatal barriers; sculpture usually prominent. *Cookeconcha* (p. 207)
Parietal wall with many threadlike traces, no palatal barriers; sculpture moderately to greatly reduced. *Nesophila* (p. 365)

LAU ARCHIPELAGO, FIJI

1. Apical sculpture of spiral cords ....Charopidae (see Part II)
Apical sculpture of radial ribs..2
2. Several apertural barriers; shell more than 2.5 mm. 3
One or no apertural barriers, shell less than 2 mm. *Discocharopa* (see Part II)
3. Umbilicus very widely open, D/U ratio 2.5-3.1; shell macroscopically smooth ....*Priceconcha tuvuthaensis* (p. 465)
4. Shell with single keel; ribs few and protruded into "winglike" extensions (fig. 198) ....*Zyzzyxdonta alata* (p. 466)
Shell with rounded periphery or bikeeled; shell sculpture not as above..*Thaumatodon* (p. 448)

MANGAREVA, GAMBIER ISLANDS

1. Umbilicus of adults secondarily narrowed to form a brood chamber; diameter generally over 5 mm. *Gambiodonta* (p. 434)
Umbilicus of adults not secondarily narrowed to form a brood chamber; adult diameter generally less than 5 mm...................2
2. Umbilicus widely open, contained less than 2.5 times in the diameter; only 1 parietal and no palatal barriers. *Rikitea* (p. 342)
Umbilicus narrowly open to nearly closed, often decoiling irregularly; several parietal and palatal barriers. *Minidonta* or *Anceyodonta* (see table LXVIII and accompanying discussion)

MARQUESAS ISLANDS

1. Umbilicus very widely open, saucer-shaped, contained 1.6-2.2 times in the diameter......................................*Planudonta* (p. 337)
Umbilicus much narrower, contained usually much more than 2.6 times in the diameter ....*Taipidon* (p. 317)

MARSHALL ISLANDS

1. Apical sculpture of spiral cords ....Charopidae (see Part II)
Apical sculpture of radial ribs..2
2. Parietal barriers 2 ....*Cookeconcha subpacificus* (Ladd) (p. 211)
Parietal barriers 3 ....*Minidonta inexpectans* (Ladd) (p. 132)

PALAU ISLANDS

1. Shell with prominent postnuclear radial ribs and much finer microradials ....Charopidae (see Part II)
Shell without major radial ribs on postnuclear whorls, only fine and very crowded microradials (figs. 203-208). *Aaadonta* (p. 473)

RAPA ISLAND

1. Umbilicus barely perforate or closed 2
   Umbilicus normally to widely open 5
2. Shell periphery distinctly angulated or protruded. *Orangia* (p. 276)
   Shell periphery evenly rounded 3
3. Columellar barrier reaching lip edge, only 2 parietals. *Orangia cookei tautautuensis* (p. 286)
   Columellar barrier displaced onto basal lip, noticeably recessed, or if reaching lip edge there are 3 parietal barriers.......... 4
4. Columellar barrier parallel to plane of coiling, reaching nearly to lip edge; apex flat, spire strongly elevated. *Opanara perahuensis* (p. 253)
   Columellar barrier deflected onto basal lip, or greatly reduced and recessed; spire and apex strongly elevated. *Ruatara* (p. 265)
5. Periphery nearly right angled; ribbing absent from body whorl and shell base.......... *Kondoconcha* (p. 368)
   Periphery evenly rounded; ribbing present on body whorl and shell base 6
6. Shell diameter less than 2.75 mm. and shell height less than 1.5 mm.......... *Rhysoconcha* (p. 255)
   Shell diameter more than 2.75 mm., or if less than 2.75 mm., then shell height more than 1.9 mm. .... *Opanara* (p. 227)

SAMOAN ISLANDS

1. Apical sculpture of spiral cords .... Charopidae (see Part II)
   Apical sculpture of radial ribs.......... 2
2. No apertural barriers present; color white. *Discocharopa* (see Part II)
   Prominent apertural barriers present; shell variegated in color. 3
3. Shell diameter less than 2 mm.; apertural barriers minutely serrated on expanded portion. *Minidonta manuaensis* (p. 130)
   Shell diameter over 3 mm.; apertural barriers "beaded" on expanded portion (fig. 208e). *Thaumatodon hystricelloides* (Mousson)

SOCIETY ISLANDS

1. Apical sculpture of strong spiral cords; aperture totally without barriers; shell sculpture prominent. Charopidae and Punctidae (see Part II)
   Apical sculpture of radial ribs; aperture normally with at least 1 parietal barrier; if without parietal barrier then sculpture absent and shell diameter over 7 mm. 2
2. Shell diameter less than 2 mm.; only 1 parietal barrier. *Discocharopa* (see Part II)
   Shell diameter over 2.25 mm.; normally several apertural barriers, or shell size over 3 mm. 3
3. Umbilicus secondarily narrowed in adults to form a brood chamber.......... *Libera* (p. 390)
   Umbilicus not secondarily narrowed in adults to form a brood chamber 4
4. Shell sculpture greatly reduced; D/U ratio 1.7-3.0; whorls averaging 6 or more .... *Nesodiscus* (p. 351)
   Shell sculpture prominent; D/U ratio usually much more than 2.8; whorls averaging 5-5½, except in *M. boraborensis, M. consobrina*, and *M. maupiensis* .... *Mautodontha* (p. 151)

TONGA

1. Shell aperture without barriers .... Charopidae (see Part II)
   Shell aperture with barriers.......... 2
2. Apical sculpture primarily of spiral cords. Charopidae (see Part II)
   Apical sculpture primarily of radial ribs. *Thaumatodon* (p. 448)

TUAMOTU ISLANDS

1. Shell diameter of adults less than 2.6 mm. *Minidonta hendersoni* (p. 134)
   Shell diameter of adults over 2.9 mm 2
2. Whorl count less than 6½.......... 3
   Whorl count of adults more than 7.......... *Kleokyphus* (p. 224)
3. Umbilicus cup-shaped, not secondarily narrowed; diameter at 5 whorls less than 4.00 mm *Mautodontha daedalea* (Gould) (p. 157)
   Umbilicus secondarily narrowed to form a brood chamber; diameter at 5 whorls more than 5.5 mm. *Pseudolibera lillianae* (p. 383)

Genus **Minidonta**, new genus

Generally small to minute (except *M. extraria, M. anatonuana*, and *M. planulata*) Endodontidae in which the umbilicus is internally constricted or U-shaped with the last whorl decoiling rapidly (except *M. gravacosta* and *M. hendersoni*). Apical and microsculpture typical of family (except secondary spiral cording present in *M. haplaenopla*), radial sculpture of prominent, normally spaced ribs (very fine and crowded only in *M. rotellina*; widely spaced only in *M. taravensis* and *M. extraria*). Apex and spire normally elevated (*M. micra* and *M. hendersoni* relatively high; *M. gravacosta* and *M. planulata* rather depressed), body whorl not descending more rapidly. Whorls usually 4¾-5⅝, normally coiled, reduced in number for minute species (*M. micra, M. manuaensis, M. inexpectans*). Parietal barriers basically 3, 2 in *M. sulcata* and *M. gravacosta*, 4 in *M. taravensis*, rarely with accessory traces, highly specialized in *M. extraria*. Columellar barrier prominent to absent. Palatal barriers simple blades, 2-5, usually 4 in number, many species with accessory traces, bulbous only in *M. micra* and *M. extraria*. All barriers reduced in size in several species (*M. planulata, M. haplaenopla, M. simulata, M. anatonuana*). Anatomy almost unknown. Penial retractor originating from diaphragm, remaining genitalia as in *Endodonta*.

Type species.—Minidonta hendersoni, new species.

The unusual coiling pattern of the umbilicus (figs. 62, 63b, 69c) is the main differentiating character of this otherwise diverse group. Generalized in sculpture and form, specializations in tooth structure closely approach the patterns of *Mautodontha, Anceyodonta*, and *Australdonta*. The species included in *Minidonta* show distinct sculptural, size, and umbilical differences from the species of *Anceyodonta* and *Australdonta*, while the approach to *Mautodontha* is closer in several respects.

Departures from the umbilical pattern are few and can be attributed to secondary shell modifications. In *M. sulcata* (fig. 68e, f) the marked columellar sulcus visually obscures the coiling pattern, which, while not as extreme as in *M. planulata*, is typical. In *M. gravacosta* and *M. extraria*, the relatively depressed apex and low H/D ratio probably correlate with the near regular decoiling of the umbilicus. Similarly, *M. hendersoni* with its very high spire and wide umbilicus shows only a slight increment in last whorl decoiling. The only species whose relatively regularly decoiling umbilicus cannot be explained as a secondary modification is *M. haplaenopla* (fig. 69f). In that species the size, shape, and dentition are so similar to other *Minidonta* that I have no hesitation in so classifying *M. haplaenopla*.

Unlike the distinctive microsculpture of *Anceyodonta* or *Australdonta,* all species of *Minidonta* have the primitive endodontid pattern of fine radials crossed by distinctly finer and more crowded spirals. Only in *M. haplaenopla* is there a weak secondary sculpture of spiral cords developed. Similarly, most species have a simple radial sculpture of prominent, rather closely set major radials. *M. rotellina* is unique in its very fine and crowded radial sculpture and *M. inexpectans* also has quite crowded sculpture. In contrast, the sculpture of *M. taravensis* is quite widely spaced, much as in *Anceyodonta.* The low rib counts of *M. micraconica* and *M. micra,* however, are a function of small size rather than alteration in rib size or spacing.

Umbilical width is rather variable (table LXIII), with two species, *M. rotellina* and *M. planulata,* having very narrow umbilici, and four species, *M. taunensis, M. hendersoni, M. inexpectans,* and *M. gravacosta,* having widely open umbilici. In *M. hendersoni* and *M. gravacosta* the increase in umbilical width seems to have changed the coiling pattern, but the other species do not seem to have been affected.

Three species, *M. planulata, M. anatonuana,* and *M. extraria* are relatively large (2.90-3.26 mm. in mean diameter), while *M. inexpectans, M. manuaensis,* and *M. micra* are minute (mean diameter 1.68-1.83 mm.). Of the large species, *M. planulata* and *M. extraria* are enlarged by depression of the apex and resulting loosening of coiling; *M. anatonuana* by a slight increase in whorl count. Size reduction in the small species is an effect of decrease in whorl count to 4 1/16 or 4½, without any change in whorl size. In many New Zealand charopids, such as *Ptychodon,* size reduction results from narrowing of the later whorls, with a bulbous nucleus indicating relationship to larger species. No such change is found in any of the Pacific basin Endodontidae.

Patterns of barrier change are more complex (table LXIII). Of the Austral Island species, *M. anatonuana* has typical dentition with elongated, flatly lamellar palatal barriers (fig. 68b). *M. sulcata* (fig. 68e) has the parietals reduced to 2 and the palatals reduced in height and length. This foreshadows the great size reduction seen in the apertural barriers of *M. planulata* and *M. haplaenopla* (fig. 69).

A different pattern of specialization is seen in the very small *M. micraconica* and *M. gravacosta.* The upper parietal is bifid (fig. 65d-e), there is a very large columellar barrier, and 5 prominent palatals plus one or two accessory traces. The palatals are shorter and less flatly lamellar than in *M. anatonuana* or the Mangarevan species, more closely resembling the form seen in the more heavily toothed species of *Mautodontha,* such as *Mautodontha zimmermani* (fig. 74b).

The Mangarevan species show even wider divergence in barrier form. *Minidonta micra* (fig. 63a) has very large, rather bulbous barriers, quite similar in form to those of *M. micraconica* (fig. 65b), only without a bifid upper parietal and having the columellar barrier greatly reduced in size. *Minidonta simulata* (fig. 70a) and *M. taravensis* (fig. 71c) have rather large and elongated barriers, similar to those of *M. anatonuana* (fig. 68b) and approach (*simulata*) or are essentially identical to (*taravensis*) the tooth form seen in *Anceyodonta. M. taravensis* has a 4th parietal and the columellar barrier greatly modified, but is closely related to *M. simulata.* In *M. taunensis* (fig. 70e) the barriers are simple and very elongated, much more so than in *M. simulata.* Their form is that of the elongated *Anceyodonta* and *Mautodontha.* Finally, *Minidonta extraria* has the unique splitting of the parietals (fig. 71f) and short, high, rather bulbous palatals. These barriers are totally unlike those in other species of *Minidonta.*

In the Henderson Island *M. hendersoni* (fig. 63c), the barriers are basically identical to those of the Mangarevan *M. micra,* differing primarily in the heavy callus on the palatal wall that reduces the size of the palatal barriers considerably. The Samoan *M. manuaensis* (fig. 62b) and Bikini Atoll fossil *M. inexpectans* (fig. 62d) have the barriers slightly reduced in size from those found in *micra* and *hendersoni* and lack the accessory traces. They are, however, essentially identical in barrier structure.

Finally, the Aitutaki *Minidonta rotellina* (fig. 62e) has very elongated barriers that are not directly similar to any other species of *Minidonta,* but show some strong similarities to those of *Mautodontha imperforata* (fig. 76e).

On the basis of the observed variation, I recognize five species groups within *Minidonta,* based on barriers, sculpture, size, and shape. They are:

Group of *Minidonta micra*—shell minute to very small; sculpture prominent; spire normally to strongly elevated; umbilicus usually widely open; 3 parietals, 3 or 4 palatals, with barriers not particularly elongated—
  M. micra, new species
  M. hendersoni, new species
  M. inexpectans (Ladd, 1958)
  M. manuaensis, new species

Group of *Minidonta micraconica*—shell very small; sculpture quite prominent; spire normally elevated or depressed; umbilicus normal to widely oepn; parietals 2 or 3, upper bifid, columellar large, 5 palatals, barriers short and prominent—
  M. micraconica, new species
  M. gravacosta, new species

Group of *Minidonta rotellina*—shell very small; sculpture very fine; spire normally elevated; umbilicus very narrow; 3 parietals, very small columellar ridge; palatals 2, barriers elongated—
  M. rotellina (Pease, 1870)

Group of *Minidonta anatonuana*—shell of average size to very large; sculpture normal; spire depressed to moderately elevated; umbilicus normal to narrow; parietals 3 or 4, all barriers normal to reduced, not particularly elongated—

M. anatonuana, new species
M. sulcata, new species
M. haplaenopla, new species
M. planulata, new species

Group of *Minidonta simulata*—shell of normal to rather large size; sculpture rather widely spaced; spire flat to normally elevated; umbilicus wide to narrow; parietals 3 or 4, columellar usually present, palatals 4, with or without accessory traces, all barriers elongated (except *extraria*)—

M. taunensis, new species
M. taravensis, new species
M. simulata, new species
M. extraria, new species

The above groups show different affinities. The *micraconica* complex is an obvious specialization of the *micra* group, which is the basic structural type within *Minidonta*. The *anatonuana* group parallels *Australdonta* in its general reduction in tooth size, large size, and rather depressed shape, but obviously differs in its umbilical coiling, microsculpture, absence of a supraperipheral sulcus, and absence of peripheral angulation. *M. rotellina* is without obvious relationships and stands as an isolated species. Finally, the *simulata* complex has more the shape of *Mautodontha*, but the sculpture, color, and dentition grade into *Anceyodonta*.

Despite the varying differences cited above, *Minidonta* presents a basic set of similarities that far outweighs individual species group trends. The large, regularly decoiling umbilicus, rather flat spire, rapidly descending body whorl, and generally much larger size of *Mautodontha* contrast to the constricted umbilicus, elevated spire, normal body whorl, and small size of *Minidonta*. Similarly, the large size, angled periphery with supraperipheral sulcus, microspiral grooving, and generally flat spire separate *Australdonta*. Species of the Mangarevan *Anceyodonta* often have strong spiral secondary sculpture, a generally minute umbilicus, very high spire, and complicated barriers; *Anceyodonta* is easily derivable from the *simulata* group of *Minidonta*, but unquestionably distinct from the other species groups.

Geographically, *Minidonta* has the widest distribution in the Endodontidae. Living (or recently extinct) species are found from Samoa to Henderson Island, a range of perhaps 2,700 miles over 41° of longitude. The fossil record from Bikini, of either Pleistocene or Pliocene age, nearly doubles the range. Current centers of speciation lie on Raivavae, Austral Islands and Mangareva, Gambier Islands, each with five species. Single living species are known from the Manua group in American Samoa (*Minidonta manuaensis*), Rurutu, Austral Islands (*M. haplaenopla*), Aitutaki, Cook Islands (*M. rotellina*), and Henderson Island (*M. hendersoni*). There is also the single fossil record from Bikini Atoll, Marshall Islands (*M. inexpectans*).

Species groups show simple distribution patterns, with the *simulata* group confined to Mangareva; the *anatonuana* group present on Raivavae and Rurutu; *rotellina*, an isolated species taxonomically and geographically, found only on Aitutaki; the *micraconica* group restricted to Raivavae; and the *micra* complex widely dispersed with species on Henderson, Mangareva, Raivavae, Manua Group and Bikini as a fossil. The most generalized stock thus has the widest distribution, including both the easternmost (Henderson) and westernmost (Manua) records.

The difficulties of dating the Bikini fossil, *M. inexpectans*, were discussed by Ladd (1958, pp. 188-189). As a Pleistocene or, less probably, a Pliocene species, this would seemingly indicate a young age for the distribution pattern. More critical examination suggests instead that this is a relict pattern. The existence of the *micra* group on the fringes of distribution—Henderson Island, Manua Group, and Bikini (during an elevated period of that atoll) — with a single species on a center of speciation, Mangareva, and a derived group, the *micraconica* pair, on the other center of speciation, Raivavae, is only part of the pattern. With the exception of *Minidonta rotellina* from Aitutaki, Cook Islands and *Mautodontha ceuthma* from Raivavae, both species standing quite isolated in their affinities and of uncertain classification, *Mautodontha* and *Minidonta* show a clear replacement pattern, with *Mautodontha* occupying the Cook, Society, and endodontid inhabitable Tuamotus, while *Minidonta* has a semi-circular fringing pattern of Manua Group Austral Islands, Mangareva and Henderson.

If *Minidonta* was limited to this fringing pattern and showed indications of being derived from *Mautodontha* by size reduction, then interpretation as a recent, secondary dispersal from a Society-Cook center of evolution would make sense. Size reduction in charopids apparently normally is accomplished by narrowing of whorls after the nucleus, with a huge nucleus remaining. There is no indication of this in *Minidonta* and fewer changes would be required in dentition and shell structures to derive *Mautodontha* from *Minidonta* than the reverse. Coupled with the presence of *Minidonta inexpectans* on Bikini, it makes more sense to view the recorded forms of *Minidonta* as stable relicts of a former, nearly continuous distribution through Polynesia, replaced in most of Samoa by *Thaumatodon* and in the Society-Cook-Tuamotu-Rapa-Marquesan area by more specialized genera, each with quite limited distribution in comparison. The presence of *M. hendersoni* on a raised *makatea* island provides evidence tending to confirm the hypothesis of Ladd (1958, p. 196) that *M. inexpectans* was "...probably lodged in crevices in elevated lagoonal limestone while they were above the sea undergoing subaerial erosion."

Only one species has been dissected. *M. hendersoni* differed significantly from *Endodonta* only in having the penial retractor originate from the diaphragm.

TABLE LXIII. - RANGE OF VARIATION IN MINIDONTA

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
manuaensis	9	94.3(86-108)	0.96(0.89-1.08)	1.68(1.59-1.83)	0.572(0.563-0.590)	4 1/16(4-4 1/4)	5.28(4.79-6.13)	3	1	3
inexpectans	6	145	1.04(1.02-1.05)	1.83(1.82-1.84)	0.565(0.559-0.571)	4 1/4	3.98(3.96-4.00)	3	1	3
micra	228	60.8(52-69)	1.09(0.96-1.19)	1.73(1.67-1.89)	0.625(0.563-0.667)	4 1/2(4 1/4-4 3/4)	4.99(3.61-5.88)	3+0-1	1	4+0-4
hendersoni	506	82.9(75-95)	1.34(1.16-1.59)	2.16(1.85-2.45)	0.621(0.575-0.685)	5+(4 1/2-5 1/2)	3.67(3.09-4.35)	3+0-1	0-1	4+1-3
micraconica	4	67.3(65-70)	1.15(0.93-1.23)	2.00(1.95-2.05)	0.575(0.560-0.597)	4 7/8+(4 5/8-5 1/8)	5.53(4.42-6.78)	3[1]+1	1	5+2
gravacosta	41	71.2(59-83)	0.92(0.83-1.03)	1.97(1.79-2.09)	0.466(0.424-0.525)	5(4 3/4-5 1/4)	3.99(3.53-4.92)	2[1]	1	5+1-2
rotellina (Pease)	25	OVER 200	1.13(1.02-1.33)	1.97(1.83-2.19)	0.573(0.539-0.611)	5 3/8(5-6)	7.10(5.29-8.21)	3	1	2+0-1
anatonuana	33	89.5(83-94)	1.74(1.46-2.04)	3.02(2.78-3.25)	0.577(0.500-0.633)	5 1/2(5-6)	5.87(4.90-7.73)	3	0	4+0-1
sulcata	4	112.5(105-120)	1.39(1.29-1.49)	2.28(2.25-2.32)	0.587(0.574-0.600)	5 1/8+(5-5 1/2)	4.50(4.00-5.00)	2	1	4
haplaenopla	77	109.6(91-125)	1.46(1.23-1.82)	2.59(2.28-3.01)	0.563(0.506-0.608)	5 1/8-(4 5/8-5 5/8)	5.06(4.26-5.75)	2-3	0	2-3-4
planulata	7	94(88-99)	1.63(1.49-1.69)	3.26(2.98-3.41)	0.495(0.484-0.517)	5(4 3/4-5 1/8)	7.12(6.37-8.42)	3	0	3
taunensis	2	113	1.18(1.13-1.23)	2.25(2.19-2.32)	0.527(0.525-0.529)	5 3/16(5-5 3/8)	3.36(3.05-3.67)	3	1	4+1
taravensis	2	68.0(64-72)	1.42(1.36-1.49)	2.58(2.48-2.68)	0.551(0.546-0.556)	5 1/2(5 3/8-5 5/8)	6.11(5.40-6.82)	4	1[4]	4+3
simulata	32	78.5(71-92)	1.55(1.38-1.78)	2.72(2.43-2.86)[3]	0.562(0.518-0.658)	5 1/8-(4 3/4-5 5/8)	4.85(3.96-6.31)	3	0-1	4+1-2
extraria	3	71.3(67-75)	1.48(1.45-1.51)	2.90(2.76-3.03)	0.512(0.500-0.524)	5 1/2(5 3/8-5 5/8)	5.33(5.25-5.41)	3[2]	1	4

1. Upper bifid
2. Each split
3. A single gerontic shell was 3.52 mm. in diameter
4. With a lateral accessory blade

KEY TO THE GENUS *Minidonta*

1. Upper parietal barrier simple; palatal barriers 4 or less 3
   Upper parietal barrier bifid (fig. 65d, e); palatal barriers 5 2
2. Parietal barriers 2, H/D ratio less than 0.540. *Minidonta gravacosta*, new species
   Parietal barriers 3, H/D ratio more than 0.540. *Minidonta micraconica*, new species
3. Umbilical wall rounded, normally 3 parietal barriers 4
   Umbilical wall with prominent sulcus (fig. 68f), 2 parietal barriers .... *Minidonta sulcata*, new species
4. Body whorl with less than 150 radial ribs, 3 or 4 palatal barriers. 5
   Body whorl with more than 200 radial ribs, only 2 major palatal barriers .... *Minidonta rotellina* (Pease, 1870)
5. Mean adult size less than 2.0 mm. 6
   Mean adult size more than 2.0 mm 8
6. Palatals 3, no accessory traces 7
   Palatals 4, normally with accessory traces. *Minidonta micra*, new species
7. More than 125 ribs on body whorl; mean D/U ratio about 4.00. *Minidonta inexpectans* (Ladd, 1958)
   Less than 125 ribs on body whorl; mean D/U ratio about 5.25. *Minidonta manuaensis*, new species
8. Mean D/U ratio less than 4.00 10
   Mean D/U ratio much more than 4.00 9
9. H/D ratio less than 0.550; no accessory parietal traces; Mangareva .... *Minidonta taunensis*, new species
   H/D ratio more than 0.550; usually an accessory parietal trace; Henderson Island .... *Minidonta hendersoni*, new species
10. Parietal barriers simple 11
    Each parietal barrier split into several traces (fig. 71f). *Minidonta extraria*, new species
11. Parietal barriers 3 12
    Parietal barriers 4 .... *Minidonta taravensis*, new species
12. Mean D/U ratio about 5.00 13
    Mean D/U ratio more than 5.50 14
13. Mean body whorl rib count less than 90; 4 palatals. *Minidonta simulata*, new species
    Mean body whorl rib count more than 100; usually 3 palatals. *Minidonta haplaenopla*, new species
14. Palatal barriers 4; mean H/D ratio about 0.575. *Minidonta anatonuana*, new species
    Palatal barriers 3; mean H/D ratio about 0.500. *Minidonta planulata*, new species

GROUP OF *Minidonta micra*

Minidonta manuaensis, new species. Figure 62 a-c.

Diagnosis.—Shell minute, diameter 1.59-1.83 mm. (mean 1.68 mm.), with 4-4¼ normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.563-0.590 (mean 0.572). Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, contained 4.79-6.13 times (mean 5.28) in the diameter. Postnuclear whorls with narrow, rounded, almost vertically sinuated radial ribs, 86-108 (mean 94.3) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of very fine radial riblets, four to eight between each pair of major ribs, crossed by distinctly finer and more crowded spiral riblets. Sutures impressed, whorls almost equally rounded on outer margins. Aperture subcircular, inclined about 5° from shell axis. Parietal barriers 3, short, extending somewhat more than one-eighth whorl: upper high and bladelike for entire length, expanded and serrated for posterior two-thirds, with sharp anterior descension; 2nd equal in height posteriorly, less expanded above, with gradual descension over anterior half; 3rd slightly reduced in height posteriorly, anterior third a threadlike trace. Columellar barrier a low, broadly rounded, recessed ridge, lying parallel to plain of coiling. Palatal barriers 3, rather prominent blades, extending a little more than one-eighth whorl: lower somewhat recessed greatly reduced in height, with very gradual anterior descension; 2nd much higher, bladelike, with sharper anterior descension; 3rd equal in height to 2nd, with more gradual anterior descension, nearly reaching lip margin. Some specimens have a barely detectable bulge where 4th palatal normally lies.

The Bikini fossil *Minidonta inexpectans* differs in having more crowded radial ribbing (145 on the body whorl), a wider umbilicus (D/U ratio 3.96-4.00), the body whorl slightly compressed laterally, and the lower palatal barrier more reduced. *Minidonta taunensis* from Mangareva has a 4th palatal barrier above the periphery, the lower palatal not reduced in size, is larger (diameter 2.17-2.30 mm.), has a wider umbilicus (D/U ratio 3.05-3.67) and is less elevated (H/D ratio 0.525-0.529). Other species differ obviously in size, sculpture, or form and cannot be confused.

Description.—Shell minute, with 3⅞ normally coiled whorls before being broken. Apex and spire evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.574. Embryonic whorls 1⅝, sculpture of radial riblets, whose interstices are 3-4 times their width, and much finer, slightly more crowded spiral riblets. Postnuclear whorls with narrow, rounded, vertically sinuated radial ribs, 80 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of very fine radial riblets, three to six between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls evenly rounded on outer margin. Color light reddish-yellow without trace of darker markings. Umbilicus narrow, U-shaped, barely decoiling, contained 6.27 times in the diameter. Aperture subcircular, inclined less than 5° from shell axis. Parietal barriers 3, extending less than three-sixteenths of a whorl: upper a high lamella for entire length, posteriorly expanded and serrated, much of anterior end partly broken; 2nd equal in height posteriorly, with gradual descension for anterior half; 3rd reduced in height posteriorly, anterior quarter threadlike. Columellar barrier recessed, a broad, low, rounded ridge lying parallel to plane of coiling. Palatal barriers 3, prominent, extending about one-eighth whorl: 1st reduced in height, with gradual anterior descension; 2nd much higher less recessed, with sharper anterior descension, expanded above; 3rd equal in height to 2nd, with more gradual anterior descension. Height of holotype 0.89 mm., diameter 1.55 mm.

Holotype.—Samoa: Manua Islands, Ta'u, Utumanu'a ridge at 350 ft. elevation. Collected by Wray Harris on June 28, 1937. Bernice P. Bishop Museum number 187207.

Range.—Olosega and Ta'u, Manua Islands, Samoa.

Paratypes.—Same as list of material.

Material.—Manua Islands: TA'U, Utumanu'a ridge at 350 ft. elevation (1 specimen, BPBM 187207); OLOSEGA, Olosega village, pastor's grounds, 600 ft. inland at 12 ft. elevation (8 specimens, BPBM 186758, BPBM 186774, BPBM 188720).

Remarks.—Unfortunately, the type specimen was damaged during cleaning prior to illustration, and the dotted lines in Figure 62a, b indicate the original contours. Since the single Ta'u example was better preserved than any of the Olosega shells, it has been selected as holotype.

Only dead specimens from sweepings at the base of a kapok plant or from a pocket of leaf mould in coralline rock are known. Possibly the species still

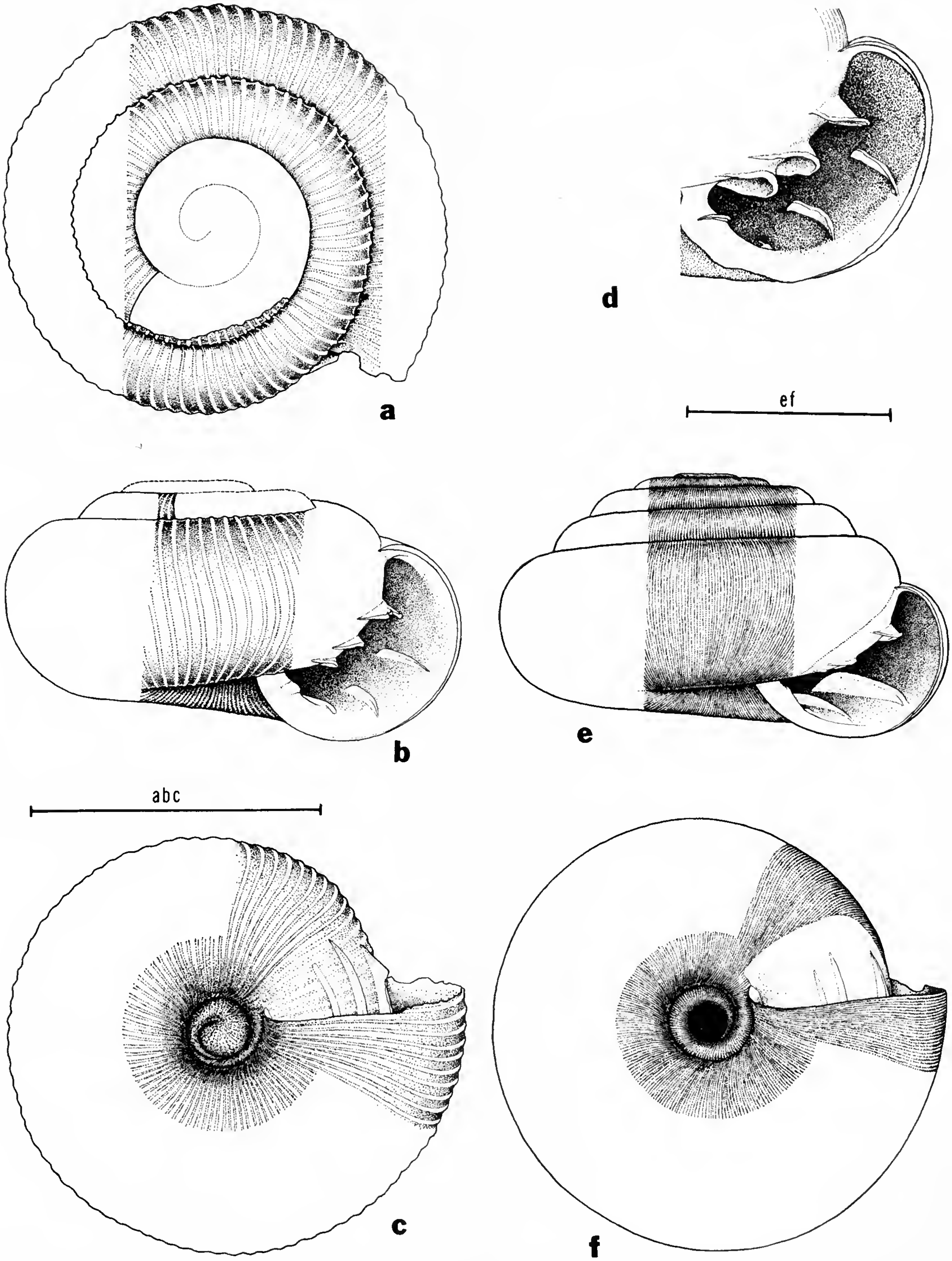

FIG. 62. **a-c**, *Minidonta manuaensis*, new species. Utumanu'a ridge, Ta'u, Manu'a Islands, American Samoa. Holotype. BPBM 187207; **d**, aperture of *Minidonta inexpectans* (Ladd). Holotype. USNM 562088; **e-f**, *Minidonta rotellina* (Pease). Aitutaki, Cook Islands. Lectotype. BPBM 2312. Scale lines equal 1 mm. (MM).

exists on the upper peaks of Ta'u or Olosega, although it is almost certainly absent from lowland areas except as fossils. Collections made at 1,300-1,500 ft. elevation in 1975 failed in locating this species. Since *M. hendersoni,* from the opposite geographic limit, is the only other *Minidonta* that has been dissected, study of *M. manuaensis* is especially desirable.

Minidonta inexpectans (Ladd, 1958). Figure 62d.

Ptychodon inexpectans Ladd, 1958, Jour. Paleontol., **32,** (1), pp. 188-189, pl. 30, figs. 1-6 - Drill hole 2A at 447-453 foot depth, Bikini Atoll, Marshall Islands (Pleistocene-Pliocene).

Diagnosis.—Shell very small, diameter 1.82-1.84 mm. (mean 1.83 mm.), with 4¼ tightly coiled whorls. Apex and spire moderately and evenly elevated, H/D ratio 0.559-0.571 (mean 0.565). Umbilicus U-shaped, last whorl decoiling more rapidly, contained 3.96-4.00 times (mean 3.98) in the diameter. Postnuclear sculpture of fine, crowded, slightly protractively sinuated radial ribs, about 145 on the body whorl, whose interstices are 1-1½ times their width. Aperture ovate, compressed laterally, lip broken. Parietal barriers 3, upper lamellate for entire length, lower 2 with anterior third threadlike, all extending one-quarter whorl posteriorly. Columellar barrier a low recessed ridge with anterior tip angling slightly downward. Palatal barriers 3; lower a small trace, upper 2 prominent lamellar ridges.

The Samoan *Minidonta manuaensis* is nearly identical, differing in having coarser ribbing (85-110 on the body whorl), a smaller umbilicus (D/U ratio 4.79-6.27) and the body whorl less laterally compressed; *M. taunensis* from Mangareva has the anterior threadlike portion of the lower parietals longer and finer; the columellar barrier slanting down more sharply; the lower palatal barrier large, middle two identical, and an additional supraperipheral palatal. It also differs in features of coiling, ribbing, and umbilicus.

Description.—Shell very small, with very slightly less than 4¼ tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending distinctly more rapidly, H/D ratio 0.559. Apical whorls 1⅜, partly eroded, with traces of widely spaced radial ribs remaining on midportion. In umbilicus, apical sculpture seen as major radial ribs, with finer radials between and barely visible spiral riblets. Remaining whorls with fine, crowded, very slightly protractively sinuated radial ribs, 145 on the body whorl, whose interstices are 1-1½ times their width. Microsculpture occasionally visible as network of very fine radials and spirals. Sutures deep, whorls strongly rounded above, compressed laterally with evenly rounded outer and basal margin, umbilical wall strongly rounded. Ground color leached from shell except for narrow to broad radial reddish-yellow markings reaching from suture to periphery, absent on base of shell. Umbilicus open, U-shaped, last whorl decoiling noticeably more rapidly, contained 3.96 times in the diameter, whorls strongly rounded inside. Aperture lunate, strongly rounded above and on umbilical wall, compressed laterally with evenly rounded outer and basal margin, inclined less than 10° from shell axis. Parietal barriers 3, high and bladelike, extending one-quarter whorl posteriorly: upper thin, high and lamellate for entire length, with very sharp anterior descension, upper edge slightly expanded; middle parietal with anterior third a high threadlike ridge, gradually descending in midportion from posterior elevated lamellar part that is only two-thirds height of upper parietal; lower parietal same shape as middle, anterior third very low and threadlike, both lower parietals extending slightly anterior of upper. Columellar barrier a low threadlike ridge slightly more elevated posteriorly and extending beyond line of vision, parallel to plane of coiling, with its tip angling very slightly down across posterior edge of columellar callus, and ending well short of lip edge. Palatal barriers 3: lower a very small, short, recessed, threadlike trace, basal in position, stopping well short of lip edge; upper 2 moderately elevated lamellate ridges, extending posteriorly three-sixteenths of a whorl, gradually descending anteriorly almost to edge of lip callus; upper palatal slightly subperipheral, pointing between upper and middle parietal; 2nd palatal located midway between upper and lower palatal teeth, pointing between middle and lower parietal. A faint swelling occupies slightly supraperipheral position near lip edge. Lip edge thickened with distinct callus, fading out near periphery, strongest on columellar wall. Height of holotype 1.02 mm., diameter 1.84 mm.

Holotype.—Marshall Islands: Bikini, drill hole 2A at 447-453 ft. deep. USNM 562088.

Range.—Known only from the type collection.

Paratypes.—USNM 562089.

Remarks.—Cleaning of the holotype by sonic vibrations revealed the presence of a columellar and lower palatal denticle, features not detected during the original study. In addition, there is a weak bulge present in the upper palatal lip that can be interpreted as a remnant of a 4th palatal tooth. Since other features of the shell are well shown in the original figures (Ladd, *loc. cit.*), only an apertural view (fig. 62d) has been presented in this study.

Classification in *Minidonta* is based on the characteristically constricted umbilicus (Ladd, 1958, pl. 30, fig. 4), absence of distinctive microsculpture, form and number of the apertural barriers, and close similarities to *M. manuaensis.* If *inexpectans* and *manuaensis* were found on the same island or on adjacent islands, they unquestionably would be considered of monophyletic origin. Their differences, discussed above in the "Diagnosis," are comparatively minor when compared to the differences among other *Minidonta.*

Dating of this species is uncertain. According to Ladd (1958, pp. 188-189), the shells were with "...fauna of shallow water and marine mollusks that is definitely post-Miocene, probably Pliocene. The land shells probably were brought in at a later date when the marine limestone was above the sea undergoing solution and recrystallization; the land shells may be Pleistocene." The closeness to an existing species has no bearing on its probable age, since many recent molluscan species are known from Pleistocene and Pliocene strata.

Minidonta micra, new species (Solem & Cooke). Figure 63a-b.

Diagnosis.—Shell minute, diameter 1.67-1.89 mm. (mean 1.73 mm.), with 4¼-4¾ normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.563-0.667 (mean 0.625). Umbilicus constricted internally, last whorl decoiling quite rapidly, contained 3.61-5.88 times (mean 4.99) in the diameter. Postnuclear whorls with broad, prominent, protractively sinuated radial ribs, 52-69 (mean 60.8) on the body whorl, whose interstices are 1½-3 times their width. Microsculpture a lattice of extremely fine radial and spiral riblets. Sutures impressed, whorls evenly rounded, except for slight lateral compression below periphery. Aperture ovate, inclined about 10° from shell axis. Parietal barriers 3, extending one-quarter whorl, usually (70 per cent) with an

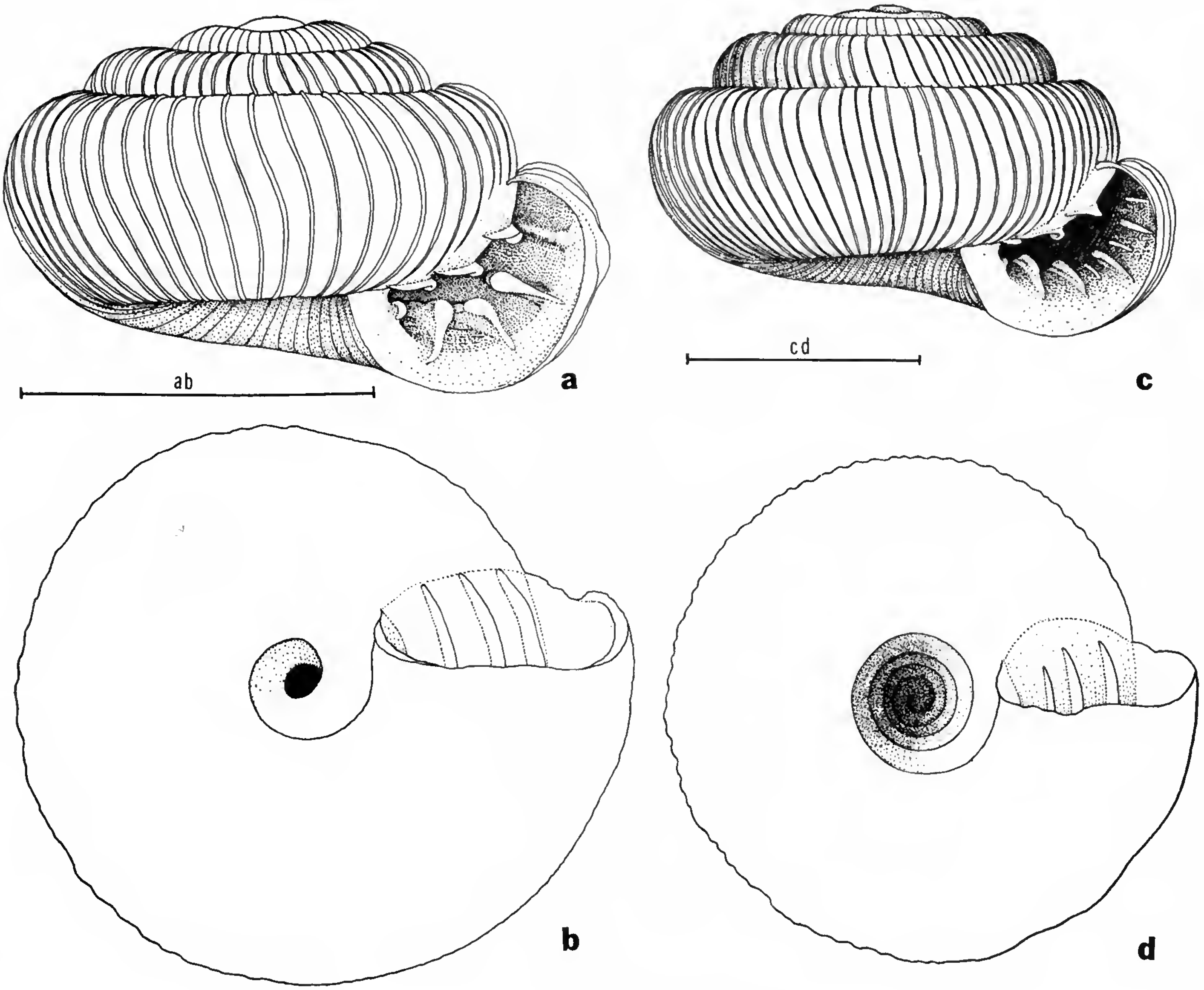

FIG. 63. **a-b**, *Minidonta micra,* new species. Station 102, Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 138757; **c-d**, *Minidonta hendersoni,* new species. Station 254, Henderson Island, Tuamotus. Holotype. BPBM 149858. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

inconspicuous accessory trace: upper a high ridge, grossly expanded and serrated on posterior two-thirds, anterior quarter narrow, with gradual descension; 2nd with posterior section slightly shorter than 1st, but otherwise identical, anterior third gradually descending; 3rd greatly reduced in height posteriorly, much narrower above, gradually descending over anterior half. Accessory trace, when present, located above upper parietal, midway to parietal-palatal margin. Columellar barrier a broad, low, serrated ridge, moderately recessed, lying parallel to plane of coiling. Palatal barriers 4, extending more than one-eighth whorl, with a variable number of accessory traces: lower nearly reaching lip edge, high, expanded, and serrated on posterior half, with sharp anterior descension; 2nd slightly lower than 1st, lying opposite 2nd parietal, with more gradual anterior descension; 3rd equal in height to 1st, longer, with more gradual anterior descension; 4th supraperipheral, a low, broadly rounded, moderately recessed ridge. Accessory traces variable in number, present above 4th palatal (one or two) and between various lower palatals or the columellar and lower palatal. Columellar and palatal walls with heavy, broadly rounded callus extending up to and including region of 4th palatal.

The minute size, presence of accessory palatal traces, and high spire immediately separate *M. micra* from the other *Minidonta. Anceyodonta ganhutuensis* can be confused, but has a tiny umbilicus (mean D/U ratio 15.8), a much higher spire (mean H/D ratio 0.789), and more whorls. *Minidonta hendersoni* is almost identical in shape and barrier structure, but is distinctly larger (mean diameter 2.16 mm.), has finer sculpture, and a wider, less constricted (mean D/U ratio 3.67) umbilicus.

Description.—Shell minute, with 4½ normally coiled whorls. Apex and spire markedly elevated, last whorl descending a little more rapidly, H/D ratio 0.596. Embryonic whorls 1½, with faint traces of microradial and microspiral sculpture remaining in sutures. Postnuclear whorls with broad, high, slightly protractively sinuated radial ribs, 60 on the body whorl, whose interstices are 2-3 times their width. Microsculpture a lattice of coequal, extremely fine radial and spiral riblets. Sutures impressed, whorls evenly rounded, somewhat compressed laterally below periphery. All color leached from shell. Umbilicus strongly constricted internally, last whorl decoiling quite rapidly, contained 4.96 times in the diameter. Aperture ovate, slightly compressed laterally below periphery, inclined about 5° from shell axis. Parietal barriers 3, extending a little more than one-quarter whorl; upper quite high, posterior two-thirds grossly expanded and serrated, anterior quarter descending gradually; 2nd slightly higher, posterior elevated portion a little shorter; 3rd greatly reduced in height, less broadly expanded, elevated portion lower, gradually descending over anterior half. Columellar and palatal walls with thick, rounded callus, extending up through 4th palatal. Columellar barrier a broad, low, recessed, serrated ridge parallel to plane of coiling. Palatal barriers 4, extending more than one-eighth whorl, plus four accessory traces: lower very high, bulbously expanded above, sharply descending almost to lip edge over anterior half; 2nd slightly lower and less broadly rounded above; 3rd intermediate in height, as expanded above as 1st; 4th supraperipheral, a broad, V-shaped ridge, moderately recessed, with sharp anterior descension. Accessory traces very short, stopping inside callus edge, located between columellar and 1st palatal, then between each pair of palatals. Height of holotype 1.02 mm., diameter 1.73 mm.

Holotype.—Gambier Islands: Mangareva, Aukena Islet, Station 102, first cave east of gap. Collected by Donald Anderson on May 28, 1934. BPBM 138757.

Range.—Known only from the type collection.

Paratypes.—Same as list of material.

Material.—Mangareva: Aukena Islet, first cave (Station 102) east of gap (228 specimens, BPBM 9669, BPBM 138757).

Remarks.—The palatal traces were accidentally omitted from the figures of the holotype and the width of the ribbing is much too narrow. Otherwise Figure 63a is an accurate representation of the type. Because of the minute size and clogged apertures, no data is available on the variation in palatal trace numbers. The parietal trace situation was checked in only 20 individuals for the same reason.

The barrier length and numbers are very close to the features found in *Anceyodonta*, but the umbilical form, lack of secondary sculpture, crowded ribbing, and basic appearance combine to place *micra* in *Minidonta*.

Minidonta hendersoni, new species (Cooke & Solem). Figures 63c-d; 64a-b.

Diagnosis.—Shell slightly smaller than average, diameter 1.85-2.45 mm. (mean 2.16 mm.), with 4½-5½ normally coiled whorls. Apex and spire markedly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.575-0.685 (mean 0.621). Umbilicus open, V-shaped, regularly decoiling, contained 3.09-4.35 (mean 3.67) times in the diameter. Postnuclear whorls with high, prominent, slightly protractively sinuated radial ribs, 75-95 (mean 82.9) on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, four to six between each pair of major ribs, with much finer and more crowded spiral riblets. Sutures impressed, whorls strongly rounded above, laterally compressed, umbilical margin very strongly rounded. Aperture ovate, compressed laterally, inclined about 10° from shell axis. Parietal barriers 3, extending less than one-quarter whorl, plus one accessory trace above upper tooth: upper parietal a lower than usual bladelike ridge, posterior half expanded and serrated, with sharp anterior descension; 2nd with posterior three-eighths equal in height to 1st, anterior quarter threadlike; 3rd greatly reduced in height posteriorly, anterior half threadlike. Accessory trace very inconspicuous, a recessed thread located near parietal-palatal margin. Columellar barrier a low, deeply recessed, threadlike ridge, in gerontic individuals completely hidden by heavy callus. Palatal barriers 4, extending about one-eighth whorl, upper reduced, plus one accessory trace: 1st basal in position, high, bladelike, rather sharp descension over anterior half; 2nd slightly more expanded above with more gradual anterior descension; 3rd with more gradual anterior descension, posterior elevated portion proportionately shorter; 4th a less deeply recessed, V-shaped ridge, much lower than 3rd, accessory trace inconspicuous and threadlike, deeply recessed, located much nearer to 4th palatal than to parietal-palatal margin. Older individuals have a strong rounded callus extending from columellar wall to 4th palatal, but not above latter.

The heavy palatal callus and rather widely open umbilicus combine with the presence of an upper parietal trace to readily separate *Minidonta hendersoni* from other species of the genus. The much larger *M. anatonuana* and *M. haplaenopla* are most similar in general aspect, but they have narrower umbilici, no parietal traces, and quite different sculpture. *M. taunensis* is the same size and has nearly identical barriers, but is a much more depressed shell with finer sculpture and a more marked internal constriction of the umbilicus. The Mangarevan *M. micra* is smaller (mean diameter 1.73 mm.), with coarser sculpture (60.8 ribs on the body whorl), and a narrower umbilicus (mean D/U ratio 4.99).

Description.—Shell very small, with 5¼ normally coiled whorls. Apex and spire strongly elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.638. Apical whorls 1½, sculpture of fine radial riblets, usually with one microrib between each pair and rather crowded spiral microribbing. Postnuclear whorls with high, V-shaped, rather prominent radial ribs, 95 on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, four to six between each pair of major ribs, crossed by much finer and more crowded spiral riblets that are barely visible under 96× magnification. Sutures impressed, whorls strongly rounded above and on umbilical margin, slightly compressed laterally. Color reddish-yellow, without darker markings. Umbilicus broadly V-shaped, regularly decoiling, contained 3.83 times in the diameter. Aperture ovate, compressed laterally, inclined about 10° from shell axis. Parietal barriers 3, extending a little more than three-eighths whorl, expanded and serrated above posteriorly: upper high, bladelike, gradually descending over anterior third; 2nd with anterior third threadlike, posterior three-eighths equal in height to 1st; 3rd greatly reduced in height posteriorly, with anterior threadlike portion proportionately longer. Columellar barrier a small threadlike trace recessed behind edge of columellar-basal callus. Palatal barriers 4, extending one-eighth whorl: lower basal in position, high and bladelike, expanded and serrated posteriorly, with rather sharp anterior descension; 2nd slightly lower, with shorter posterior expanded portion and more gradual anterior descension; 3rd palatal equal in height to 1st, with more gradual anterior descension; 4th palatal a much lower, V-shaped ridge situated opposite and pointing towards upper parietal. Accessory traces located between palatals 2 and 3, 3 and 4, and above 4th barrier. A heavy, rounded callus extends from columellar wall to 4th palatal. Height of holotype 1.45 mm., diameter 2.27 mm.

Holotype.—Henderson Island: northwest part of island (Station 254) on a flat hillside at 15 ft. elevation. Collected on rotting sticks and under stones by Donald Anderson on June 20, 1934. BPBM 149858.

Range.—Henderson Island at several scattered localities.

Paratypes.—Same as list of material.

Material.—Henderson Island: northwest part (Stations 219, 222, 223, 231, 233, 236, 241, 243, 244, 246, 252, 254) under rotting vegetation and stones (506 specimens, BPBM 149428-9, BPBM 149461, BPBM 149470, BPBM 149573-4, BPBM 149602, BPBM 149631, BPBM 149708, BPBM 149712-3, BPBM 149729, BPBM 149756, BPBM 149830, BPBM 149858).

Remarks.—Dead specimens were common at numerous stations on different parts of Henderson Island, but living specimens were found only at Stations 219 and 243. Unfortunately, most of these were immature, but some account of the anatomy could be prepared.

The shells had surprisingly little variation in size, shape, and apertural barriers, the only exception was the presence in some individuals of the small lower palatal traces, and variation in the development of the columellar and basal callus. In gerontic individuals, particularly those from Station 236, the callus was extremely heavy and covered the columellar trace completely. In less aged individuals the columellar trace could be seen lying just in back of the posterior callus edge.

This species is obviously related to the Mangarevan *Minidonta micra,* the differences being indicated above under the "Diagnosis." Henderson Island is an uninhabited, raised coral island of *makatea.* The northern end is about 2½ miles wide, tapering after about 5 miles to a southern point. Vegetation covers the entire island up to its maximum elevation of about 100 ft. Surprisingly enough, in addition to this endemic endodontid, Henderson Island also has the endemic zonitid, *Diastole glaucina* H. B. Baker (1938b, p. 50), and a tornatellinid, *Tubuaia hendersoni* Kondo (1962, pp. 36-38).

Description of soft parts.—Foot and tail typical. Sole undivided, extending slightly up side of foot. Pedal grooves typical, suprapedal less distinct, no caudal horn or middorsal groove visible. Slime network weak on head region. Head retracted partly into pallial cavity.

Body color light yellow-white, without darker markings.

Mantle collar simple, without glandular extension onto pallial roof. Pneumostome in normal position, no mantle lobes developed.

Pallial region extending apically a trifle less than one-half whorl, flattened length about 2.04 mm. Lung roof clear, without granulations. Kidney (K) typical, about 0.69 mm. long, base abutting on loop of intestine, upper margin lying along hindgut, about 0.37 mm. from base to anterior end. Ureter (KD) prominent, reflexed with opening next to hindgut at anterior end of rectal kidney margin. Heart (H) about one-third length of kidney, lying next to middle portion of kidney, not parallel to hindgut. Principal pulmonary vein (HV) very faint, without branching. Hindgut (HG) extending about one-eighth whorl above apex of kidney, paralleling parietal-palatal margin to anus.

Ovotestis poorly preserved, a small number of rather large follicles (some with developing ova?), strung along a faintly iridescent collecting duct, imbedded above stomach-intestine reflexion. Hermaphroditic duct (GD, fig. 64a) typical, slightly iridescent, swollen in midportion, narrowing abruptly just before reflexion to albumen gland. Albumen gland (GG) lying between kidney base and stomach, composed of comparatively few and proportionately large alveoli, head of spermatheca lying against lower edge. Talon (GT) long and slender, with small apical head, imbedded in albumen gland, slightly enlarged after junction with hermaphroditic duct, opening into head of prostate and uterus. Prostate (DG) of large acini opening into narrow tube appressed to wall of uterus, only a single row of acini present. Uterus (UT) a swollen, thin-walled tube without clearly differentiated sections, merging into free oviduct without demarcation.

Vas deferens (VD) originating from tube of prostate, passing down to penioviducal angle, then reflexed up side of penis to insert subapically on penis head. Penial retractor (PR) arising from diaphragm just above point of stomach origin, inserting directly on head of penis. Penis (P) elongated, slender, twisted, length about 1.38-1.60 mm., internally (fig. 64b) with two simple pilasters, vas deferens entering just below apical union of pilasters in V formed by their union. Atrium (Y) rather long.

Free oviduct (UV) tapering gradually from uterus, distinctly wider than vas deferens. Spermatheca (S) with head reaching albumen gland, slender shaft bound to prostate tube and uterus junction, free on lower portion, joining free oviduct just above atrial entrance. Vagina (V) effectively absent due to late union of free oviduct and spermatheca.

Free muscle system typical.

Buccal mass and esophagus without noticeably different features. Stomach starting about one-eighth whorl above apex of pallial cavity, extending apically for one whorl before reflexing into intestine. Intestine typical, coiling pattern occupying an eighth of a whorl between pallial cavity and stomach.

Jaw and radula not satisfactorily mounted.

(Based primarily on BPBM 149428, one specimen in shell 1.68 mm. in diameter with 4⅛ whorls, remaining previously extracted.)

GROUP OF *Minidonta micraconica*

Minidonta micraconica, new species. Figure 65 a-e.

Diagnosis.—Shell very small, diameter 1.95-2.05 mm. (mean 2.00 mm.), with 4⅝-5⅛ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.560-0.597 (mean 0.575). Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, contained 4.42-6.78 times (mean 5.53) in the diameter. Postnuclear sculpture of prominent, broad, rounded, slightly protractively sinuated radial ribs, 65-70 (mean 67.3) on the body whorl, whose interstices are less than twice their width. Microsculpture a lattice of extremely fine coequal radial and spiral riblets, eight to twelve radials between each pair of major ribs. Sutures impressed, whorls compressed laterally above periphery and basally, columellar margin slightly protruded. Aperture ovate, columellar margin prolonged, inclined about 5° from shell axis. Parietal barriers 3, lower greatly reduced, with one accessory trace, extending about three-sixteenths of a whorl: upper a high, thin bladelike lamella with gradual descension over anterior quarter, middle two-thirds with an accessory blade, strongly expanded and serrated (fig. 65d, e) pointing toward or slightly above 3rd palatal barrier; 2nd slightly longer than 1st, extending further anteriorly with more gradual descension, posterior third strongly expanded and serrated; 3rd parietal a low lamellar ridge, less than half length of 2nd, nearly identical in shape to that barrier. Accessory trace a recessed thread, located midway between upper parietal and parietal-palatal margin. Columellar barrier a low to moderate crescentic ridge, parallel to plane of coiling, slightly recessed. Palatal barriers 5, high, extending less than one-eighth whorl, expanded and serrated above, plus two accessory traces: lower a high crescentic ridge, descending sharply to lip edge, twisted at anterior end, located at baso-columellar margin; 2nd slightly lower, with more gradual descension, more bladelike in form; 3rd equal in height to 1st, with rather gradual anterior descension, only slightly recessed; 4th reduced in height, a low lamellar blade, slightly recessed, located nearly on periphery; 5th identical to 4th, located above periphery. Accessory traces short, located between 1st and 2nd, 2nd and 3rd palatals.

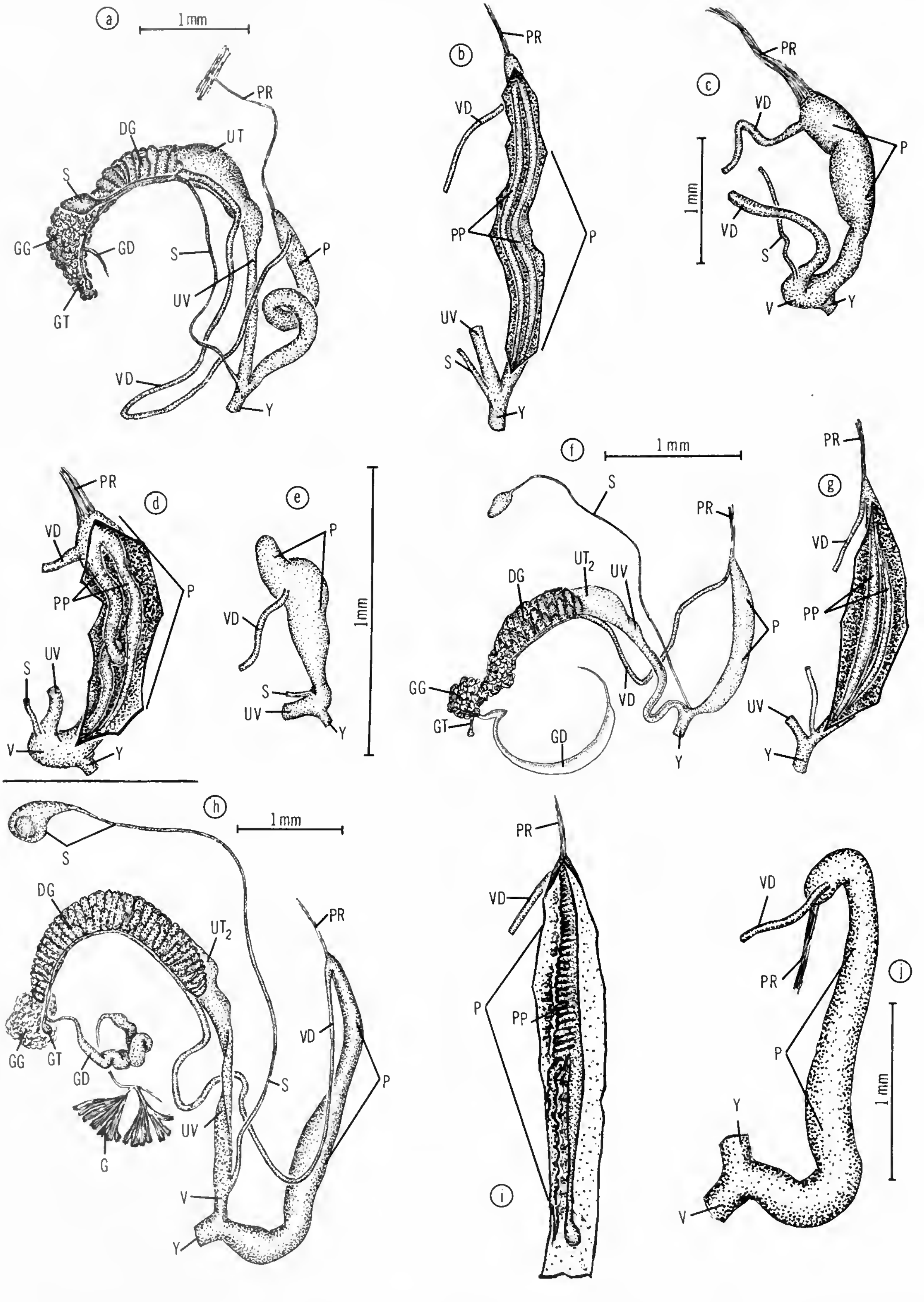

FIG. 64. Anatomy of *Minidonta, Mautodontha, Rhysoconcha,* and *Ruatara:* **a-b**, *Minidonta hendersoni.* Henderson Island. BPBM 149428. *a,* genitalia; *b,* interior of penis; **c-d**, *Mautodontha (M.) zimmermani.* Mt. Aorai, Tahiti, Society Islands. BPBM 145293. *c,* terminal genitalia; *d,* interior of penis; **e**, *Mautodontha (M.) aoraiensis.* Mt. Aorai, Tahiti, Society Islands. BPBM 145536. Terminal genitalia; **f-g**, *Rhysoconcha variumbilicata,* Maitua, Rapa, Austral Islands. BPBM 138337. *f,* genitalia; *g,* interior of penis; **h-i**, *Ruatara oparica normalis.* Mt. Ruatara, Rapa, Austral Islands. BPBM 143492. *h,* genitalia; *i,* interior of penis; **j**, *Ruatara oparica reductidenta,* Maitua, Rapa, Austral Islands. BPBM 137609. Penial complex. Scale lines as marked. (See Appendix for explanation of abbreviations.)

The bifid upper parietal barrier immediately separates *Minidonta micraconica* from most other Austral Island endodontids. Species with similar barrier structure include many of the much larger Hawaiian *Endodonta,* and the closely related *Minidonta gravacosta,* which has only 2 major parietals, a much lower spire and much wider umbilicus.

Description.—Shell very small, with 4¾ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.574. Apical sculpture eroded. Postnuclear whorls with broad, prominent, rounded, slightly protractively sinuated radial ribs, 65 on the body whorl, whose interstices are less than twice their width. Microsculpture extremely fine, a lattice of coequal radial and spiral riblets, eight to twelve between each pair of major ribs. Sutures impressed, whorls strongly rounded, compressed laterally above periphery and on basal margin, columellar wall protruded. Color light reddish-yellow above periphery, base and apex bleached white. Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, contained 6.78 times in the diameter. Aperture ovate, inclined about 5° from shell axis, columellar margin prolonged. Parietal barriers 3, first 2 extending three-sixteenths of a whorl, 3rd greatly reduced, plus one superior accessory trace: upper parietal long, with rather sharp anterior descension, broken off above for most of length; 2nd a high, bladelike lamella, posterior third expanded and serrated, with more gradual anterior descension; 3rd greatly reduced, a short, crescentic, deeply recessed ridge lying along posterior portion of 2nd tooth. Accessory lamella a very inconspicuous threadlike trace above 1st parietal. Columellar barrier a broad, rather recessed, crescentic ridge parallel to plane of coiling. Palatal barriers 5, extending less than one-eighth whorl, plus two accessory traces: lower at baso-columellar margin, very high, expanded and serrated above, descending abruptly to lip edge; 2nd slightly lower, anterior parts broken off; 3rd as high as 1st, slenderer, with sharp, but not plunging anterior descension; 4th located near periphery, broken off above; 5th supraperipheral, a bladelike ridge with more gradual anterior descension than 3rd, rather low. Two accessory traces, a threadlike, inconspicuous ridge between 2nd and 3rd palatals, plus a broader, higher ridge between 1st and 2nd palatals. Height of holotype 1.15 mm., diameter 2.01 mm.

Holotype.—Austral Islands: Raivavae, Station 652, one-quarter mile east of Anatonu village at 50-150 ft. elevation. Collected on a hillside by Yoshio Kondo and Donald Anderson on August 11, 1934. BPBM 147338.

Range.—Near Anatonu village, Raivavae, Austral Islands.

Paratypes.—Same as list of material.

Material.—Raivavae: hillside one-quarter mile east (Station 652) of Anatonu village at 50-150 ft. elevation (4 specimens, BPBM 147338).

Remarks.—The type specimen, unfortunately, has several apertural barriers broken, but is by far the best preserved example in terms of sculpture. Detail sketches (fig. 65d, e) of the upper parietal in a paratype compensate for the missing portions in the holotype.

The bifid upper parietal is almost unique among Austral Island species, although common in Hawaiian *Cookeconcha* and *Endodonta.*

Minidonta gravacosta, new species. Figure 65f-h.

Diagnosis.—Shell very small, diameter 1.79-2.09 mm. (mean 1.97 mm.), with 4¾-5¼ rather tightly coiled whorls. Apex flat to barely elevated, lower whorls of spire descending rather rapidly, H/D ratio 0.424-0.525 (mean 0.466). Umbilicus open, U-shaped, last whorl often decoiling a little more rapidly, contained 3.53-4.92 (mean 3.99) times in the diameter. Postnuclear sculpture of prominent, broad, high, slightly protractive radial ribs, 59-83 (mean 71.2) on the body whorl, whose interstices are 1-2 times their width. Microsculpture a lattice of very fine radial riblets, five to nine between each pair of major ribs, crossed by distinctly finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above and on basal margin, strongly compressed laterally below periphery. Aperture compressedly ovate, inclined less than 5° from shell axis. Parietal barriers 2, extending about three-sixteenths of a whorl: upper a high, thin, bladelike lamella with gradual descension over anterior third, posterior half with a downwards pointing accessory blade, expanded and serrated above; 2nd parietal a very broadly expanded ridge, posterior half equal in height to 1st and serrated above, anterior third much lower. A very weak, deeply recessed, columellar barrier apparently usually present. Palatal barriers 5, extending one-eighth whorl, plus one (67 per cent) or two (33 per cent) accessory traces: lower at baso-columellar margin, very high and broad, abruptly descending to lip margin, crescentic in form; 2nd markedly lower, a broad, bladelike ridge, with more gradual anterior descension, expanded and serrated above; 3rd nearly equal in height to 1st, somewhat recessed, expanded and serrated above; 4th a shorter, greatly reduced lamellar ridge, moderately recessed, slightly subperipheral; 5th same form and length as 4th, much higher, located above periphery. First accessory trace a threadlike ridge to bladelike lamella, expanded and serrated above, located between 1st and 2nd palatals. Second accessory trace, when present, a very short threadlike trace located between 2nd and 3rd palatals.

The Raivavae *Minidonta micraconica* is very closely related, but differs in being higher (mean H/D ratio 0.575), with a narrower umbilicus (mean D/U ratio 5.53), 3 parietals and one accessory trace, plus a quite distinct columellar barrier. *Minidonta gravacosta* has only 2 parietals, a very small, deeply recessed, columellar barrier, much lower spire (mean H/D ratio 0.466) and a wider umbilicus (mean D/U ratio 3.99). No other species of *Minidonta* have a bifid upper parietal.

Description.—Shell very small, with 5¼ rather tightly coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.476. Apical whorls 1½, sculpture of fine, rather crowded radial riblets, with a microsculpture of one microradial riblet between the primary radials and very fine microspirals. Postnuclear whorls with broad, prominent, high, slightly protractive radial ribs, 65 on the body whorl, whose interstices are only slightly greater than their width. Microsculpture of five to six radials between each pair of major ribs, crossed by finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above and on basal margin, strongly compressed laterally below periphery, Color light yellow-white, without darker markings. Umbilicus open, U-shaped, slightly and regularly decoiling, contained 3.93 times in the diameter, margin markedly shouldered. Aperture elongate-ovate, laterally compressed, inclined less than 5° from shell axis. Parietal barriers 2, extending three-sixteenths of a whorl: upper high, quite prominent, gradual descension on anterior third, posterior half with downwards pointing accessory blade, grossly expanded and serrated above; 2nd a much lower barrier, very broadly expanded and serrated above. Columellar barrier a very low, deeply recessed, threadlike ridge, not visible in direct frontal view. Palatal barriers 5, extending one-eighth whorl, plus two accessory traces: lower at baso-columellar margin, high, quite thick, abruptly descending to lip edge; 2nd a much lower, bladelike lamella, somewhat expanded above, slightly recessed, with much more gradual anterior descension; 3rd same shape as 2nd, as high as 1st; 4th a low, moderately recessed lamellar ridge, much smaller than 3rd; 5th higher than 4th, but lower than 2nd, a recessed lamellar ridge. Accessory trace between 1st and 2nd palatals nearly equal in height to 4th palatal, but much shorter; trace between 2nd and 3rd palatals a very short, raised threadlike ridge. Height of holotype 0.99 mm., diameter 2.07 mm.

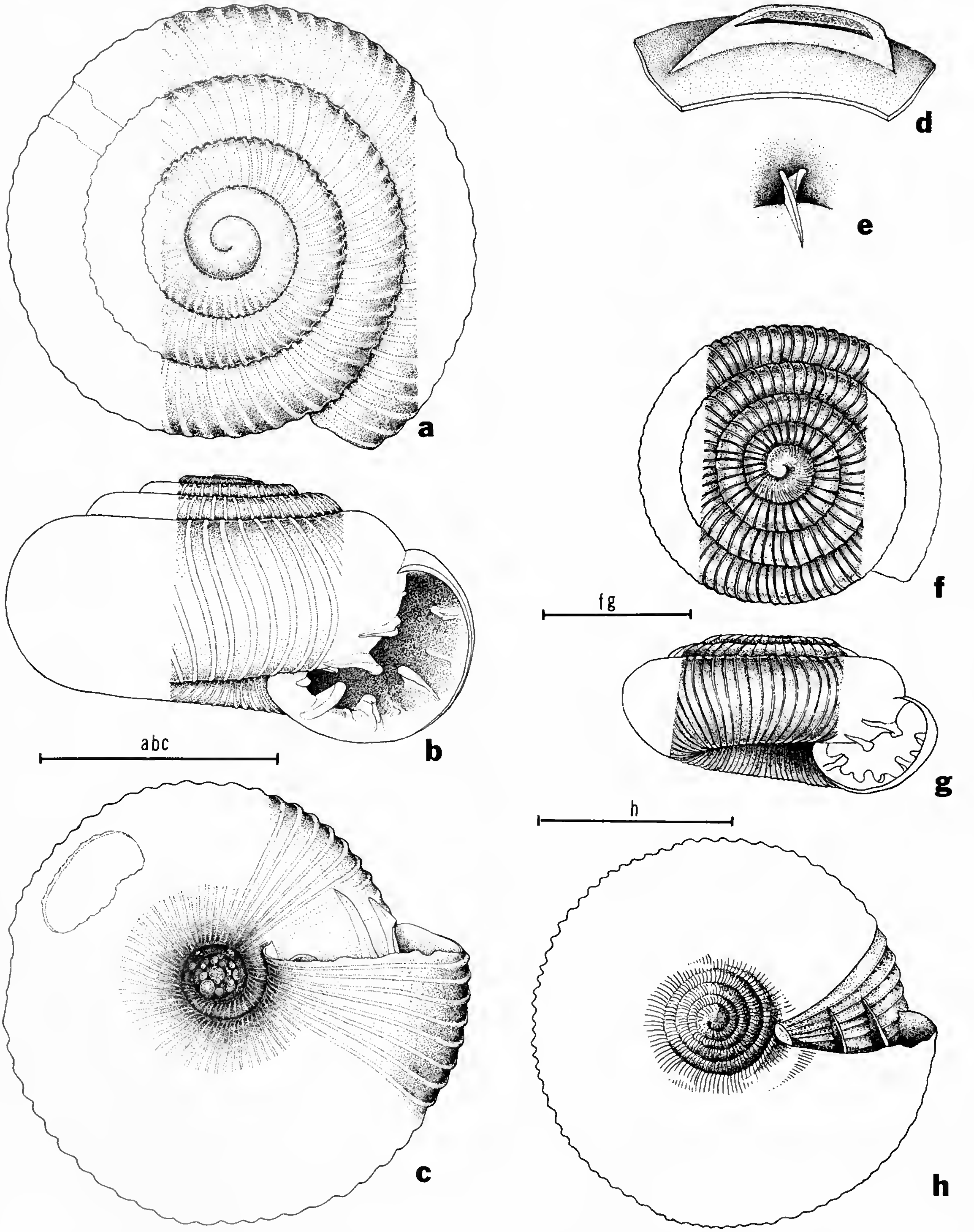

FIG. 65. **a-e**, *Minidonta micraconica*, new species. *a-c*, Station 652, Raivavae, Austral Islands. Holotype. BPBM 147338; *d-e*, detail of 1st parietal lamella, Station 652, Raivavae, Austral Islands. Paratype; **f-h**, *Minidonta gravacosta*, new species. Station 622, Raivavae, Austral Islands. Holotype. BPBM 147098. Scale lines equal 1 mm. (*a-e*, MM; *f-h*, SG).

Holotype.—Austral Islands: Raivavae, Station 622, in a hau and lime thicket at Ahuoivi Point under dead hau leaves. Collected by Yoshio Kondo, Donald Anderson, and C. M. Cooke, Jr. on August 9, 1934. BPBM 147098.

Range.—Known from two lowland stations on Raivavae Island.

Paratypes.—Same as list of material.

Material.—Raivavae: thicket at Ahuoivi Point (Station 622) under dead hau leaves (39 specimens, BPBM 147098, BPBM 142175); subfossil deposit at Raiavua (Station 547) at 5 ft. elevation, about 10-30 ft. inland (2 specimens, BPBM 146170).

Remarks.—Most specimens were not sufficiently cleaned to enable sighting of the recessed columellar barrier. It may be absent in a fair proportion, but this could not be checked.

GROUP OF *Minidonta rotellina*

Minidonta rotellina (Pease, 1870). Figure 62e-f.

Pithys rotellina Pease, 1870, Jour. de Conchyl., **18**, pp. 393-394 — Aitutaki, Cook Islands.
Pitys rotellina Pease, 1871, Proc. Zool. Soc. London, **1871**, pp. 453, 474; Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, **8**, (4), p. 390.
Helix (*Pithys*) *rotellina* (Pease), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 262.
Helix (*Endodonta*) *rotellina* (Pease), Tryon, 1887, Man. Conchol., (2), **3**, p. 60, pl. 11, figs. 82-83.
Endodonta (*Thaumatodon*) *rotellina* (Pease), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 27.

Diagnosis.—Shell very small, diameter 1.83-2.19 mm. (mean 1.97 mm.), with 5-6 tightly coiled whorls. Apex slightly, spire markedly elevated, last whorl descending at same rate, H/D ratio 0.539-0.611 (mean 0.573). Umbilicus quite constricted, last whorl decoiling more rapidly, contained 5.29-8.21 times (mean 7.10) in the diameter. Sculpture of vertical, extremely fine and crowded radial ribs, too numerous for accurate counting, occasionally a slightly finer radial riblet between each pair of major ribs and barely visible, extremely crowded spiral riblets. Sutures deep, whorls evenly rounded on outer margin, slightly compressed basally. Aperture elongate-ovate, with smoothly rounded margin, parallel to shell axis. Parietal barriers 3, extending one-quarter whorl: upper a very high, thin lamella, posterior two-thirds serrated and strongly expanded, anterior quarter with very gradual anterior descension; 2nd with posterior third about half as high as 1st, anterior half threadlike; 3rd with posterior portion markedly lower than 2nd, otherwise identical. Columellar wall with single broad, low rounded ridge, surmounting callus nearly to lip edge and slightly slanted down from plane of coiling. Palatal barriers 2, extending about three-sixteenths of a whorl, often (about 33 per cent) with a faint, short peripheral trace: lower basal in position, a raised V-shaped to rounded ridge, rather deeply recessed; 2nd a very high bladelike lamellar ridge, serrated and strongly expanded above, with very gradual anterior descension, much less recessed than 1st palatal. Palatal trace, when present, located at periphery, undoubtedly the remnant of a former 3rd palatal lamella.

The absence of major radial sculpture, minute size, strongly constricted umbilicus and reduced number of palatal barriers at once separate *Minidonta rotellina* from the other Society and Cook Island species. No other *Minidonta* has such fine sculpture. The irregular spacing between the parietal barriers is equally distinctive.

Description.—Shell minute, with 6 tightly coiled whorls. Spire markedly elevated, apex slightly flattened, H/D ratio 0.606. Embryonic whorls 1⅝, sculpture eroded, remaining whorls with extremely closely spaced, fine, lamellate, vertical radial ribs that are much too numerous to count. Microsculpture consisting of a single radial riblet between the scarcely larger radial ribs and barely visible, quite crowded spiral ribbing. Sutures deep, whorls moderately rounded above, slightly flattened on basal margin. Umbilicus narrow, very constricted, contained 5.54 times in the diameter. Shell dark yellowish white with extensive but irregular reddish flammulations. Aperture ovate, somewhat flattened laterally and basally, parallel to shell axis. Parietal barriers 3, extending slightly more than one-quarter whorl: upper high and lamellate for posterior three-quarters, serrated and grossly expanded above, gradually descending anteriorly: 2nd with anterior two-thirds threadlike, posterior quarter about half the height of 1st; 3rd similar to 2nd, but with posterior portion much lower. Columellar barrier a low, rounded recessed ridge on a relatively thin callus, almost parallel to plane of coiling. Major palatal barriers 2, extending three-sixteenths of a whorl: lower a moderately high lamellate ridge, serrated and broadly rounded above, extending to posterior edge of apertural callus; 2nd a very high lamellate ridge, strongly expanded and serrated above, extending much nearer to apertural edge. Height of lectotype 1.33 mm., diameter 2.19 mm.

Lectotype.—Cook Islands: Aitutaki. Collected by Andrew Garrett. BPBM 2312.

Range.—Aitutaki.

Paratypes.—BPBM 2312.

Material.—Aitutaki (25 specimens, BPBM 2312, FMNH 116988, Zurich, SMF 165459).

Remarks.—Garrett (1881, p. 390) reported that both *Mautodontha imperforata* and *Minidonta rotellina* were common in coastal forests on Aitutaki. Although Peter Buck collected a few *Mautodontha imperforata* in 1929, no specimens of *Minidonta rotellina* have been taken since the early 1880's.

In several respects the apertural barriers are unusual. Proportionately, the 1st parietal is grossly enlarged in size, while the nearly opposite 3rd palatal either is reduced to a barely visible trace or usually is absent. Possibly as a concommitant of the inward apertural prolongation, the columellar barrier and 1st palatal are much smaller than usual and the 2nd palatal is enlarged. Thus enlargement in the 1st parietal and 2nd palatal is balanced by reductions in the 1st and 3rd palatals and columellar ridge. Also, the distance between the 1st and 2nd parietals is more than twice the distance between the 2nd and 3rd parietals, where in most other species of endodontids, the distance between parietal barriers is essentially identical.

The general similarities (fig. 61) of *Mautodontha imperforata* to *Minidonta rotellina* are misleading. The former has much less reduced sculpture, the apertural barriers split in several cases, and a different pattern of whorl coiling.

GROUP OF *Minidonta anatonuana*

Specimens of this complex are relatively similar and show slight-to-moderate overlap in almost every

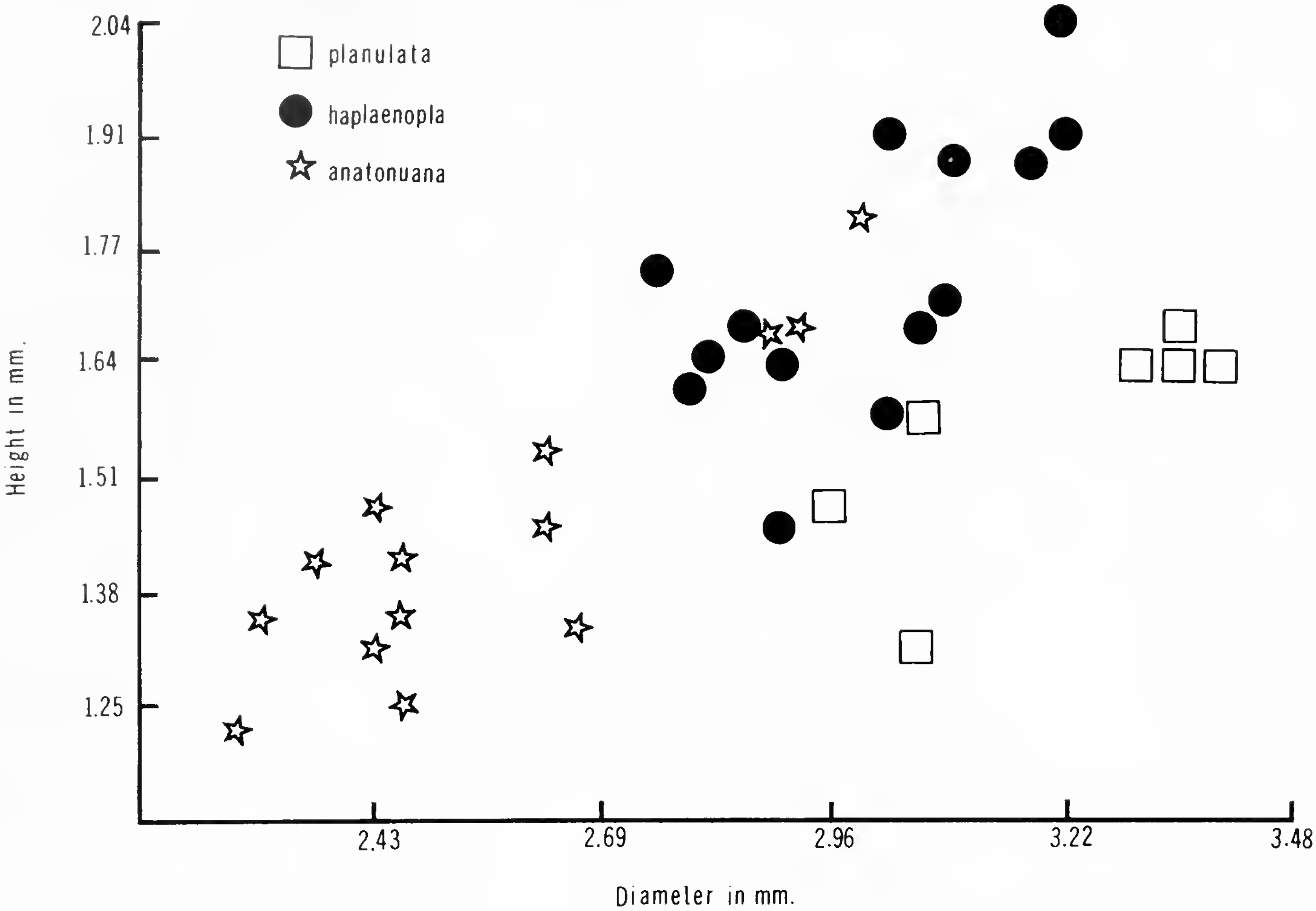

FIG. 66. Correlation of height and diameter in *Minidonta anatonuana, M. haplaenopla,* and *M. planulata.*

meristic character. The columellar sulcus of *Minidonta sulcata* (fig. 68f) at once identifies that species, but the others can be confused. Plotting of the height and diameters for *M. planulata, M. haplaenopla,* and *M. anatonuana* (fig. 66) shows the last two share a common pattern of growth, but *M. anatonuana* is smaller, while *M. planulata* has an altered pattern. A similar comparison of the D/U ratio and diameter (fig. 67) will assist in separating doubtful examples. With reference to these charts and barrier structure, even worn examples can be identified with certainty.

Minidonta anatonuana, new species. Figure 68a-c.

Diagnosis.—Shell very large, diameter 2.78-3.25 mm. (mean 3.02 mm.), with 5-6 normally coiled whorls. Apex and spire markedly elevated, last whorl descending a little more rapidly, H/D ratio 0.500-0.633 (mean 0.577). Umbilicus narrow, U-shaped, last whorl decoiling slightly more rapidly, contained 4.90-7.73 times (mean 5.87) in the diameter. Postnuclear whorls with high, prominent, rounded, protractively sinuated radial ribs, 83-94 (mean 89.5) on the body whorl, whose interstices are 2-3 times their width. Microsculpture a lattice of fine radial riblets, three to five between each pair of major ribs, crossed by finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, flattened to very slightly concave above periphery, evenly rounded and somewhat compressed below periphery. Aperture ovate, noticeably flattened above periphery, inclined about 10° from shell axis. Parietal barriers 3, extending more than one-quarter whorl, first 2 quite large: upper parietal a very high, thin, bladelike lamella, very slightly expanded above, with gradual descension until anterior eighth; 2nd parietal with posterior half equal in height to 1st, anterior quarter to third a low bladelike lamella, extending further than 1st; 3rd parietal greatly reduced in height, a bladelike to V-shaped recessed ridge lying along posterior half of 2nd parietal. Columellar barrier absent, although 1st palatal located at baso-columellar margin. Palatal barriers 4, prominent, extending three-sixteenths of a whorl, often with an accessory trace: lower at baso-columellar margin, a low, bladelike lamella with gradual anterior descension; 2nd much higher, longer, less recessed, with slightly more gradual anterior descension; 3rd quite high, pointing between 1st and 2nd palatals, thin, nearly reaching lip margin, with sharper anterior descension; 4th suprapepheral, a reduced V-shaped to lamellar ridge, deeply recessed and shortened. Palatal trace, when present, situated between 1st and 2nd palatals.

The palatal barriers of *Minidonta anatonuana* relate it to the *inexpectans-manuaensis-sulcata* complex, from which it differs by its much larger size, smaller umbilicus and lack of a columellar barrier. *M. haplaenopla* has finer and more crowded ribs and usually less than 4 palatals.

Description.—Shell small, with 5¼ normally coiled whorls. Apex and spire strongly elevated, last whorl descending a little more rapidly, H/D ratio 0.568. Embryonic whorls 1½, only trace of typical radial and microsculpture remaining. Remaining whorls with high, prominent, rounded, slightly protractively sinuated radial ribs, 94 on the body whorl, whose interstices are less than twice their width. Microsculpture a lattice of very fine radial and even finer spiral riblets. Sutures deep, whorls strongly rounded above, flattened to

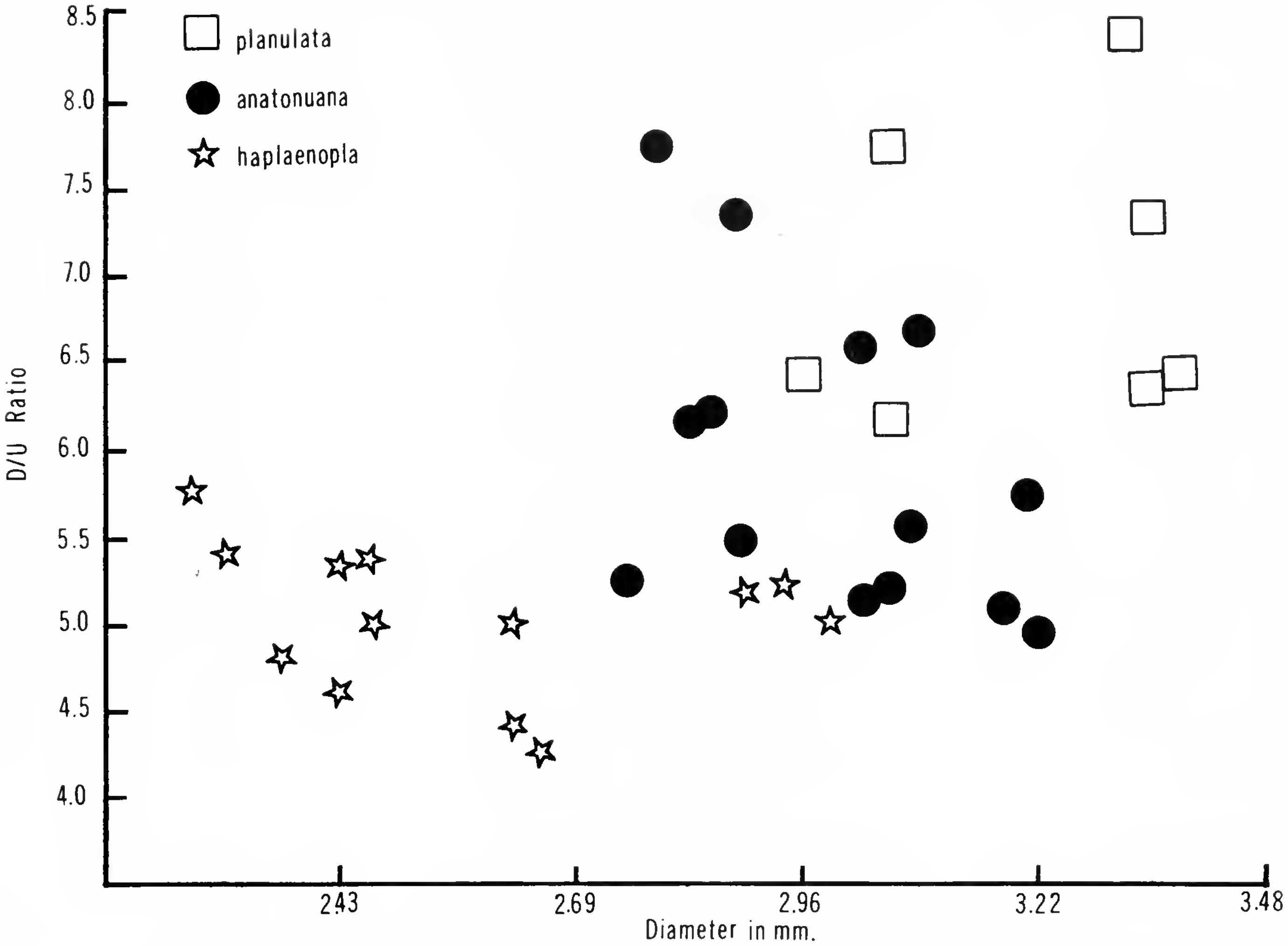

FIG. 67. Correlation of diameter and D/U ratio in *Minidonta anatonuana, M. haplaenopla*, and *M. planulata*.

slightly concave above periphery, compressed on lower palatal margin. Color leached from shell. Umbilicus quite narrow, U-shaped, last whorl decoiling more rapidly, contained 5.50 times in the diameter. Aperture ovate, flattened above, compressed below periphery, inclined about 15° from shell axis. Parietal barriers 3, extending more than one-quarter whorl: upper a very high, thin, bladelike lamella, not expanded above, descending sharply at anterior end; 2nd with posterior half as in 1st, anterior quarter a raised, threadlike ridge; 3rd a low threadlike ridge along posterior half of 2nd tooth. No columellar barrier. Palatal barriers 4, extending more than one-eighth whorl, with one accessory trace: lower at basocolumellar margin, a low lamellar ridge crossing callus and nearly reaching apertural margin; 2nd much higher, pointing towards 2nd parietal, an elevated lamellar ridge with gradual anterior descension, nearly reaching lip margin; 3rd a quite high, bladelike lamella, with very gradual anterior descension; 4th a deeply recessed, V-shaped trace, supraperipheral. Accessory trace threadlike, short, located between 1st and 2nd palatals, moderately recessed. Callus on columellar and lower palatal wall rather thick. Height of holotype 1.65 mm., diameter 2.90 mm.

Holotype.—Austral Islands: Raivavae, Station 652, one-quarter mile east of Anatonu village at 50-150 ft. elevation. Collected by Yoshio Kondo and Donald Anderson on August 11, 1934. BPBM 147384.

Range.—Near Anatonu village, Raivavae, Austral Islands.

Paratypes.—Same as list of material.

Material.—Raivavae: one-quarter mile east of Anatonu village (Stations 633, 636, 652) at 50-500 ft. elevation (33 specimens, BPBM 147167, BPBM 147196, BPBM 147384-5, BPBM 147387).

Remarks.—All specimens of *Minidonta anatonuana* were from subfossil deposits and the apertures clogged with dirt. Not all individuals were cleaned sufficiently to check the presence or absence of the palatal trace, but about two-thirds of those checked had the trace present.

The slight indication of a supraperipheral sulcus, big barriers, and narrowly U-shaped umbilicus with rapidly decoiling last whorl present an appearance somewhat intermediate between *Australdonta* and *Minidonta*. The form of the barriers is the same as in *M. inexpectans* and *M. manuaensis*. *M. anatonuana* lacks the sculpture and shell form of *Australdonta*. The umbilical characters are those of *Minidonta* and association with these species is the most logical choice in classifying this species.

Minidonta sulcata, new species. Figure 68d-f.

Diagnosis.—Shell of average size, diameter 2.25-2.32 mm. (mean 2.28 mm.), with 5-5½ tightly coiled whorls. Apex and spire

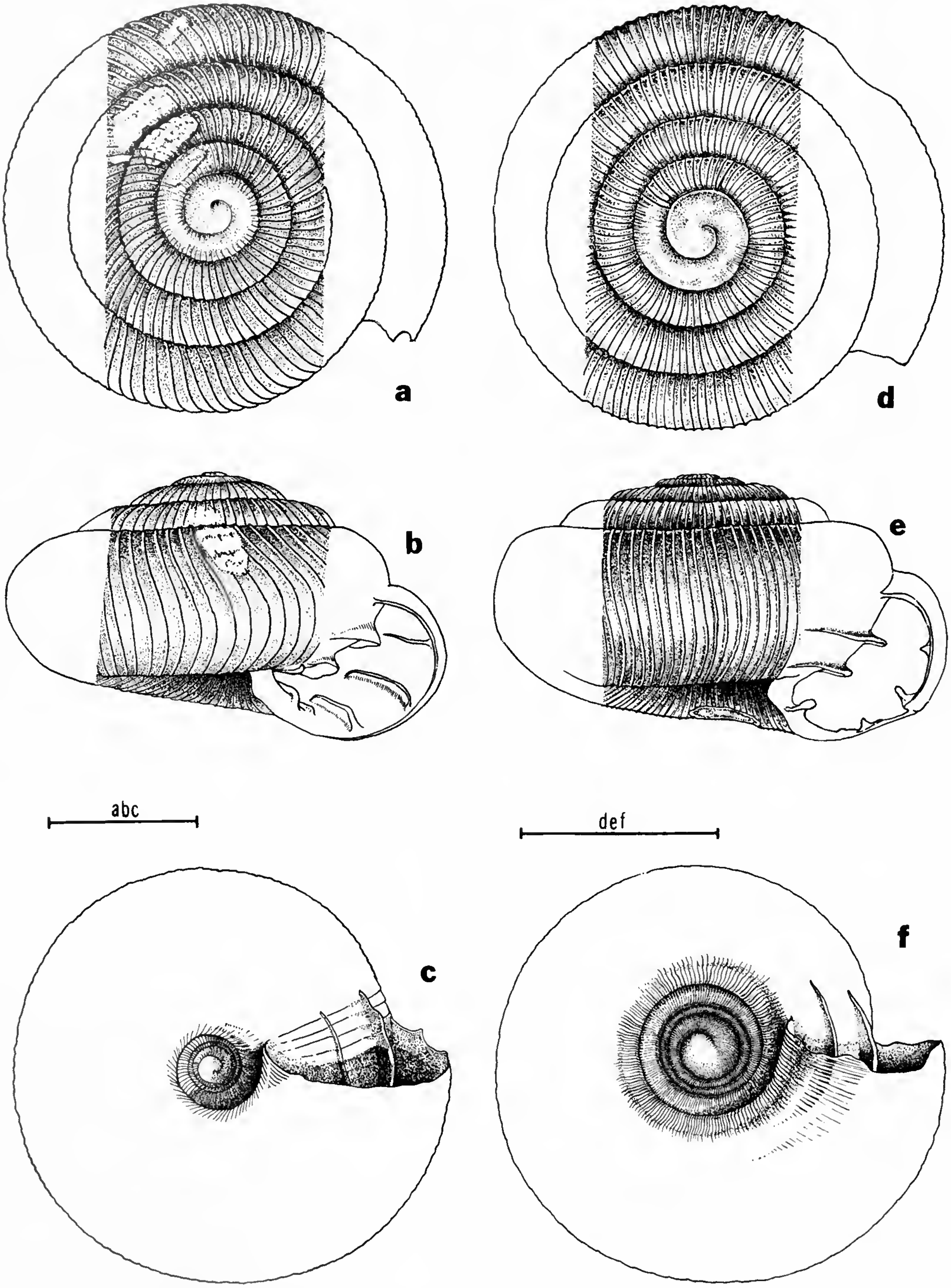

FIG. 68. **a-c**, *Minidonta anatonuana,* new species. Station 652, Raivavae, Austral Islands. Holotype. BPBM 147384; **d-f**, *Minidonta sulcata,* new species. Station 652, Raivavae, Austral Islands. Holotype. BPBM 215242. Scale lines equal 1 mm. (SG).

moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.574-0.600 (mean 0.587). Umbilicus narrow, U-shaped, last whorl decoiling slightly more rapidly, contained 4.00-5.00 times (mean 4.50) in the diameter. Umbilical margin protruded into a "beak", columellar wall with a strong sulcus. Postnuclear whorls with high, rounded, prominent, vertically sinuated radial ribs, 105-120 (mean 112.5) on the body whorl, whose interstices are about twice their width. Microsculpture a lattice of fine radial riblets, three to five between each pair of major ribs, crossed by very fine spiral ribs, about half the size of radials. Sutures deep, whorls strongly rounded above, slightly compressed laterally above and below evenly rounded periphery, umbilical margin as described above. Aperture ovate, inclined less than 5° from shell axis. Parietal barriers 2, extending less than three-sixteenths of a whorl: upper a high bladelike ridge with gradual anterior descension, posterior elevated half serrated and expanded above; 2nd equal in height to 1st, longer, with same shape, extending further anteriorly. Columellar barrier a high, bladelike lamella, parallel to plane of coiling until just inside aperture, suddenly descending anteriorly, nearly reaching lip margin. Palatal barriers 4, 1st and 4th greatly reduced, 2nd and 3rd extending about one-eighth whorl: 1st basal, an inconspicuous threadlike trace; 2nd a low lamellar ridge with gradual anterior descension, nearly reaching lip edge; 3rd a high lamellar blade with sharper anterior descension; 4th supraperipheral, an inconspicuous, recessed, V-shaped ridge.

The striking columellar sulcus at once separates *Minidonta sulcata* from the other species of *Minidonta.* The simplified set of barriers is basically like that found in *M. inexpectans,* differing only in the presence of a large columellar and only 2 parietal barriers.

Description.—Shell very small, with 5 tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.574. Embryonic whorls 1⅜, sculpture completely eroded. Remaining whorls with high, prominent, rounded, vertically sinuated radial ribs, 120 on the body whorl, whose interstices are less than twice their width. Microsculpture of extremely fine radial riblets, three to five between each pair of major ribs, crossed by finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded, with lateral compression above and below periphery. Umbilical margin with deep sulcus and protruding keel. Color mainly leached from shell. Umbilicus narrow, U-shaped, last whorl decoiling slightly more rapidly, contained 4.00 times in the diameter. Aperture ovate, lip edge badly broken. Parietal barriers 2, extending about three-sixteenths of a whorl: upper a high, bladelike lamella, posteriorly serrated and expanded, anteriorly with gradual descension; 2nd longer, extending somewhat further anteriorly, identical in shape. Columellar barrier high, bladelike, abruptly descending anteriorly, slightly angled downwards from plane of coiling, nearly reaching lip edge. Palatal barriers 4, extending about one-eighth whorl: lower a very inconspicuous threadlike trace, basal in position; 2nd a moderate lamellar ridge with gradual anterior descension; 3rd a much higher, bladelike lamella with sharper anterior descension; 4th a shorter, deeply recessed V-shaped ridge, supraperipheral. Height of holotype 1.28 mm., diameter 2.24 mm.

Holotype.—Austral Islands: Raivavae, Station 652, one-quarter mile east of Anatonu village at 50-150 ft. elevation. Collected on a hillside by Yoshio Kondo and Donald Anderson on August 11, 1934. BPBM 215242.

Range.—Near Anatonu village, Raivavae, Austral Islands.

Paratypes.—Same as list of material.

Material.—Raivavae: one-quarter mile east of Anatonu village (Station 652) at 50-150 ft. elevation on a dry hillside (4 specimens, BPBM 147384).

Remarks.—No important variation in barrier structure was noted. While the sulcus and large columellar barrier are diagnostic and make *Minidonta sulcata* seem a highly distinctive species, the form of the palatal barriers and shell shape indicate its close relationship to *M. inexpectans* and *M. manuaensis.*

Minidonta haplaenopla, new species. Figure 69 d-f.

Diagnosis. — Shell rather large, diameter 2.28-3.01 mm. (mean 2.59 mm.), with 4⅝-5⅝ normally coiled whorls. Apex flat, spire slightly elevated, last whorl descending more rapidly, H/D ratio 0.506-0.608 (mean 0.563). Umbilicus narrow, open, U-shaped, only slightly decoiling, contained 4.26-5.75 times (mean 5.06) in the diameter. Postnuclear sculpture of prominent, narrow, slightly protractively sinuated radial ribs, 91-125[1] (mean 109.6) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of extremely fine radial riblets, four to seven between each pair of major ribs, crossed by even finer and more crowded spiral ribs, with a secondary sculpture of rather widely spaced spiral cords. Sutures deep, whorls strongly rounded above, evenly rounded on compressed outer margin, umbilical margin strongly rounded. Aperture compressedly ovate, inclined about 5° from shell axis. Parietal barriers 3, rarely 2 (9.5 per cent), extending one-quarter whorl: upper a high bladelike lamella, gradually descending over anterior half; 2nd with posterior eighth usually equal in height to 1st, expanded and serrated, anterior half a high threadlike ridge; 3rd with posterior section reduced in height, not expanded, anterior half a lower threadlike ridge. No columellar barrier. Palatal barriers 3, extending less than one-eighth whorl, low bladelike ridges: lower rather short, basal in position, flat, expanded and serrated posteriorly, with very gradual anterior descension; 2nd much higher, larger, with sharper anterior descension, rather deeply recessed, tending towards crescentic form above.

Smaller in size than *M. anatonuana* and *M. planulata, Minidonta haplaenopla* differs from them primarily in its reduced barrier complement and finer sculpture, plus adding a secondary sculpture of spiral cords. The absence of a columellar barrier also is a distinguishing character.

Description. — Shell rather small, with 5⅝ normally coiled whorls. Apex nearly flat, spire strongly elevated, last whorl not descending more rapidly, H/D ratio 0.561. Apical whorls 1⅝, sculpture eroded. Postnuclear whorls with low, rounded, very closely set, almost vertically sinuated radial ribs, 179 on the body whorl, whose interstices are equal to their width. Microsculpture a lattice of very fine radials and barely visible spirals, with a secondary sculpture of rather inconspicuous spiral cords. Sutures deep, whorls strongly rounded above and on umbilical margin, strongly compressed laterally below periphery. Umbilicus, narrow, U-shaped, last whorl decoiling slightly more rapidly, contained 5.23 times in the diameter. Color light reddish-horn, with vague traces of lighter markings. Aperture elongate-ovate, inclined slightly more than 5° from shell axis. Parietal barriers 3, extending less than one-quarter whorl, partly broken: upper with posterior quarter absent, anterior portion a gradually descending, rather low, bladelike lamella; 2nd with posterior third moderately elevated, anterior half threadlike; 3rd a low threadlike trace for entire length. No columellar barrier. Palatal barriers 3, low and short: 1st a moderately recessed, short crescentic lamellar trace; 2nd a less deeply recessed lamellar ridge with gradual anterior descension; 3rd a much shorter, deeply recessed lamellar trace. Height of holotype 1.68 mm., diameter 2.93 mm.

Holotype.—Austral Islands: Rurutu, Station 748, Mato Naa cliffs at 250 ft. elevation. Collected dead by

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[1] In one gerontic adult, 179 ribs.

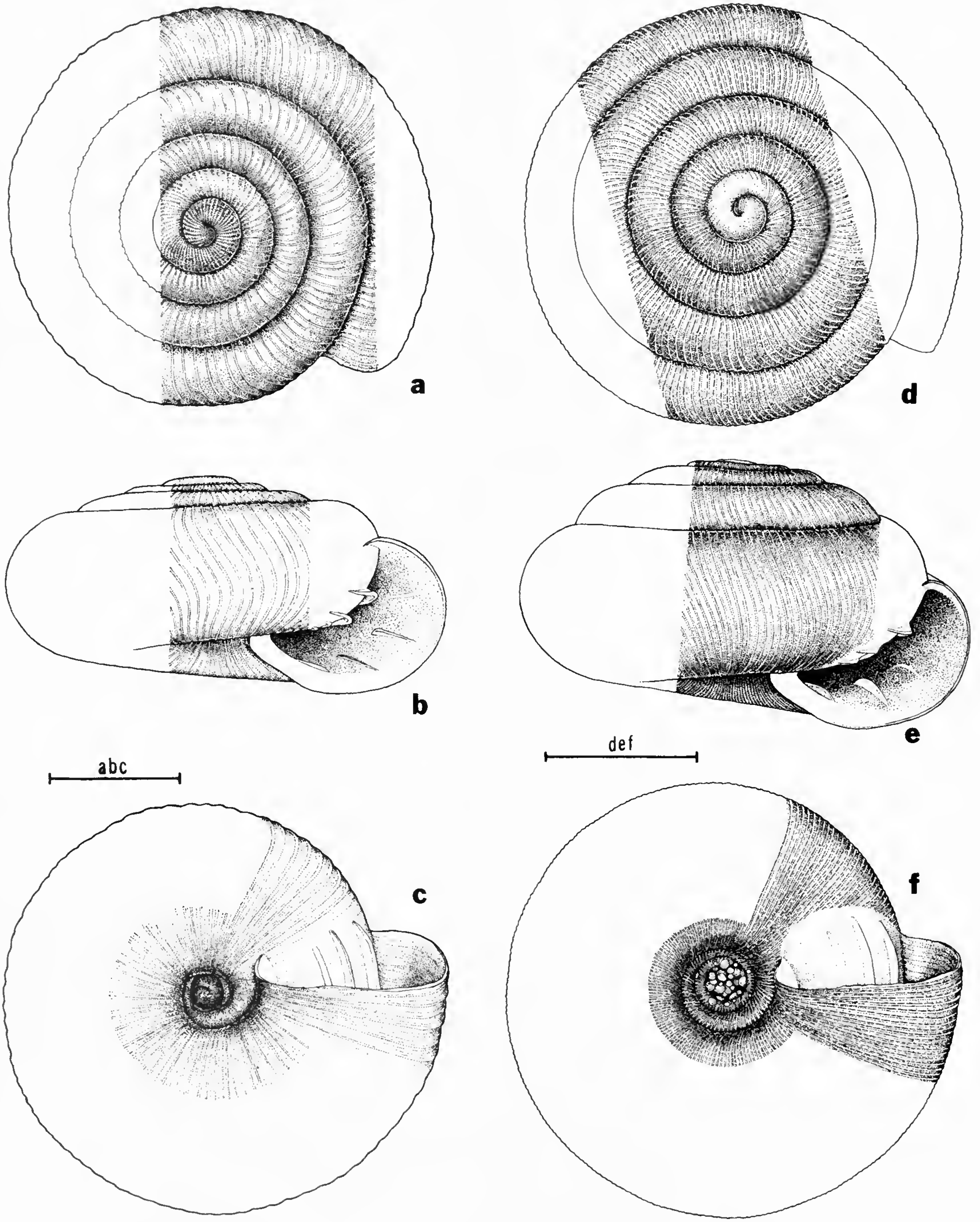

FIG. 69. **a-c**, *Minidonta planulata*, new species. Station 633, Raivavae, Austral Islands. Holotype. BPBM 147166; **d-f**, *Minidonta haplaenopla*, new species. Station 748, Rurutu, Austral Islands. Holotype. BPBM 148129. Scale lines equal 1 mm. (MM).

TABLE LXIV. - LOCAL VARIATION IN MINIDONTA

Name	Number of Specimens	Height	Diameter	H/D ratio	Whorls	D/U ratio
manuaensis BPBM 188720, BPBM 186774, BPBM 186758	4	0.96±0.040 (0.89-1.08)	1.68±0.052 (1.59-1.82)	0.572±0.0065 (0.563-0.590)	4+ (4-4 1/4)	5.28±0.295 (4.79-6.13)
micra BPBM 138757	20	1.09±0.014 (0.96-1.19)	1.73±0.011 (1.67-1.89)	0.625±0.0063 (0.563-0.667)	4 1/2- (4 1/4-4 3/4)	4.99±0.114 (3.61-5.88)
hendersoni BPBM 149574, -631, -729, -858, -929	29	1.34±0.020 (1.16-1.59)	2.16±0.025 (1.85-2.45)	0.621±0.0048 (0.575-0.685)	5+ (4 1/2-5 1/2)	3.67±0.069 (3.09-4.35)
micraconica BPBM 147388	4	1.15±0.028 (1.09-1.23)	2.00±0.022 (1.95-2.05)	0.575±0.0080 (0.560-0.597)	4 3/4+ (4 5/8- 5)	5.53±0.515 (4.42-6.78)
gravacosta BPBM 147098	12	0.92±0.016 (0.83-1.03)	1.97±0.025 (1.79-2.09)	0.466±0.0095 (0.424-0.525)	5- (4 1/2-5 1/4)	3.99±0.110 (3.53-4.92)
rotellina BPBM 2312	6	1.14±0.044 (1.04-1.33)	1.97±0.051 (1.84-2.19)	0.575±0.0071 (0.562-0.609)	5 1/2 (5 1/4-6)	7.08±0.423 (5.54-8.13)
FMNH 116988	7	1.13±0.031 (1.02-1.27)	1.98±0.044 (1.84-2.19)	0.569±0.0100 (0.539-0.611)	5 3/8+ (5-5 5/8)	7.26±0.364 (5.29-8.21)
anatonuana BPBM 147384	12	1.69±0.036 (1.46-1.92)	2.99 ± 0.042 (2.78-3.25)	0.567±0.0104 (0.500-0.631)	5 3/8+ (5-5 1/2)	5.89±0.269 (4.90-7.73)
sulcata BPBM ex 147384	3	1.39±0.057 (1.29-1.49)	2.28±0.033 (2.25-2.32)	0.587±0.0127 (0.574-0.600)	5 1/4+ (5-5 1/2)	4.50±0.502 (4.00-5.00)
haplaenopla BPBM 148129	7	1.55±0.069 (1.36-1.82)	2.71±0.099 (2.32-3.01)	0.570±0.0132 (0.506-0.608)	5 1/4 (4 7/8-5 5/8)	5.06±0.114 (4.26-5.39)
BPBM 148686	7	1.37±0.043 (1.23-1.57)	2.46±0.042 (2.28-2.65)	0.555±0.0121 (0.507-0.597)	5- (4 3/4-5 1/8)	5.05±0.178 (4.44-5.75)
planulata BPBM 147166 ex 147384	6	1.62±0.030 (1.49-1.69)	3.26±0.075 (2.98-3.41)	0.495±0.0049 (0.484-0.517)	5 (4 3/4-5 1/8)	7.12±0.347 (6.37-8.42)
taunensis BPBM 140884	2	1.18±0.050 (1.13-1.23)	2.25±0.066 (2.19-2.32)	0.527±0.0020 (0.525-0.529)	5 1/8+ (5-5 3/8)	3.36±0.311 (3.05-3.67)
taravensis BPBM 138884	2	1.42±0.066 (1.36-1.49)	2.58±0.099 (2.48-2.68)	0.551±0.0050 (0.546-0.556)	5 1/2 (5 3/8-5 5/8)	6.11±0.707 (5.40-6.82)
simulata BPBM 138698, BPBM 138756	17	1.53±0.025 (1.39-1.79)	2.71±0.030 (2.45-2.88)	0.566±0.0082 (0.518-0.658)	5 1/8- (4 3/4-5 5/8)	4.82±0.155 (3.96-6.31)

Yoshio Kondo and C. M. Cooke, Jr. on August 25, 1934. BPBM 148129.

Range.—Mato Naa area at 10-250 ft. elevation, Rurutu, Austral Islands.

Paratypes.—Same as list of material.

Material.—Rurutu, Mato Naa area (Stations 748, 768, 792) at 10-250 ft. elevation (77 specimens, BPBM 148129, BPBM 148686, BPBM 148402).

Remarks.—The type is a relatively gerontic shell in which size of the barriers is quite reduced, compared with younger individuals, and the radial ribbing is very crowded. Other gerontic specimens, two in number, have the 3rd parietal lost and the 3rd palatal reduced to a very slight trace. Also the entire palatal wall becomes covered with a rather thick callus.

Specimens from Stations 748 and 792 differed significantly (table LXIV) in respect to diameter (with 12 df, "t" = 2.3259), reflecting only the presence of gerontic individuals in the set from Station 748. The slight difference in H/D ratio is not significant ("t" = 0.8388). The name *haplaenopla* is derived from the Greek words meaning "simply armed" and refers to the undistinguished apertural barriers. The only slight decoiling of the last umbilical whorl and secondary microsculpture are not the usual characters of *Minidonta,* but the pattern of the barrier structure is so similar to *M. inexpectans* and *M. manuaensis* that I have no hesitation about including *M. haplaenopla* in this genus. The characters of *M. haplaenopla* begin to approach those of *Australdonta,* which is quite possibly a direct local derivative of *Minidonta.*

Minidonta planulata, new species. Figure 69a-c.

Diagnosis. — Shell extremely large, diameter 2.98-3.41 mm. (mean 3.26 mm.), with 4¾-5⅛ normally coiled whorls. Apex and spire evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.484 -0.517 (mean 0.495). Umbilicus very narrow, constricted, last whorl decoiling more rapidly, contained 6.37-8.42 times (mean 7.12) in the diameter. Postnuclear sculpture of prominent, rounded, strongly protractively sinuated radial ribs, 88-99 (mean 94) on the body whorl, whose interstices are 2-5 times their width. Microsculpture of low, fine, quite widely spaced radial riblets, three to six between each pair of major ribs, crossed by barely visible, crowded spiral riblets. Sutures deep, whorls evenly rounded on outer margin, slightly compressed laterally above periphery, flattened on basal margin, with very strongly rounded umbilical margin. Aperture ovate, flattened basally, inclined slightly more than 20° from shell axis. Parietal barriers 3, extending one-quarter whorl: upper a high, bladelike lamella, posterior third weakly expanded and serrated above, anterior end very sharply descending; 2nd with posterior elevated portion distinctly lower, but more broadly expanded, anterior half a very low bladelike lamella; 3rd parietal a low threadlike ridge, very weakly elevated posteriorly. No columellar barrier. Palatal barriers 4, very low, extending about one-eighth whorl: lower a raised threadlike ridge partly hidden behind apertural callus, basal in position; 2nd equal in size to 1st, deeply recessed; 3rd slightly higher and longer, a trifle less recessed; 4th a very inconspicuous, short, deeply recessed, V-shaped trace.

The highly constricted umbilicus, lack of secondary spiral sculpture, and absence of the supraperipheral sulcus are the main characters separating *Minidonta planulata* from *Australdonta.* The large size, depressed shape, very narrow umbilicus, and absence of a columellar barrier readily distinguish *M. planulata* from the other *Minidonta.*

Description. — Shell of average size, with 5 normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.486. Apical sculpture of fine, quite widely spaced radial ribs, with finer, more crowded spiral riblets, radial sculpture becoming much more crowded at end of apex. Postnuclear whorls with narrow, prominent, strongly protractively sinuated radial ribs, 99 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine, widely spaced radial riblets, three to six between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures impressed, whorls evenly rounded on outer margins, slightly compressed laterally above periphery, flattened on basal margin, umbilical margin very strongly rounded. Umbilicus strongly constricted, U-shaped, last whorl suddenly decoiling, contained 6.44 times in the diameter. All color leached from shell. Aperture compressedly ovate, flattened basally, inclined more than 20° from shell axis. Parietal barriers 3, extending nearly one-quarter whorl: upper very high and bladelike, posterior quarter serrated and weakly expanded with very sharp anterior descension; 2nd with lower posterior portion, anterior half a low lamellar ridge; 3rd a very low threadlike trace, not expanded posteriorly. Columellar barrier absent. Palatal barriers 4, extending one-eighth whorl, quite low and inconspicuous: lower hidden behind apertural callus, a raised threadlike ridge; 2nd a raised lamellar ridge, rather deeply recessed; 3rd slightly higher, less deeply recessed; 4th a short, very deeply recessed, V-shaped trace. Height of holotype 1.65 mm., diameter 3.39 mm.

Holotype. — Austral Islands: Raivavae Island, Station 633, one-quarter mile east of Anatonu village at 50-150 ft. elevation. Collected on a hillside by Yoshio Kondo and Donald Anderson on August 10, 1934. BPBM 147166.

Range. — Near Anatonu Village, Raivavae, Austral Islands.

Paratypes. — Same as list of material.

Material. — Raivavae: one-quarter mile east of Anatonu village (Stations 633, 653) at 50-150 ft. elevation (7 specimens, BPBM 147166, BPBM 147384).

Remarks. — Although agreeing with *Australdonta* in size and general appearance, the presence of only 3 palatal barriers, constricted umbilicus, absence of secondary spiral grooving, and lack of a supraperipheral sulcus in *Minidonta planulata* effectively distinguish it from *Australdonta.* Although by far the largest *Minidonta,* the apertural and umbilical characters of *M. planulata* agree fully with more typical species.

No significant variation was noted in the limited material available.

GROUP OF *Minidonta simulata*

Minidonta taunensis, new species (Solem & Cooke). Figure 70e-f.

Diagnosis. — Shell average in size, diameter 2.19-2.32 mm. (mean 2.25 mm.) with 5-5⅜ normally coiled whorls. Apex flat, spire slightly elevated, last whorl descending much more rapidly, H/D ratio 0.525-0.529 (mean 0.527). Umbilicus open, U-shaped, last whorl decoiling much more rapidly, contained 3.05-3.67 times (mean 3.36) in the diameter. Postnuclear whorls with narrow, rounded, slightly protractively sinuated radial ribs, 113 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of rather prominent radial riblets, three to five between each pair of major ribs, crossed by very fine and crowded, barely visible spiral riblets. Sutures impressed, whorls strongly rounded above and on basal margin, slightly compressed laterally. Aperture ovate, inclined about 10° from shell axis. Parietal barriers 3, extending more than one-quarter whorl: upper a high, thin blade, weakly expanded above for posterior three-quarters, anterior quarter much lower after abrupt descension; 2nd equal in height to 1st for posterior five-eighths, more expanded and serrated above, anterior third threadlike; 3rd with posterior elevated portion less than half the height of 2nd, anterior threadlike portion very short, stopping far back of anterior end of 2nd parietal. Columellar barrier a broad, low, crescentic ridge, moderately recessed, with anterior end angled slightly downwards. Palatal barriers 4, long, bladelike ridges, extending nearly three-eighths whorl, plus one faint superior trace: lower a narrow bladelike lamella, suddenly descending anteriorly to a threadlike extension; 2nd much higher, more broadly expanded and serrated, with more gradual anterior descension, coming nearer to lip edge; 3rd distinctly higher than 2nd, less recessed, with more gradual anterior descension; 4th a narrow, prominent, V-shaped ridge, much lower than 3rd palatal, lying opposite upper parietal.

Although very similar in general appearance to *Mautodontha daedalea,* the internally constricted umbilicus, presence of a distinct columellar barrier, very small size and much higher spire easily separate

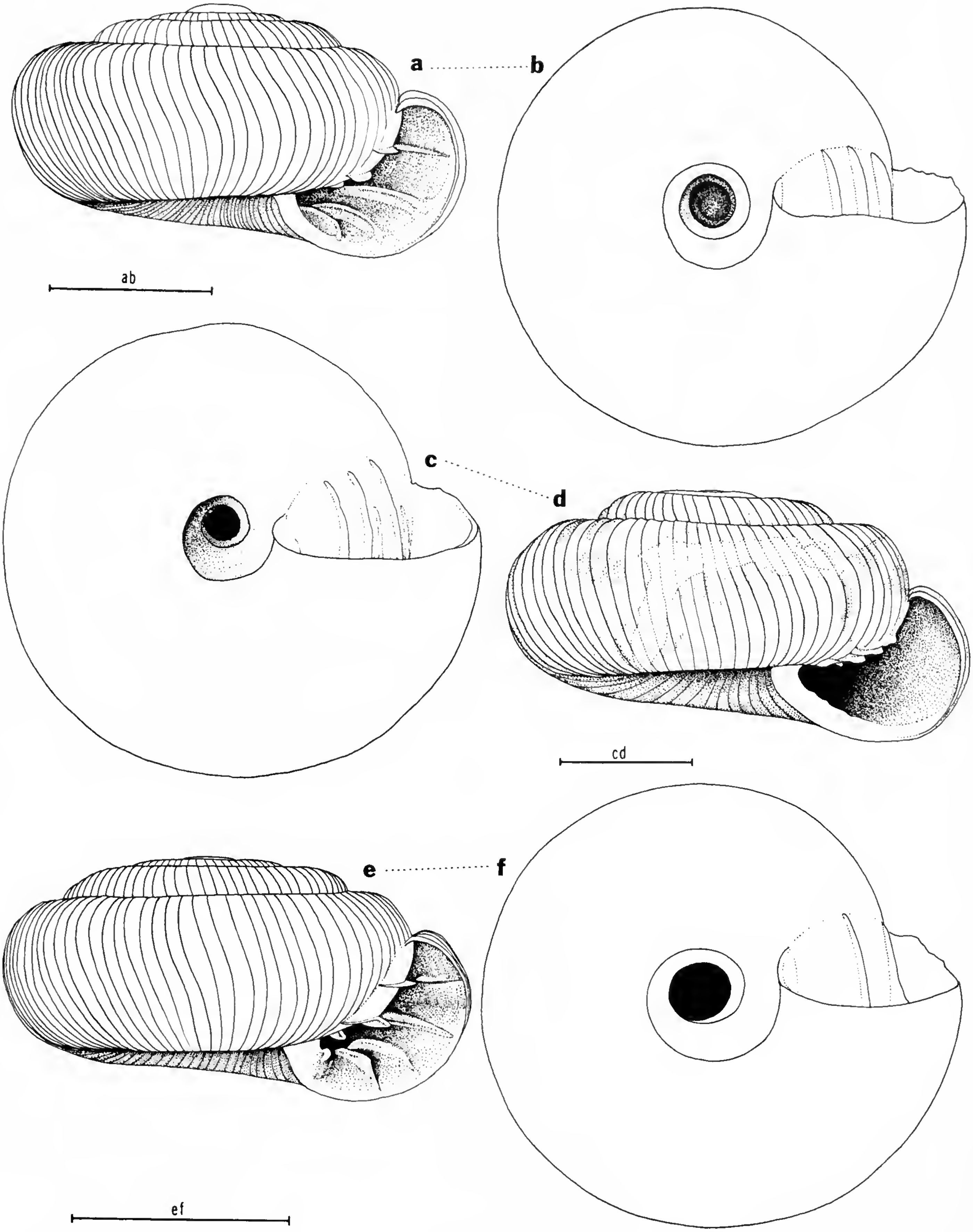

FIG. 70. **a-d**, *Minidonta simulata,* new species. *a-b,* Station 88, Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 138698; *c-d,* Station 102, Aukena Islet, Mangareva, Gambier Islands. A gerontic individual. BPBM 9409; **e-f**, *Minidonta taunensis,* new species. Station 90, Tauna Islet, Mangareva, Gambier Islands. Holotype. BPBM 140884. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Minidonta taunensis. Of the other Mangarevan species, *M. taravensis* has much coarser ribbing, a 4th parietal and a much narrower umbilicus; *M. simulata* is larger, with more widely spaced ribbing, usually lacks the columellar barrier and has one to two accessory palatal traces.

Description.—Shell very small, with 5 normally coiled whorls. Apex almost flat, lower whorls descending progressively more rapidly, H/D ratio 0.525. Apical whorls 1⅜, sculpture of fine radial riblets, microriblet between each pair of major ribs, and extremely fine spiral riblets. Postnuclear whorls with narrow, rounded, slightly protractively sinuated radial ribs, 113 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of rather prominent radial riblets, three to five between each pair of major ribs, crossed by very fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on basal margin, slightly compressed laterally. Color light yellow-white, with regularly spaced reddish markings, zigzagged and broadened on periphery, narrowing and tending to coalesce on base of shell. Umbilicus narrow, U-shaped, last whorl decoiling quite rapidly, contained 3.67 times in the diameter. Aperture ovate, slightly compressed laterally, inclined about 10° from shell axis. Apertural barriers as described in diagnosis above. Height of holotype 1.12 mm., diameter 2.17 mm.

Holotype.—Gambier Islands: Mangareva, Station 90, Tauna Islet. Collected from dead leaves by S. Wight and Yoshio Kondo on May 28, 1934. BPBM 140884.

Range.—Known only from the type collection.

Paratype.—BPBM 140884.

Material.—Same as types (2 specimens).

Remarks.—Although a second trip was made to Tauna Islet in search of additional material, only the two specimens were found. Tauna Islet is third to the southernmost of the chain of coral islets situated on the outer reef west of the high islets in the Mangareva group. It is about one-quarter mile long, a few hundred feet wide, and about 6 ft. high. The islet in 1934 was heavily covered by regular atoll vegetation with a generous planting of coconuts. The only other snails found on the islet belonged to wide-ranging "atoll" species and none of the other Mangarevan endemics were obtained. The presence there of a distinct species of endodontid is quite surprising.

At first glance (fig. 70) *Minidonta taunensis* would seem identical to *M. simulata*. The larger size at a lower whorl count (table LXIII), higher spire, narrower umbilicus, reduced parietal barriers, and absence of the columellar barrier in *M. simulata* easily distinguish them. Although not shown adequately in the illustrations, *M. simulata* has fewer and more widely spaced radial ribs. In the single paratype the umbilicus is less constricted internally, although still not showing the normal, regular decoiling seen in most Pacific endodontids. Features of the apertural barriers are identical to those found in the holotype.

Minidonta taravensis, new species (Solem & Cooke).
Figure 71a-c.

Diagnosis. — Shell larger than average, diameter 2.48-2.68 mm. (mean 2.58 mm.), with 5⅜-5⅝ normally coiled whorls. Spire and apex distinctly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.546-0.556 (mean 0.551). Umbilicus narrowly open, U-shaped, last whorl decoiling more rapidly, contained 5.40-6.82 times (mean 6.11) in the diameter. Postnuclear sculpture of narrow, prominent, protractive radial ribs, 64-72 (mean 68) on the body whorl, whose interstices are 3 - 5 times their width. Microsculpture of rather prominent radial riblets, five to nine between each pair of major ribs, and spiral riblets that are much less than half the size of the radials. Sutures impressed, whorls strongly rounded above and on umbilical margin, markedly compressed laterally and basally. Aperture elongately ovate, compressed laterally, inclined about 15° from shell axis. Parietal barriers 4, extending more than one-quarter whorl: upper a very high, thin blade, narrowly expanded and serrated above, sharply descending over anterior fifth; 2nd much shorter and lower, deeply recessed, relatively much more expanded and serrated above, with gradual anterior descension; 3rd parietal low and threadlike, bifid with both tops expanded and serrated after anterior fifth which is a merged threadlike trace, with a thin bladelike lamella arising between the two arms: 4th threadlike for anterior quarter, abruptly rising to a very high lamellar posterior, broadly expanded and rolled above. Columellar barrier a bladelike ridge displaced onto basal margin, with a laterally extending crescentic blade located just below upper edge. Palatal barriers 4, extending posteriorly beyond line of vision, with broad, low accessory traces between columellar and 1st palatal, 1st and 2nd palatals, then 2nd and 3rd palatals, with only last one prominent: 1st palatal greatly reduced in height, narrowly expanded above, with very gradual anterior descension; 2nd very high, broadly expanded above, with sharper anterior descension; 3rd situated opposite 2nd parietal, equal in height to 2nd palatal, more expanded above, with more gradual anterior descension; 4th reduced in height, situated opposite 1st parietal, with abrupt anterior descension.

The bifid 3rd parietal and lateral accessory blade on the columellar barrier immediately separate *Minidonta taravensis* from other species of *Minidonta*. It is the only species in that genus with 4 parietals and closely approaches the structure found in *Anceyodonta*.

Description. — Shell small, with 5⅝ normally coiled whorls. Spire and apex moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.556. Embryonic whorls 1⅜, sculpture eroded. Remaining whorls with moderately wide, protractive radial ribs, 64 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of relatively prominent radial riblets, crossed by much finer and more crowded spiral riblets. Sutures moderately impressed, whorls rounded above, flattened laterally and on the base. Umbilicus U-shaped, narrow, last whorl decoiling more rapidly, contained 5.40 times in the diameter. Color leached from shell. Aperture compressedly ovate, inclined about 15° from shell axis. Apertural barriers as in diagnosis above. Height of holotype 1.49 mm., diameter 2.68 mm.

Holotype. — Gambier Islands: Mangareva, Station 126, Taravai Islet. Collected in sand by D. Anderson on June 1, 1934. BPBM 138884.

Range. — Known only from the type set.

Paratype. — BPBM 138884.

Remarks. — Despite considerable efforts to find additional specimens, only the two examples are known.

The bifid 3rd parietal and columellar barriers are diagnostic, and prevent confusing *Minidonta taravensis* with any other endodontid. This species is nearest to *Anceyodonta* of any *Minidonta* and could be classified in that genus without any great stretching of generic limits. The widely spaced ribbing,

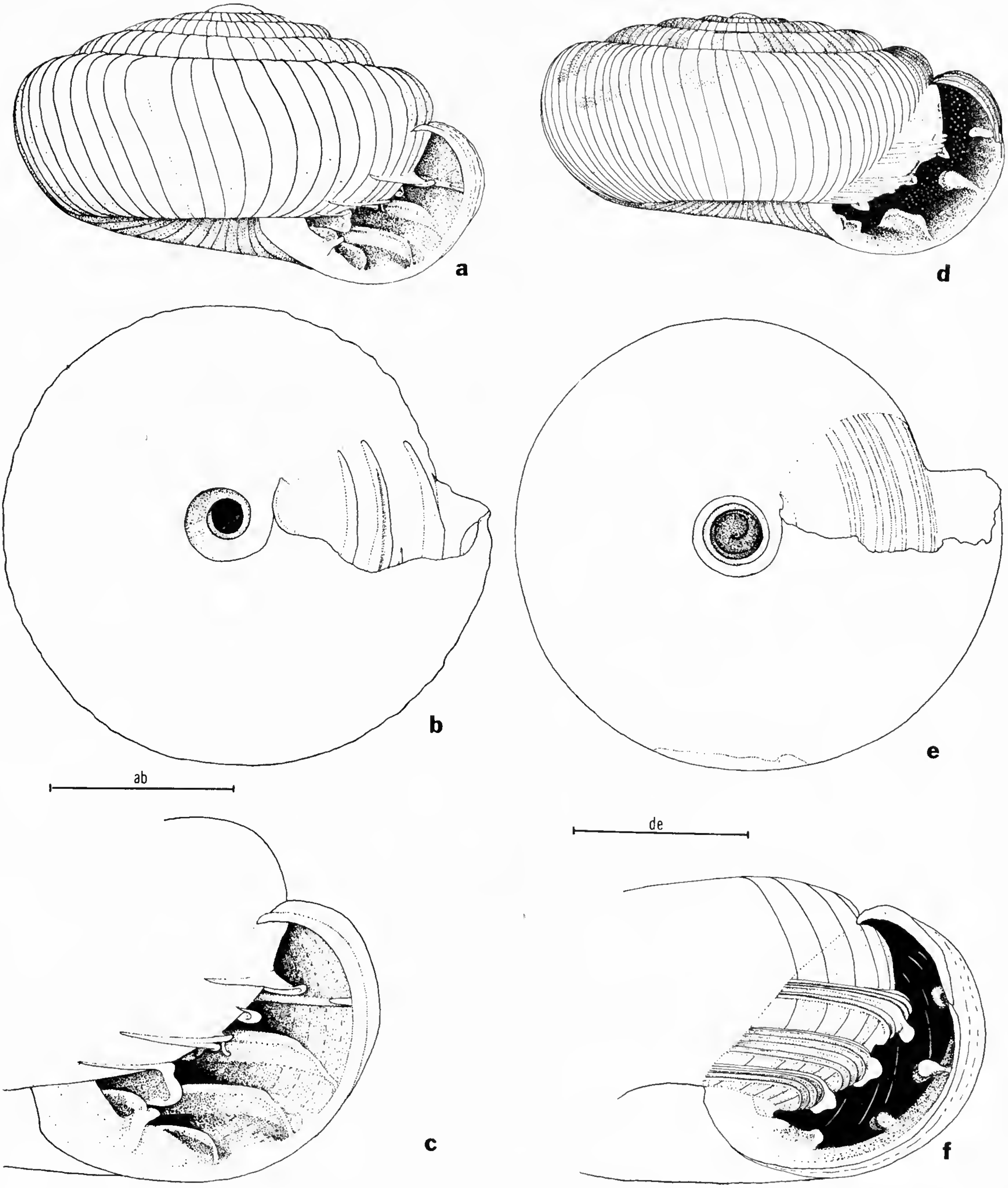

FIG. 71. **a-c**, *Minidonta taravensis*, new species. Station 126, Taravai Islet, Mangareva, Gambier Islands. Holotype. BPBM 138884; **d-f**, *Minidonta extraria*, new species. Station 197, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 139008. Scale lines equal 1 mm. Figures *c* and *f* greatly enlarged. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

number and length of apertural barriers, greatly reduced 1st palatal, and prominent V-shaped upper palatal all are characters typical of *Anceyodonta* and absent or rarely present in *Minidonta*. The bifid columellar and bifid 3rd parietal, shape of the umbilicus, low spire, absence of secondary spiral cording or a sulcus, limited number of inconspicuous palatal traces and low spire lead me to consider *taravensis* as a species of *Minidonta* that closely approaches, but does not reach, the evolutionary level of *Anceyodonta*.

Minidonta simulata, new species (Solem & Cooke). Figure 70a-d.

Diagnosis. – Shell larger than average, diameter 2.43-2.86 mm. (mean 2.72 mm.), with 4¾-5⅝ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending only a little more rapidly, H/D ratio 0.518-0.658 (mean 0.562). Umbilicus very narrow internally, last whorl decoiling quite rapidly, contained 3.96-6.31 times (mean 4.85) in the diameter. Postnuclear whorls with low, narrow, protractively sinuated radial ribs, 71-92 (mean 78.5) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, four to eight between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on umbilical margin, markedly compressed laterally and less so on basal margin. Aperture ovate, compressed laterally, inclined about 10° from shell axis. Parietal barriers 3, extending about three-sixteenths of a whorl: upper a high thin blade, posterior third very weakly expanded and serrated, with gradual descension until just before anterior end; 2nd a raised threadlike ridge, posterior third to half expanded and serrated, extending further anteriorly than upper parietal; 3rd same as 2nd, often slightly lower with posterior portion shorter. Columellar wall without any barrier (75 per cent) or with a recessed crescentic trace (25 per cent). Palatal barriers 4, often with one accessory trace (32 per cent), rarely (4 per cent) with two: lower palatal at baso-columellar angle, reduced in height, a low lamellar ridge; 2nd much higher, with more gradual anterior descension; 3rd still higher, with more gradual descension over anterior half; 4th a low, V-shaped ridge, moderately recessed. Accessory trace normally between 2nd and 3rd palatals, rarely a second one between 1st and 2nd.

The much smaller *Minidonta taunensis* is very similar in appearance to *M. simulata,* but differs in ribbing, umbilical width and details of barrier structure. The Tuamotu *Mautodontha daedalea* is much more depressed and with finer ribbing, although very similar in barrier pattern.

Description. – Shell small, with 4¾ whorls that regularly increase in size. Spire moderately and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.535. Embryonic whorls 1⅝, showing very faint traces of microradial and microspiral sculpture. Remaining whorls with relatively narrow, protractively sinuated radial ribs, 86 on the body whorl, whose interstices are 2 - 4 times their width. Microsculpture of extremely fine radial riblets crossed by very fine spiral riblets. Sutures impressed, whorls strongly rounded above, compressed laterally. Umbilicus narrow, U-shaped, last whorl decoiling quite rapidly, contained 4.53 times in the diameter. All color leached from shell. Aperture ovate, somewhat compressed laterally, inclined about 10° from shell axis. Parietal barriers 3, extending three-sixteenths of a whorl: upper a high bladelike lamella with sharp anterior descension; 2nd a raised threadlike ridge weakly elevated posteriorly; 3rd same as 2nd, with posterior portion shorter. No columellar barrier. Palatal barriers 4, extending a little more than one-eighth whorl: lower smaller than 2nd or 3rd, with rather sharp anterior descension; 2nd and 3rd progressively higher, with more gradual anterior descension; 4th a much lower, prominent V-shaped ridge, recessed within aperture. Height of holotype 1.51 mm., diameter 2.83 mm.

Holotype. – Gambier Islands: Mangareva, Station 88, Aukena Islet, along trail near gap. Collected by Donald Anderson and C. M. Cooke, Jr. on May 28, 1934. BPBM 138698.

Range. – Known from Aukena, Mangareva and Agakauitai Islets, Mangareva Island, Gambier Islands.

Paratypes. – Same as list of material.

Material.–Mangareva: Aukena Islet (Stations 88, 102) near the gap (30 specimens, BPBM 9409, BPBM 138698, BPBM 138756); Mangareva Islet (Station 187) north part of Rikitea on open ground (1 specimen, BPBM 141662); Agakauitai Islet (Station 195) on northwest side on sandy soil (1 specimen, BPBM 138895).

Remarks. – The columellar barrier, when present, is a very small recessed tubercle on the columellar wall and could be easily overlooked. The palatal trace, when present, is an accessory denticle between palatals 2 and 3, about as high as the 1st palatal, but only slightly longer than high.

Most specimens were collected on Aukena, but the single individuals from Mangareva and Agakauitai have the same apertural barriers and fall within the range of size variation shown by the Aukena shells (table LXIV).

In gerontic individuals, which reach an observed maximum diameter of 3.52 mm., the apertural barriers are greatly reduced, with the palatals represented only by slight bumps on the aperture (fig. 70d). The single unbroken gerontic individual is so much larger than the other specimens examined that it has been deliberately excluded from determining the average size of adult shells.

The name *simulata* is taken from the resemblance of this species to *Mautodontha daedalea* (Gould) from Makatea. The greater elevation of spire, smaller size, the stronger, more widely spaced costae and longer apertural barriers of *simulata* readily serve to distinguish the two species.

Minidonta extraria, new species (Cooke & Solem). Figure 71d-f.

Diagnosis. – Shell large, diameter 2.76-3.03 mm. (mean 2.90 mm.), with 5⅜-5⅝ normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.500-0.524 (mean 0.512). Umbilicus narrow, U-shaped, last whorl decoiling a trifle more rapidly, contained 5.25-5.41 times (mean 5.33) in the diameter. Sculpture of narrow, prominent, protractively sinuated radial ribs, 67-75 (mean 71.3) on the body whorl, whose interstices are 3 - 5 times their width. Microsculpture of fine radial riblets, four to eight between each pair of major ribs, crossed by very fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on basal margin, compressed laterally. Aperture ovate, compressed laterally, inclined about 10° from shell axis. Parietal barriers 3, extending almost one-quarter whorl, each split into minor threads on a broad ridge: upper with posterior quarter expanded and serrated, an upper thread raised for posterior half, then split, with two or three lower threads; 2nd with posterior quarter elevated and expanded, with three or four accessory threads; 3rd as 2nd, with only two or three accessory threads. Columellar barrier a very low, broad, inconspicuous recessed ridge. Palatal barriers 4, bulbous above, extending about one-sixteenth of a whorl: lower a short crescentic ridge, moderately recessed, with gradual anterior descension; 2nd almost twice as high, much longer, equally expanded, with more gradual anterior descension; 3rd similar to 2nd, more expanded above; 4th a much lower, slender, bladelike ridge, less expanded above. Very faint, broad swellings located between major palatals (not shown in fig. 71d, f).

The extraordinary splitting of the parietal barriers into several threadlike accessory ridges immediately identifies *Minidonta extraria.* Its short swollen palatal barriers are also markedly different from the long barriers seen in species of similar size (*M. taunensis* and *M. taravensis*). On the structure of the parietal barriers alone, no species of endodontid can be confused with *M. extraria.*

Description. – Shell small, with 5⅜ relatively narrow whorls. Apex and spire only slightly elevated, last whorl descending a trifle more rapidly, H/D ratio 0.524. Embryonic whorls 1⅜, worn, only faint traces of radial microsculpture remaining. Postnuclear whorls with very narrow, nearly vertically sinuated radial ribs, 70 on the body whorl, whose interstices are 3-4 times their width. Microsculpture of numerous fine radial riblets crossed by barely visible spiral riblets. Sutures moderately impressed, whorls strongly rounded above, slightly flattened laterally and on the basal margin. Color mainly leached from shell, faint irregular reddish markings visible above periphery. Umbilicus almost U-shaped, last whorl decoiling a trifle more rapidly, contained 5.25 times in the diameter. Aperture ovate, flattened laterally, inclined about 10° from shell axis. Parietal barriers 3, extending about one-quarter whorl: upper split into five threads, the uppermost of which is also bifid, third major thread bulbously expanded for posterior quarter with minute serrations on top; middle and lower parietal barriers similarly split, but middle with upper three threads united and becoming bulbously expanded posteriorly; lower parietal with only the upper thread bulbously expanded posteriorly. Columellar barrier a broad, low, recessed ridge, slanted slightly downwards. Palatal barriers 4, less than one-sixteenth whorl in length: middle two palatals high, very bulbously expanded and strongly serrated above; lower palatal an expanded threadlike ridge serrated above; upper palatal a relatively narrow, crescent-shaped lamella only slightly expanded above posteriorly. Height of holotype 1.45 mm., diameter 2.76 mm.

Holotype. – Gambier Islands: Mangareva, Station 197, Mangareva Islet, Northeast of Vaituatai Bay. Collected by Donald Anderson and C. M. Cooke, Jr. on June 9, 1934. BPBM 139008.

Range. – Found on Mangareva, Aukena and Taravai Islets, Mangareva, Gambier Islands.

Paratypes. – BPBM 9668, BPBM 138885.

Material. – Mangareva: Mangareva Islet, northeast (Station 197) of Vaituatai Bay (1 specimen, BPBM 139008); Aukena Islet (1 specimen, BPBM 9668); Taravai Islet (Station 126) in sand (1 specimen, BPBM 138885).

Remarks. – One specimen was found at each of three localities on three different islets. In size and shape *Minidonta extraria* is perhaps nearest to *M. simulata,* but it differs not only in the apertural barriers but also in the character of the ribbing. The striking parietal dentition (fig. 71f) by itself serves to separate *M. extraria* from all other known Pacific Island charopids and endodontids. The splitting of the parietals is approached only by *Helenoconcha minutissima* (Smith, 1892) from St. Helena, which has only one or two accessory threads per barrier and the barriers are much higher (E. A. Smith, 1892, pl. 21, fig. 9b).

Genus **Mautodontha,** new genus

Generalized Endodontidae with typical apical and microsculpture (except in *M. ceuthma* and *M. zimmermani*), major sculpture varying from extremely fine and crowded (*M. boraborensis, M. maupiensis,* and *M. imperforata*) to greatly reduced (*M. zebrina*), normally with 80-154 ribs on the body whorl. Apex flat to markedly elevated, body whorl descending sharply and rounded or laterally compressed (*Garrettoconcha*) or slightly descending with markedly angulated periphery (*Mautodontha, s.s.*). Whorls usually 4⅞-5½, tightly coiled, only in *M. maupiensis, M. consobrina,* and *M. boraborensis* increased in number. Umbilicus broadly to narrowly (*M. zimmermani, M. zebrina, M. rarotongensis*) open, rarely constricted (*M. punctiperforata*) or closed (*M. imperforata*). Parietal barriers basically 4 in number, frequently 1 or more absent or split into traces, many species with only 1 or 2 parietals. Columellar barrier weak or absent. Palatals absent in *M. aoraiensis, M. consimilis, M. acuticosta,* and *M. unilamellata*; reduced to 2 or 3 in *M. rarotongensis*; normally 4 or 5 with (*Garrettoconcha*) or without (*Mautodontha, s.s.*) one to several accessory traces. Terminal genitalia differing from that of *Australdonta* only in lacking a fleshy extension of the penis head into which the penial retractor merges. Anatomy otherwise unknown.

Type species. – *Helix daedalea* Gould, 1846.

The almost complete absence of anatomical data makes ordering of the species within this plastic and geographically scattered complex difficult. Individual species show incipient or marked similarities to such divergent evolutionary levels as *Libera, Nesodiscus, Australdonta,* and the Rapan radiation. *Mautodontha* seems to be the modern remnant of the group from which the above genera evolved. The trends in shell form, sculpture, umbilical contours, and barriers outlined below may involve parallelisms, particularly in regard to the *consimilis-acuticosta-unilamellata* group. Data from the shell alone is insufficient to decide whether polyphyletic or monophyletic derivation is indicated for such particular species sets.

The presently known Rarotonga, Austral and Society Islands *Mautodontha* are undoubtedly extinct (with the probable exceptions of the high altitude Tahitian *M. zimmermani* and *M. aoraiensis*). Further refinement of the classification will depend on collection of additional species from the remnant high forest patches in the Society Islands, recovery of live material of *M. daedalea* from one of the Tuamotu atolls, or collection of *M. rarotongensis* on Atiu and *M. imperforata* from Aitutaki.

Since this genus is a "base group" within the Endodontidae and the name *Thaumatodon* usually has been applied to its species, the anagram *Mautodontha* was considered an appropriate designation.

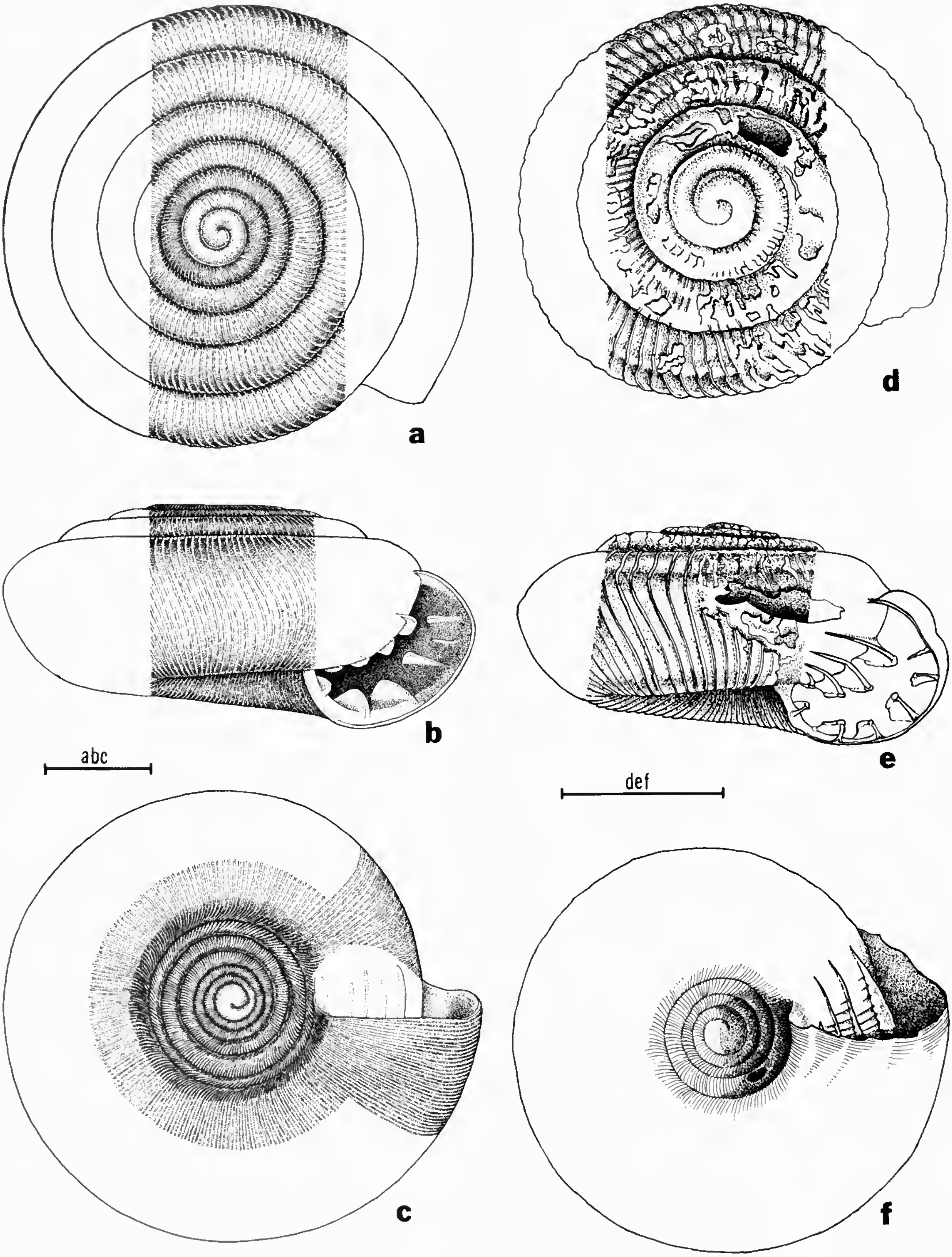

FIG. 72. **a-c**, *Mautodontha* (*M.*) *boraborensis* (Garrett). Borabora, Society Islands. Paratype. BPBM 3763; **d-f**, *Mautodontha* (*M.*) *ceuthma*, new species. Station 589, at 900 ft. elevation, Raivavae, Austral Islands. Holotype. BPBM 146590. Scale lines equal 1 mm. (*a-c*, MM; *d-f*, SG).

The type species, *M. daedalea* from the Tuamotu Islands of Anaa, Makatea, and Niau, approximates what I consider the basic pattern of *Mautodontha*: a depressed shell with flat or barely elevated spire, widely open U- to cup-shaped umbilicus with somewhat flattened sides, the umbilicus regularly decoiling, prominent and numerous apertural barriers (reduced somewhat in *daedalea*), often with an angulated periphery, and well-developed ribbing. From this basic form there have been several directions of divergence. In *M. boraborensis* there is crowding of sculpture, development of a high angulated periphery, a great increase in size and whorl count (fig. 72a), tightening of coiling, widening of the umbilicus, and moderate recession of the palatal barriers. Further development of these conchological trends, coupled with barrier reduction and recession, is culminated in the Society Island endemic genus *Nesodiscus*.

Two species, *M. ceuthma* and *M. zimmermani*, tend toward the characteristics of *Australdonta*, but the wider umbilicus with slightly flattened sides, very large and greatly expanded apertural barriers, and secondary microsculpture of spiral cords (rather than grooves) are important reasons for not placing *ceuthma* in *Australdonta*. The supraperipheral sulcus, grossly enlarged barriers, and secondary spiral cording are not found in any other *Mautodontha*, and *M. ceuthma* stands as a quite isolated species. *M. zimmermani* from Tahiti has an angulated periphery and traces of the microspiral grooving typical of *Australdonta*. It has, however, different anatomical features (see below), quite large apertural barriers, and the flattened umbilical sides found in *Mautodontha*. In the distinct elevation of the spire and resultant narrowing of the umbilicus, *M. zimmermani* departs from most *Australdonta* and typical *Mautodontha*, perhaps foreshadowing the more extensive shifts seen in *M. zebrina*. *M. aoraiensis* is basically similar to the species discussed above in form, umbilicus, and ribbing, differing most obviously in its total lack of palatal barriers, altered 2nd parietal and depressed spire. The apparent small size probably results from the fact that the only collection consists of apparently juvenile shells. The weak secondary spiral cording in that species is very similar to that found in *M. ceuthma*. Despite its general structural differences and much smaller size, *M. aoraiensis* can best be associated with the *M. daedalea* complex.

A much more obvious change is shown by *M. zebrina* from Rarotonga. Although larger, higher, and with a narrower umbilicus than *M. zimmermani*, the two species greatly overlap in measurements and have nearly identical apertural barriers (*zebrina* usually lacks a columellar). The body whorl of *M. zebrina* lacks an angulation and the umbilical walls show no trace of flattening. The most obvious difference lies in the drastic reduction in major sculpture shown by *M. zebrina*, a trend carried further in *M. maupiensis* and *M. imperforata*.

The second major group within *Mautodontha*, the subgenus *Garrettoconcha*, comprises another pattern of specialization, characterized by lateral compression of the body whorl, tighter whorl coiling, rapid descension of the body whorl, narrowed umbilicus, reduced to greatly reduced barriers usually with accessory traces, and often very crowded or reduced ribbing. The least differentiated species, *M. consobrina* from Huahine, has a widely open umbilicus without marked flattening of the sides, a flat spire with rather sharp descension of the body whorl, distinct lateral compression of the body whorl, crowded ribbing, and a full complement of relatively low apertural barriers. While showing a number of similarities to typical *Mautodontha*, the totality of its features place it in *Garrettoconcha*. The Borabora *M. saintjohni* has the umbilicus slightly smaller, the spire slightly elevated, the last whorl descending very rapidly, but otherwise is a miniature replica of *M. consobrina*. *M. maupiensis* from Maupiti, is basically similar to the first two, but has greatly crowded sculpture, a much narrower umbilicus and the barriers quite reduced in size. *M. consobrina*, *M. saintjohni*, and *M. maupiensis* all retain 4 parietals (although numbers 2 and 4 are greatly reduced and shortened in *M. maupiensis*), and usually 4 palatals plus several accessory traces.

The Aitutaki *M. imperforata* probably belongs here, although altered in a number of ways. Its umbilicus is completely closed by inward expansion of the columellar region, the apertural barriers are very long and rather prominent with the 2nd and 3rd parietals reduced and several additional traces present. The whorls are not laterally compressed and the apex and spire are moderately and evenly elevated (these may be secondary modifications associated with umbilical closure). Although these changes produce a quite distinctive appearance, I doubt that they are important enough for other than specific recognition.

M. parvidens has the barriers reduced in height and normally one or two parietals have been lost. The umbilicus is slightly narrower than in *M. consobrina* or *M. saintjohni*, but the H/D ratio is lower, probably because there is less lateral flattening of the whorls. The very similar *M. subtilis* differs most obviously in having much more widely spaced sculpture on the spire and early body whorl plus a narrower umbilicus, but is otherwise structured as in *M. parvidens*. The Moorean *M. punctiperforata* has the umbilicus quite narrow and usually the parietal barriers are altered with numerous accessory traces replacing the 3rd parietal. Some specimens, however, have 3 parietals and the barriers enlarged. These specimens have an appearance intermediate between that of *M. parvidens* and *M. zimmermani* in terms of barrier structure. *M. rarotongensis* from Atui, Cook Islands has the same parietal barriers as the above, but the upper palatals are lost, the umbilicus is rather narrow with strongly rounded sides, and there is significant lateral compression of the body whorl.

Finally, in *M. consimilis, M. acuticosta,* and *M. unilamellata* the apertural barriers are reduced to only 1 or 2 parietals, with the palatals lost. The last two species have wider umbilici and less compressed body whorls than *M. consimilis,* thus somewhat approximating the form of *M. zimmermani.*

Geographically, *Mautodontha* is rather widely dispersed. Single species are known from the Tuamotu and Austral Islands, four species from the Cook Islands (one each on Atiu and Aitutaki, two from Rarotonga), with the remaining 11 species found in the Society Islands. The replacement pattern of this distribution in relation to the genus *Minidonta* has been discussed above (p. 128).

Momentarily ignoring *M. parvidens,* which has been collected on three islands (Borabora, Huahine and Raiatea), Tahiti and Rarotonga each have two species of *Mautodontha.* The Raiatean forms are certainly monophyletic; the Huahine *M. subtilis* can easily be derived from *M. parvidens*; and the Tahitian *M. zimmermani* and *M. aoraiensis* probably share common ancestry. This leaves only the Rarotongan *M. zebrina* and *M. unilamellata* plus the Boraboran pair, *M. boraborensis* and *M. saintjohni,* as representing clear cases of separate faunal invasions of the same island. Although showing slight differences between different island populations (table LXVII), *M. parvidens* presumably was a widely distributed lowland species, native to Huahine, Tahiti, and Moorea, while many of the others probably were found inland at high or moderate elevations.

The only case of clear geographic relationship concerns *M. consobrina* from Huahine, *M. saintjohni* from Borabora, and *M. maupiensis* from Maupiti, which are closely similar and allopatric.

Relationships of *Mautodontha* have been discussed above (pp. 113-114). Here it is sufficient to emphasize that *Australdonta* differs in its peculiar secondary microsculpture (fig. 124), large size, carinated periphery with strong supraperipheral sulcus, and narrower umbilicus with rounded internal margins; *Minidonta* by its internally constricted umbilicus, very small size, and often reduced apertural barriers; *Nesodiscus* by its large size, many whorls, umbilical brood chamber that may show membranous closing, greatly reduced and usually deeply recessed barriers, plus very crowded and reduced to lost sculpture; *Libera* by its umbilical brood chamber and much different shell shape.

KEY TO THE GENUS *Mautodontha*

1. Palatal barriers absent 2
   Palatal barriers present 5
2. H/D ratio more than 0.400 3
   H/D ratio less than 0.375.
   Mautodontha (*M.*) *aoraiensis,* new species
3. Mean diameter about 3.4-3.5 mm.; mean D/U ratio more than 4.00.
   Mautodontha (*Garrettoconcha*) *consimilis* (Pease, 1868)
   Mean diameter about 3.9-4.0 mm.; mean D/U ratio less than 3.75 4
4. Usually 2 or more parietal barriers; mean H/D ratio less than 0.500; Raiatea, Society Islands.
   Mautodontha (*Garrettoconcha*) *acuticosta* (Garrett, 1884)
   Only 1 major parietal barrier; mean H/D ratio about 0.550; Rarotonga, Cook Islands.
   Mautodontha (*Garrettoconcha*) *unilamellata* (Garrett, 1874)
5. Umbilicus at least slightly open 6
   Umbilicus closed.
   Mautodontha (*Garrettoconcha*) *imperforata* (Pease, 1870)
6. Mean D/U ratio less than 7.00 7
   Mean D/U ratio more than 10.0.
   Mautodontha (*Garrettoconcha*) *punctiperforata* (Garrett, 1884)
7. Body whorl without any supraperipheral sulcus 8
   Body whorl with distinct supraperipheral sulcus; Raivavae, Austral Islands .... *Mautodontha* (*M.*) *ceuthma,* new species
8. Mean diameter more than 3.6 mm. *AND* 4 parietal barriers present 9
   Mean diameter less than 3.6 mm. *OR* with only 3 parietal barriers 10
9. Body whorl markedly angulated; Borabora, Society Islands.
   Mautodontha (*M.*) *boraborensis* (Garrett, 1884)
   Body whorl not angulated; Huahine, Society Islands.
   Mautodontha (*Garrettoconcha*) *consobrina* (Garrett, 1884)
10. Mean D/U ratio more than 4.75 11
    Mean D/U ratio usually much less than 4.75 13
11. Less than 100 ribs on body whorl; mean diameter more than 3.5 mm.; always 3 parietal barriers 12
    More than 100 ribs on body whorl; mean diameter about 3.00 mm.; often only 2 parietals present.
    Mautodontha (*Garrettoconcha*) *rarotongensis* (Pease, 1870)
12. Between 70-90 normal ribs on weakly angulated body whorl; spire elevated; Tahiti, Society Islands.
    Mautodontha (*M.*) *zimmermani,* new species
    Less than 45 reduced ribs on rounded body whorl; spire flat or barely elevated; Rarotonga, Cook Islands.
    Mautodontha (*M.*) *zebrina* (Garrett, 1874)
13. More than 100 ribs on body whorl in nongerontic specimens 14
    Less than 100 ribs on body whorl in nongerontic specimens.
    Mautodontha (*Garrettoconcha*) *subtilis* (Garrett, 1884)
14. Less than 200 ribs on body whorl 15
    More than 200 ribs on body whorl.
    Mautodontha (*Garrettoconcha*) *maupiensis* (Garrett, 1872)
15. Mean H/D ratio 0.490 or greater 16
    Mean H/D ratio about 0.425.
    Mautodontha (*M.*) *daedalea* (Gould, 1846)
16. Palatal barriers 4, with four accessory traces; columellar barrier present.
    Mautodontha (*Garrettoconcha*) *saintjohni,* new species
    Palatal barriers usually 2 (rarely 3 or 4), no accessory traces; columellar barrier absent.
    Mautodontha (*Garrettoconcha*) *parvidens* (Pease, 1861)

Subgenus **Mautodontha,** *s.s.*

Rather depressed to flat-spired shells with a broadly open umbilicus, the last whorl only slightly descending and the body whorl at least weakly angulated. Apertural barriers prominent, large, rarely with accessory traces, greatly reduced only in *aoraiensis.*

In narrowing of the umbilicus, both *M. zimmermani* and *M. zebrina* somewhat resemble *Garrettoconcha,* but their remaining characters are those of *Mautodontha s.s.* In its secondary sculpture, *M. zimmermani* has the *Australdonta* pattern, while *M. ceuthma* has the ribbing and supraperipheral sulcus of that genus. In contrast, *M. boraborensis* presents a

TABLE LXV. - RANGE OF VARIATION IN MAUTODONTHA (MAUTODONTHA)

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
boraborensis (Garrett)	31	202(179-249)	1.87(1.74-2.17)	4.54(4.15-5.00)	0.426(0.366-0.457)	7 1/8-(6 1/2-8)	2.49(2.09-2.98)	4	1	4-5
daedalea (Gould)	113	145.7(131-167)	1.35(1.15-1.68)	3.20(2.80-3.59)	0.422(0.375-0.486)	5 3/8+(5-6 1/4)	3.14(2.65-3.82)	3-4	0	5-6
ceuthma	3	90(89-91)	1.41(---------)	2.93(2.83-3.03)	0.484(0.467-0.500)	5 1/8	3.79(3.74-3.83)	4	1	5+1
zimmermanni	12	80(70-90)	1.65(1.42-1.92)	3.61(3.25-3.97)	0.455(0.434-0.483)	5+(4 7/8-5 1/4)	5.13(4.15-6.67)	3	1	4
zebrina (Garrett)	6	34.8(32-41)	2.08(1.81-2.47)	4.10(3.75-4.57)	0.507(0.474-0.521)	5+(4 3/4-5 1/4)	5.85(5.20-6.44)	3	0-1	3-4
aoraiensis	3	63.5(61-66)	0.94(0.89-0.99)	2.68(2.60-2.76)	0.349(0.342-0.357)	4 1/8(4-4 1/4)	2.91(2.82-3.00)	2	0	0

combination of characters that, when accentuated, are typified by *Nesodiscus*.

Since only the two Tahitian species, *M. zimmermani* and *M. aoraiensis*, have been dissected, close phyletic association of these somewhat diverse species from scattered localities can be questioned. Displaying incipient or threshold stages toward the divergent evolutionary levels represented by *Australdonta* and *Nesodiscus*, unquestionably *Mautodontha* is a protean group. Lacking comprehensive anatomical data, particularly in regard to *M. boraborensis*, *M. ceuthma*, and the more generalized *Nesodiscus* (*taneae* and *huaheinensis*), it is best to resist a flat statement that both *Australdonta* and *Nesodiscus* have been derived from *Mautodontha s.s.* although this very probable hypothesis is outlined above (p. 112).

The species do show a relatively coherent pattern of structure (table LXV) and offer a distinct contrast to *Garrettoconcha* (table LXVI). While very considerable-to-complete overlap in range of any one character exists because of parallel specializations, the average dimension within each subgenus differs in four of five basic parameters:—

Mean of:	Ribs	Height	Diameter	H/D ratio	D/U ratio
Garrettoconcha	126.9	1.82	3.39	0.537	4.70
Mautodontha s.s.	102.7	1.55	3.51	0.441	3.89

While the diameters are essentially identical (only 3.5 per cent difference), *Mautodontha s.s.* has 19 per cent fewer ribs, a 17.2 per cent wider umbilicus, 14.8 per cent lower height and hence a 17.9 per cent less H/D ratio. Except for the ribbing, these are obviously correlated changes, but serve to emphasize the dichotomy of evolution within *Mautodontha*.

Mautodontha (M.) boraborensis (Garrett, 1884).
Figure 72a-c.

Pitys boraborensis Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), pp. 32-33, pl. 2, figs. 18, a, b — Borabora, Society Islands at 900 ft. elevation.

Helix (*Endodonta*) *boraborensis* (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 66, pl. 12, figs. 52-54.

Endodonta (*Thaumatodon*) *boraborensis* (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Diagnosis. — Shell very large, diameter 4.21-5.00 mm. (mean 4.54 mm.), with 6½-8 very tightly coiled whorls. Apex flat or barely elevated, whorls of spire descending slightly, last whorl a little more rapidly, H/D ratio 0.366-0.457 (mean 0.426). Umbilicus broadly V-shaped, slightly and regularly decoiling, contained 2.09-2.98 times (mean 2.49) in the diameter. Sculpture of narrow, very protractively sinuated radial ribs, about 174-249 (mean 202) on the body whorl. Sutures relatively shallow, whorls flattened above and below the high and obtusely angulated periphery. Aperture subquadrangular, inclined less than 10° from shell axis. Parietal barriers 4, extending less than one-quarter whorl: upper a high bladelike ridge, posterior third expanded and serrated above, with gradual anterior descension; 2nd and 3rd with anterior half to two-thirds threadlike, posterior quarter to third as in 1st one; 4th parietal differing from 3rd only in having posterior elevated portion lower and shorter. Columellar barrier a recessed high ridge with gradual anterior descension, slightly twisted downwards from plane of coiling at anterior. Palatal barriers 4 (88.2 per cent) or 5 (11.8 per cent), extending about one-eighth whorl: lower basal, a high crescentic lamella, slightly flattened above with rather sharp anterior descension; 2nd, 3rd, and 4th (rarely) subperipheral, progressively lower and less crescentic with more gradual anterior descension; upper located barely above periphery, a lamellar ridge shorter than lower palatals and more deeply recessed.

The very large size, numerous whorls, very widely open umbilicus, and sharply angulated high periphery easily separate *M. boraborensis* from the other Society Island *Mautodontha*. The other large species, *M. acuticosta*, lacks palatal barriers and has a much narrower umbilicus. The smaller species of *Nesodiscus* differ in having a raised apex with heavy, rounded ribbing and at most only 2 parietals.

Description. — Shell very large, with 7¼ very tightly coiled whorls. Apex and early whorls of spire flat, later whorls descending gradually, last whorl moderately rapidly, H/D ratio 0.421. Apical whorls 1½, sculpture eroded. Postnuclear whorls with moderately prominent, broadly rounded, very slightly protractively sinuated radial ribs, 249 on the body whorl, whose interstices are about twice their width. Microsculpture a lattice of fine radial riblets and distinctly finer and a little more crowded spiral riblets. Sutures moderately impressed. Whorls flatly rounded above with gently and evenly rounded subperipheral margin. Periphery obtusely angulated, strongly rounded; not protruded. Ground color light yellow horn with irregularly spaced, narrow to broad, dark reddish-purple flammulations. Umbilicus widely open, broadly V-shaped, regularly decoiling, contained 2.38 times in the diameter with slight shouldering of whorl margins. Aperture subquadrangular, with flatly rounded lower margin, inclined about 10° from shell axis. Parietal barriers 4, extending three-sixteenths of a whorl: upper a high bladelike lamella with very gradual anterior descension, broadened and flattened above posteriorly; 2nd parietal with anterior half threadlike, slightly lower and much narrower posteriorly; 3rd parietal, same as 2nd; 4th parietal reduced to a threadlike trace, one-half length of upper. Columellar barrier a prominent, low ridge, moderately recessed from apertural margin, lying nearly parallel to plane of coiling. Palatal barriers 4: lower 3 crescentic with gradual anterior descension, moderately recessed and slightly flattened on top, extending about one-eighth whorl, progressively reduced in height; upper palatal a high, threadlike ridge, slightly longer than the lower barriers, located just above periphery. Height of lectotype 2.11 mm., diameter 5.00 mm.

Lectotype. — Society Islands: Borabora at 900 ft. elevation. Collected by Andrew Garrett. ANSP 47775.

Range. — Borabora, Society Islands at 800-900 ft. elevation.

Paratypes. — BPBM 3763, ANSP 290091, Zurich.

Material. — Borabora: south slope Pahio-Temanu ridge (Station 1093) at 800 ft. elevation in a cave entrance (11 specimens, BPBM 152392-4); Borabora (20 specimens, BPBM 3763, BPBM 170955, Zurich, ANSP 290091).

Remarks. — In size and general appearance, *M. boraborensis* is intermediate between the Society Island *Mautodontha* and *Nesodiscus*. One specimen in the Zoologisches Museum der Universität Zurich, has the same umbilical brood capsule that is characteristic of *Nesodiscus taneae* and *N. huaheinensis*. The apical sculpture of fine and widely spaced radials with finer spirals combine with the large palatal barriers to place this species in *Mautodontha*. Unfortunately, no preserved material was available.

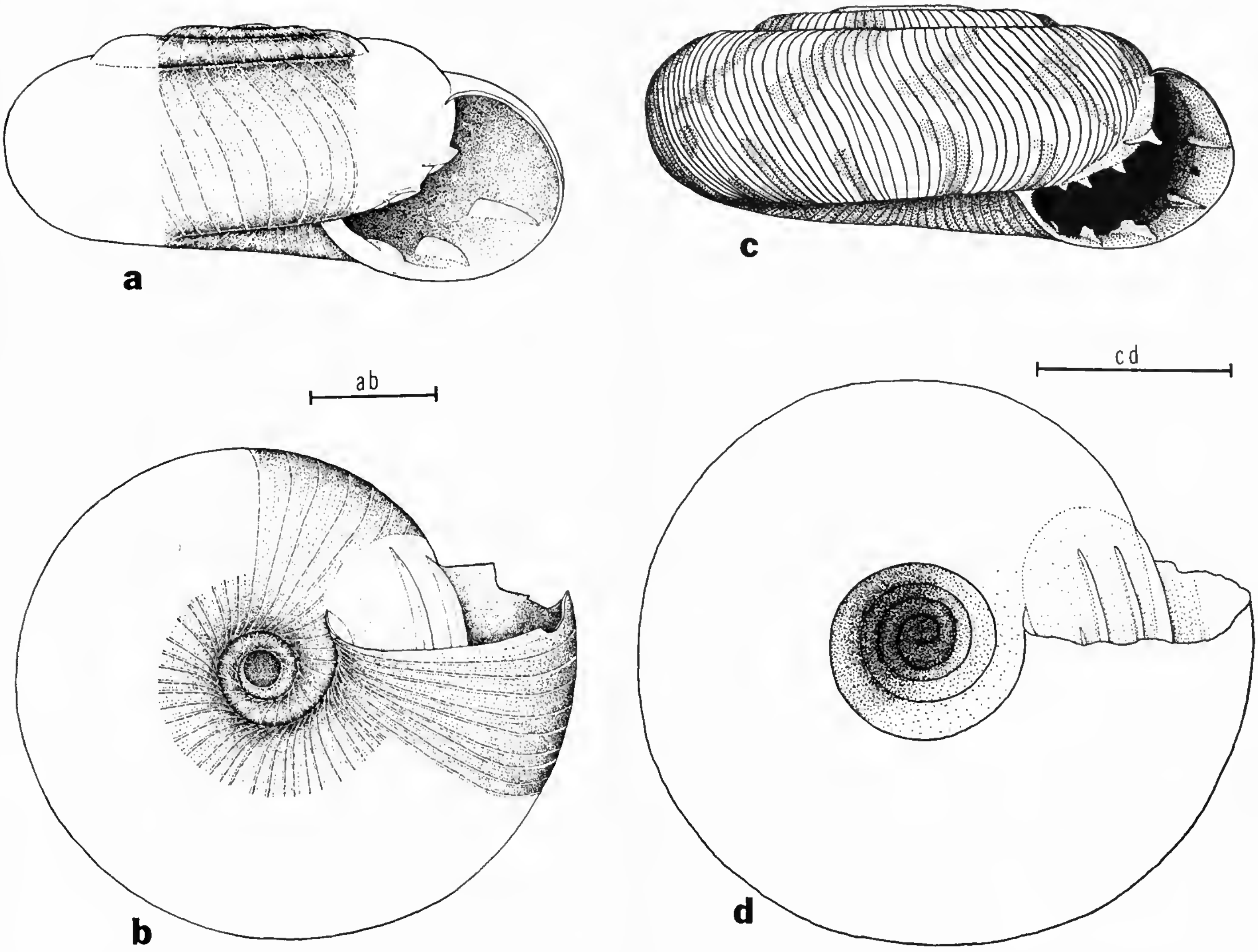

FIG. 73. **a-b**, *Mautodontha* (*M.*) *zebrina* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2337; **c-d**, *Mautodontha* (*M.*) *daedalea* (Gould). 1 mile inland, Makatea, Tuamotu Islands. BPBM 115738. Scale lines equal 1 mm. Figures *a-b* (MM); *c-d*, by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Garrett (1884, p. 33) stated that this was comparatively rare and found only at 900 ft. above sea level. The only more recent collection, made by the members of the Mangarevan Expedition in 1934, was of dead specimens collected from debris in a cave entrance at 800 ft. elevation.

Barrier variation was minimal, concerning only the 4th parietal, which sometimes had the anterior threadlike portion missing or the posterior part only weakly elevated, and in the number of palatal barriers. Usually, there were 3 subperipheral palatals and a single supraperipheral ridge. Two specimens (of 17 adults) had a 4th subperipheral palatal and two specimens had an accessory trace between palatals 2 and 3. Usually the supraperipheral palatal was strongly elevated, but occasionally it was greatly reduced in height.

Mautodontha (M.) daedalea (Gould, 1846). Figure 73c-d.

Helix (*Pitys*) *daedalea* Gould, 1846, Proc. Boston Soc. Nat. Hist., **2**, p. 173 – Matea (=Makatea, Tuamotu Islands); Gould, 1846, Exped. Shells, pp. 21-22 – Tahiti and Matea; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 186 – Tahiti and Matea; Gould, 1852, U. S. Explor. Exped., Wilkes, **12**, pp. 54-55 – Aurora (=Makatea) and Tahiti; Gould, 1860, U. S. Explor. Exped., Wilkes, Atlas of shells, pl. 4, figs. 51, a-d; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 221; Pfeiffer, 1876, *op. cit.*, **7**, p. 258; Johnson, 1964, U. S. Nat. Mus. Bull., **239**, p. 65.

Helix (*Endodonta*) *daedalea* (Gould), Tryon, 1887, Man. Conchol., (2), **3**, p. 64, pl. 12, figs. 23-25.

Endodonta (*Thaumatodon*) *daedalea* (Gould), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 27.

Thaumatodon daedalea (Gould), Cooke, 1934, Occ. Pap. B. P. Bishop Museum, **10**, (11), p. 5 – Makatea.

Endodonta consobrina Aubert de la Rüe and Soyer, 1958 (not Garrett, 1887), Bull. Mus. Nat. d'Hist. Nat., Paris, 2nd ser., **30**, (4), p. 365 – Makatea, Tuamotu Islands (fossil).

Diagnosis. – Shell of less than average size, diameter 2.80-3.59 mm. (mean 3.20 mm.), with 5-6¼ rather tightly coiled whorls. Apex and early spire usually flat or slightly elevated, last whorl descending slightly, H/D ratio 0.375-0.486 (mean 0.422). Umbilicus widely open, cup-shaped, regularly decoiling, sides slightly flattened, contained 2.65-3.82 times (mean 3.14) in the diameter. Sculpture of low, prominent, strongly protractively sinuated, rather closely set radial ribs, 131-167 (mean 145.7) on the body whorl, whose interstices are less than twice their width. Microsculpture of extremely fine and crowded radial riblets, three to six between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Sutures impressed, whorls with evenly rounded margins, slightly compressed laterally below periphery. Aperture elongate-ovate, laterally compressed below rounded periphery, inclined about 20° from shell axis. Parietal barriers 3 (67.7 per cent) or 4 (32.3 per cent), extending about three-sixteenths of a whorl: upper with posterior third high and bladelike, serrated and expanded above, with gradual descension over anterior two-thirds; 2nd with posterior portion slightly shorter and lower, anterior half threadlike; 3rd with posterior portion distinctly reduced in height and length, anterior portion as in 2nd; 4th, when present, a threadlike trace, sometimes weakly elevated posteriorly, often shortened. Columellar barrier absent, although reduced lower palatal located at baso-columellar margin may be mistaken for a columellar barrier. Palatal barriers 5, prominent, extending about one-eighth whorl: lower at baso-columellar margin, a short, slightly recessed, raised threadlike trace, quite inconspicuous in most examples; 2nd a low bladelike lamella with rather sharp anterior descension, reaching nearly to lip margin; 3rd a very high, bladelike lamella whose edge points towards 2nd parietal, nearly reaching lip margin, with very gradual anterior descension; 4th equal in height to 3rd, narrower, longer, with more gradual anterior descension; 5th palatal a moderately recessed, low, bladelike lamella, shorter than 4th. Rarely an additional palatal between 4th and 5th.

The very depressed shape, widely open umbilicus, numerous ribs and presence of 5 or more palatal barriers separate *M. daedalea* from the other *Mautodontha*. The only other species normally with 5 palatals, *M. ceuthma* from Raivavae, has much larger barriers, a prominent supraperipheral sulcus, and only about 90 widely spaced ribs on the body whorl.

Description. — Shell a badly broken adult with 5⅛ whorls remaining, parietal barrier position indicating it originally had 5¾+ whorls. Apex flat, spire slightly elevated, last whorl descending a little more rapidly, H/D ratio 0.474. Apical whorls 1⅜, sculpture obscured by glue. Remaining whorls with low, rounded, strongly protractively sinuated radial ribs, 132 on the last remaining whorl, whose interstices are less than twice their width. Microsculpture a lattice of radial and slightly finer and more crowded spiral riblets. Sutures impressed, whorls evenly rounded on outer margins, compressed laterally below periphery. Umbilicus cup-shaped, regularly decoiling, widely open, contained 3.39 times in the diameter. Aperture not describable because of breakage. Color light yellow-white with irregularly spaced, narrow to wide, zigzag reddish flammulations. Parietal barriers 3, extending slightly less than three-sixteenths of a whorl, with one low accessory trace; upper with posterior third a very high lamella, anterior half a low lamellar ridge; 2nd parietal with posterior elevated portion shorter, anterior section threadlike; 3rd parietal with posterior portion distinctly lower and shorter, anterior portion identical. Accessory trace threadlike, located between 2nd and 3rd parietals. Palatal wall completely absent for first half whorl, so barriers not observed. Height of remaining shell 1.48 mm., diameter 3.13 mm.

Lectotype. — Tuamotu Islands: Aurora (=Makatea) Island. Collected by the United States Exploring Expedition. MCZ 169115.

Range. — Makatea, Anaa, and Niau Islands, Tuamotu Archipelago.

Material. — MAKATEA (13 specimens, MCZ 169115, FMNH 46441, ANSP 1947, Paris): from 1 mile inland at 250-300 ft. elevation (88 specimens, BPBM 115738). ANAA: Tukuhoru Islet, under stones and dead leaves (4 specimens, BPBM 136519). NIAU (8 specimens, ANSP 156348, BPBM 118516).

Remarks. — The badly damaged lectotype is obviously not the specimen figured by Gould (*loc. cit.*), but is the only specimen surviving from the original collection. It is well within the range of variation shown by more recent collections.

In the original description, Gould mentioned 4 parietals, 5 palatals, and a small columellar nodule, but in the first published illustration (Gould, 1860, pl. 4, figs. 51, a-d) there are only 4 palatals and no columellar barrier shown. Only one of 32 adults examined during this study had a weak columellar trace, and no specimens had only 4 palatals. Since the 1st palatal is normally so small, it easily could have been overlooked by the artist. In all other respects, the figured specimen is typical of the species.

Barrier variation was moderate. Two-thirds of the specimens had only 3 parietals, while most of the rest had a small 4th barrier. Only in three examples was there a 4th parietal equal in size to the others. One individual had a 6th palatal present between the 4th and 5th palatals. All others had the normal 5 barriers.

Material from Makatea collected in 1934 by the Mangarevan Expedition and in 1955 by E. Aubert de la Rue compared perfectly in respect to sculpture and barrier configurations. Differences in H/D ratio (table LXVII) are not significant (with 20 df, "*t*" = 0.1509), while the difference in diameter is significant at the 5 per cent probability level ("*t*" = 1.7958). Although statistically significant, there probably is no biological meaning to this, since so many specimens were damaged that exact separation of adult and subadult examples was impossible. The Niau shells have significantly narrower umbilici than the Makatea specimens (with 17 df, "*t*" = 2.7036), but despite an equivalent numerical gap (table LXVII), the difference between the Niau and Anaa shells in umbilical width is not statistically significant (with 6 df, "*t*" = 1.8800). So few specimens from Niau and Anaa are involved that the importance of these differences cannot be evaluated.

The presence of *M. daedalea* on Anaa and Niau, both of which are low coral atolls, is surprising and should be investigated further. In view of the significant differences in umbilical width, I hesitate to state that "probably they were carried from Makatea" by natives, yet they represent the only record of living endodontids from atolls.

Mautodontha (M.) ceuthma, new species. Figure 72d-f.

Diagnosis. — Shell much smaller than average, diameter 2.83-3.03 mm. (diameter 2.93 mm.), with 5⅛ relatively tightly coiled whorls. Apex and spire moderately elevated, last whorl descending slightly more rapidly, H/D ratio 0.467-0.500 (mean 0.484). Umbilicus V-shaped, regularly decoiling, broadly open, contained 3.74-3.83 times (mean 3.79) in the diameter, sides flattened internally. Sculpture of narrow, rather widely spaced, strongly protractively sinuated radial ribs, 89-91 (mean 90) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radials, exceedingly fine spirals, and a secondary sculpture of low spiral cords visible mainly above and below periphery. Sutures deep, whorls strongly rounded above, sloping down to prominent supraperipheral sulcus, periphery slightly angled, lower palatal margin compressed and evenly rounded. Aperture ovate, upper palatal margin concave, periphery angled, inclined about 25° from shell axis. Parietal barriers 4, very high, extending one-quarter whorl, lower greatly reduced in height with anterior threadlike portion absent. Columellar barrier high, bladelike, serrated and expanded above, with sharp anterior descension. Palatal barriers 5, extending one-eighth whorl, with one weak lower accessory trace: 5th palatal much lower, 4th palatal slightly lower than first 3 lamellae. For details of tooth structure see description.

The very high, markedly serrated and expanded barriers, distinct supraperipheral sulcus and weak secondary spiral cording readily separate *M. ceuthma* from all other *Mautodontha*. The presence of secondary spiral cording rather than low spiral grooves separates *M. ceuthma* from *Australdonta*. Only *M. daedalea* normally has 5 palatals, but in that species the barriers are much smaller, the ribbing much more crowded and there is no supraperipheral sulcus.

Description. — Shell rather small, with 5⅛ relatively tightly coiled whorls. Apex and spire moderately elevated, last whorl descending more rapidly, H/D ratio 0.500. Embryonic sculpture eroded above, but visible in umbilicus as typical microradial and microspiral ribbing. Remaining whorls with prominent, narrow, rather widely spaced, strongly protractively sinuated radial ribs, 91 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by very fine and crowded spiral riblets, with a secondary sculpture of inconspicuous spiral cords. Sutures strongly indented, whorls rounded on top, sloping down to marked supraperipheral sulcus, followed by a slight peripheral angulation, evenly rounded but compressed lower palatal wall and compressed umbilical margin. Umbilicus V-shaped, widely open, regularly decoiling, contained 3.74 times in the diameter, with a slight internal concavity marking position of columellar barrier, side walls flattened. Color uniform light reddish-brown. Aperture ovate with concave supraperipheral margin, rounded and compressed lower palatal margin, inclined about 25° from shell axis. Parietal barriers 4, extending one-quarter whorl, teeth very high, upper an extremely high, thin bladelike lamella, posterior third grossly expanded and serrated above, middle third gradually descending, weakly expanded but not serrated, anterior third a very gradually descending, low lamellar ridge; 2nd with posterior quarter as in 1st, middle third descending rather sharply, anterior portion a raised threadlike ridge; 3rd parietal slightly lower than 2nd posteriorly, identical in shape; 4th parietal identical in form, but greatly reduced in height with anterior threadlike portion absent. Columellar barrier a high bladelike lamella, strongly expanded and serrated above, with rather sharp anterior descension, angling downward from plane of coiling. Palatal barriers 5, extending one-eighth whorl, very high, with one weak accessory trace: lower 2 palatals equal in size, higher than columellar, identical in structure except more gradual anterior descension; 3rd palatal distinctly higher than 2nd, identical in structure, with more gradual anterior descension; 4th lower than 2nd, subperipheral, with very gradual anterior descension; 5th palatal supraperipheral, located opposite bottom of sulcus, a low lamellar ridge, expanded and serrated above, with very gradual anterior descension. Height of holotype 1.41 mm., diameter 2.83 mm.

Holotype. — Austral Islands: Raivavae, Station 589, two-thirds way up cliff of Mt. Taraia at 900 ft. elevation. Collected by Harold St. John, on a patch of soil in a crevice out of the reach of goats on August 6, 1934. BPBM 146590.

Range. — Mt. Taraia, Raivavae, Austral Islands.

Paratypes. — BPBM 146569.

Material. — Raivavae: from foot to top of cliff of Mt. Taraia (Stations 577, 589) up to 900 ft. elevation (3 specimens, same as list of types).

Remarks. — The name *ceuthma* is taken from the habitat of the type locality, a rock crevice safe from the depradations of goats.

The general aspect of the shell is that of the Austral Island genus *Australdonta,* from which it differs in having secondary spiral ribbing instead of grooves, very large parietal and palatal barriers instead of their being relatively reduced in size, and the umbilicus wider with rather flattened sides instead of being narrower and with rounded sides. As indicated above, classification of *M. ceuthma* into either *Mautodontha* or *Australdonta* could be justified utilizing selected shell features. Despite the disjunct geography, a preponderance of what I consider to be significant characters support its inclusion in *Mautodontha.*

Mautodontha (M.) zimmermani, new species.
Figures 64c-d; 74a-c.

Diagnosis. — Shell slightly larger than average, diameter 3.25-3.95 mm. (mean 3.61 mm.), with 4⅞-5¼ loosely coiled whorls. Apex and spire distinctly and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.434-0.483 (mean 0.455). Umbilicus V-shaped, narrow, last whorl decoiling more rapidly, contained 4.15-6.67 times (mean 5.13) in the diameter. Sculpture of fine, protractively sinuated radial ribs, 70-90 (mean 80) on the body whorl, with prominent periostracal extensions, whose interstices are 2-3 times their width. Microsculpture of very fine radial riblets, seven to twelve between each pair of major ribs, barely visible spiral ribs, and a secondary sculpture of weak irregular spiral grooves, prominent on spire and near suture, absent near body whorl periphery. Aperture ovate, strongly flattened above with gently rounded basal margin. Periphery slightly, but distinctly, angulated. Parietal barriers 3, extending about one-quarter whorl, lower greatly reduced in adults: upper a high, bladelike lamella with posterior third to half expanded and serrated, anterior half with very gradual descension; 2nd with posterior third equal in height, anterior half threadlike; 3rd parietal with posterior third greatly reduced in height, anterior threadlike portion equal to 2nd in length or greatly shortened in older individuals. Columellar wall with a deeply recessed, threadlike or crescentic, short ridge. Palatal barriers 4, large, extending more than one-eighth whorl: lower basal in position, a prominent, bladelike ridge, moderately recessed, with gradual anterior descension, expanded and serrated above; 2nd higher longer, with more gradual anterior descension; 3rd equal in height to 2nd, usually more deeply recessed, with much more gradual anterior descension; 4th supraperipheral, equal in height to 1st or slightly lower, with same descension as 2nd, deeply recessed.

The prominent radial ribs (70-90) on the body whorl and angulated periphery are the main characters separating *Mautodontha zimmermani* from the Cook Island *M. zĕbrina*. The relatively narrow umbilicus, 3 parietals and weak secondary sculpture of spiral grooves combine to separate it from any other *Mautodontha*.

Description. — Shell large with 5¼ relatively loosely coiled whorls. Apex and spire evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.483. Embryonic whorls 1⅜, sculpture eroded. Postnuclear whorls with relatively low and indistinct, protractively sinuated radial ribs, about 90 on the body whorl, whose interstices are about 2-3 times their width. Microsculpture of very

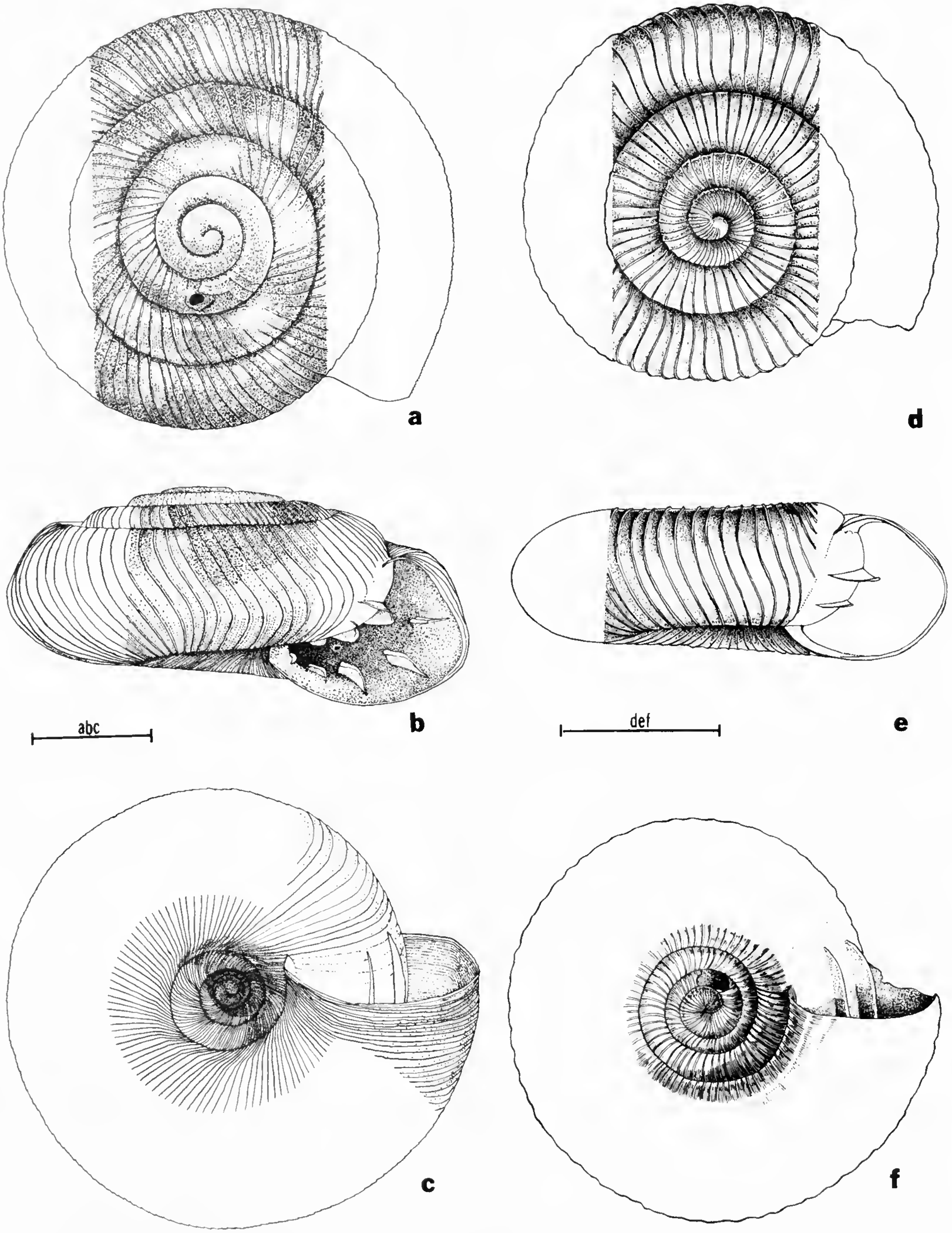

FIG. 74. **a-c**, *Mautodontha* (*M.*) *zimmermani*, new species. Station 865, Aorai trail at 5,600-6,300 ft. elevation, Tahiti, Society Islands. Holotype. BPBM 145293; **d-f**, *Mautodontha* (*M.*) *aoraiensis*, new species. Station 870, west of Aorai trail at 5,000 ft. elevation, Tahiti, Society Islands. Holotype. BPBM 145536. Scale lines equal 1 mm. (SG).

fine radial riblets, extremely fine and crowded spiral riblets, plus weak spiral grooves on spire and near sutures. Sutures deeply impressed, whorls strongly rounded above suture, flattened laterally above periphery and evenly rounded on basal margin. Periphery weakly angulated. Umbilicus narrowly V-shaped, last whorl decoiling much more rapidly, contained 6.67 times in the diameter. Color light yellow horn with a few widely spaced, reddish flammulations on the spire. Aperture ovate, flattened above periphery, somewhat compressed below. Parietal barriers 3, extending three-sixteenths of a whorl. Upper a high, bladelike lamella, posterior third expanded and serrated above, with very gradual anterior descension; 2nd with posterior third equal in height to 1st, anterior half threadlike; 3rd with posterior third greatly reduced in height, anterior threadlike portion ending well before anterior end of 2nd tooth. Columellar barrier a very short crescentic ridge, deeply recessed within aperture. Palatal barriers 4, extending about one-eighth whorl: lower a narrow, bladelike lamellar ridge, slightly expanded and serrated above; 2nd and 3rd progressively longer, higher and with more gradual anterior descension; 4th palatal equal in height to 1st, deeply recessed, with more gradual anterior descension, rather short. Height of holotype 1.91 mm., diameter 3.95 mm.

Holotype. — Society Islands: Tahiti, Station 865, near top of Aorai Trail, ridge at 5,600-6,300 ft. elevation. Collected by Elwood Zimmerman, Yoshio Kondo, and Donald Anderson on September 15, 1934. BPBM 145293.

Range. — Slopes of Mt. Aorai at 3,500-6,300 ft. elevation, Tahiti, Society Islands.

Paratypes. — Same as list of materials.

Material. — Tahiti: Aorai Trail (Stations 860, 862, 863, 865, 867, 869) from 3,500-6,300 ft. elevation (12 specimens, BPBM 142071, BPBM 145119, BPBM 145165, BPBM 145225, BPBM 145293-5, BPBM 145491, BPBM 145701).

Remarks. — In possessing an angulated periphery and weak spiral grooves, *Mautodontha zimmermani* closely approaches *Australdonta*. The large apertural barriers, internally constricted umbilicus, very weak spiral sculpture, total lack of any supraperipheral sulcus, simple penial pilaster pattern (fig. 64d), and absence of a fleshy fusion of the penis with the penial retractor (fig. 64c) combine to place *zimmermani* in *Mautodontha*. The most similar species is the Rarotonga *M. zebrina*. Differences are outlined above in the diagnosis.

Great pleasure is taken in naming this species after Elwood Zimmerman, entomologist on the Mangarevan Expedition, collector of many type specimens described in this paper, and famous student of the Pacific Island faunas.

Description of soft parts. — Only fragmentary animals were available. Pallial region extending apically one-half whorl, flattened length from pneumostome to base of kidney about 2.25 mm. Lung roof clear, no granulation. Kidney about 0.69 mm. long and typical in structure. Posterior third of kidney reaching hindgut. Ureter typical, opening at point where kidney reaches hindgut. Heart partly torn from surface of kidney and impossible to measure.

Apical genitalia not examined. Vas deferens (VD) entering laterally near penis head, opening internally just beneath apical fusion of penial pilasters (fig. 64d, PP). Penial retractor (PR) inserting directly on penis head, no sign of any fleshy extension. Penis (fig. 64c, P) slightly over 2 mm. long, tapering near atrial junction. Internal sculpture of two longitudinal pilasters, fusing apically above entrance of vas deferens, with one slightly twisted and coiled just below midpoint of penis (fig. 64d). Union of free oviduct and spermathecal stalk occurring just above entrance of penis and vagina into the narrow atrium.

No satisfactory mount was obtained of either jaw or radula.

(Dissection based on BPBM 145293, one example previously pulled from shell.)

Mautodontha (M.) zebrina (Garrett, 1874). Figure 73a-b.

Pitys zebrina Garrett, 1874, Proc. Acad. Nat. Sci., Philadelphia, **1873**, pp. 234-235, pl. 3, fig. 66 — Rarotonga, Cook Islands; Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, **8**, (4), p. 389.

Helix (*Endodonta*) *zebrina* (Garrett), Tryon, 1887, Man. Conchol., (2), 3, p. 64, pl. 12, figs. 17-19.

Endodonta (*Thaumatodon*) *zebrina* (Garrett), Pilsbry, 1893. *op. cit.*, (2), 9, p. 27.

Diagnosis. — Shell very large, diameter 3.75-4.57 mm. (mean 4.10 mm.), with 4¾ - 5⅜ quite loosely coiled whorls. Apex and early spire flat or barely elevated, last whorl descending slightly more rapidly, H/D ratio 0.474-0.540 (mean 0.507). Umbilicus constricted, V-shaped, narrow, last whorl decoiling more rapidly, contained 5.20-6.44 times (mean 5.85) in the diameter. Sculpture of very widely spaced, protractive radial ribs, 32-41 (mean 34.8) on the body whorl, whose interstices are 7-8 times their width, becoming greatly reduced to indistinguishable on the body whorl. Microsculpture of prominent radial riblets and extremely fine spiral riblets. Sutures impressed, whorls smoothly rounded, slightly compressed above and below periphery, umbilical margin strongly rounded. Aperture subcircular, slightly flattened basally, inclined about 10° from shell axis. Parietal barriers 3, lower greatly reduced, extending nearly one-quarter whorl: upper a high lamellar ridge, posterior third with upper edge weakly expanded and serrated, anterior part with very gradual descension to just before end; 2nd with posterior quarter to third as in 1st, anterior half threadlike; 3rd with elevated posterior portion greatly reduced in height, shorter, anterior threadlike portion greatly shortened to absent. Columellar wall usually without, rarely (16 per cent) with a small, deeply recessed lamellar ridge. Palatal barriers usually 4, rarely (16 per cent) with upper absent, extending one-eighth whorl: lower basal, a raised, high lamellar ridge with gradual anterior descension, moderately recessed; 2nd and 3rd progressively higher, longer, with more gradual anterior descension; 4th supraperipheral, a deeply recessed, short, threadlike or V-shaped trace, sometimes absent.

The widely spaced, reduced radial sculpture, constricted narrow umbilicus, large size, and large palatal barriers diagnosis *Mautodontha zebrina*. The other Cook Islands species of similar size, *M. unilamellata*, has no palatal barriers, only one parietal barrier, a widely open umbilicus and much more numerous crowded ribs (table LXVI). *M. zimmermani* from Tahiti is most similar in size and barrier structure, but obviously differs in its regularly spaced radial ribbing (70-90 on body whorl), angulated periphery and elevated spire.

Description. — Shell relatively large, with 5⅜ rather loosely coiled whorls. Apex and spire slightly elevated, body whorl descending a little more rapidly, H/D ratio 0.540. Apical whorls 1⅜, sculpture eroded. Postnuclear whorls with low, widely spaced, radial ribs, 41 on the body whorl, whose interstices are 7-8 times their width, primarily indicated by long, periostracal extensions. Microsculpture of prominent, lamellar, radial riblets, eight to twelve between each pair of major ribs, with very fine, barely visible spiral riblets. Sutures moderately impressed, whorls somewhat compressed laterally above periphery and on basal margin. Color very light yellow horn with irregular protractive, reddish flammulations that coalesce near periphery and tend to fade out near umbilicus. Umbilicus narrowly open, internally constricted by whorl coiling, contained 5.35 times in the diameter. Aperture subcircular, slightly flattened basally and laterally above periphery, inclined about 10° from shell axis. Parietal barriers 3, extending a little more than three-sixteenths of a whorl: upper bladelike, with very gradual anterior descension, posterior third weakly expanded and serrated on top, anterior end sharply descending; 2nd with posterior third as in 1st, anterior half threadlike, total length equal to 1st; 3rd parietal a reduced, threadlike ridge, only two-thirds length of upper, weakly elevated posteriorly. Columellar wall with a deeply recessed, very faint, rounded ridge, situated on moderately heavy callus. Palatal barriers 4, extending about one-eighth whorl: lower a high, lamellar ridge, recessed within aperture, with gradual anterior descension; 2nd sub-crescentic, higher, with more gradual anterior descension, slightly less deeply recessed; 3rd palatal a high, bladelike ridge, reaching almost to apertural edge; upper palatal an indistinct threadlike ridge, moderately recessed within aperture. Height of lectotype 2.47 mm., diameter 4.57 mm.

Lectotype. — Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47799.

Range. — A valley on Rarotonga, Cook Islands.

Paratypes. — ANSP 290104, BPBM 2337.

Material. — Rarotonga (6 specimens, ANSP 47799, ANSP 290104, BPBM 2337).

Remarks. — Garrett (1881, p. 389) reported that "a half dozen specimens" were collected at the same place as the *otareae* form of "*Patula*" *decorticata*, a charopid belonging to an undescribed genus. No other material is known. Surprisingly, all six of the original specimens were located still preserved in museum collections.

Other Cook Island species with apertural barriers either belong to *Libera, Thaumatodon,* or have only a single parietal and no palatal barriers (*M. unilamellata*). Differences from the Tahitian *M. zimmermani* are given in the diagnosis.

One specimen (the lectotype) had a distinct columellar, and one individual had the 4th palatal absent. Otherwise, the barrier structure was identical.

Mautodontha (M.) aoraiensis, new species. Figures 64e; 74d-f.

Diagnosis. — Shell very small, diameter 2.60-276 mm. (mean 2.68 mm.), with 4-4¼ normally coiled whorls. Apex and first postnuclear whorl depressed, later whorls flatly coiled, last whorl not descending more rapidly, H/D ratio 0.342-0.357 (mean 0.349). Umbilicus broadly open, saucershaped, regularly decoiling, contained 2.82-3.00 times (mean 2.91) in the diameter. Postnuclear whorls with high, prominent, protractively sinuated radial ribs, 61-66 (mean 63.5) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of six to nine very fine radial riblets between each pair of major ribs and barely visible microspiral riblets, plus a very weak sculpture of secondary spiral cords near the sutures and umbilicus. Sutures deep, whorls strongly rounded above, compressed laterally above and below rounded periphery, umbilical margin strongly rounded. Aperture subcircular, compressed above and below periphery, inclined about 15° from shell axis. Parietal wall with 2 barriers, extending three-sixteenths of a whorl: upper a high, bladelike ridge, serrated on top, not expanded or raised posteriorly, with smooth descension for anterior sixth: 2nd half the height of 1st, with same shape and sculpture, differing only in more gradual anterior descension. No columellar or palatal barriers.

The lack of any columellar and palatal barriers separates *Mautodontha aoraiensis* from most species. The very high parietal barriers, depressed spire, and very wide umbilicus immediately separate it from *M. consimilis, M. acuticosta,* and *M. unilamellata,* the other *Mautodontha* that lack palatals. In these species the parietal(s) is threadlike, the spire strongly elevated and the umbilicus V- or U-shaped.

Description. — Shell relatively small, with 4¼ loosely coiled whorls. Apex and early spire slightly depressed, remaining spire planulate, body whorl not decoiling more rapidly, H/D ratio 0.357. Embryonic whorls 1½, sculpture of two minor radial ribs between each relatively large radial, with relatively closely spaced spiral ribs about equal in size to the minor radials. Postnuclear whorls with relatively high, protractively sinuated, lamellar radial ribs, 66 on the body whorl, whose interstices are 2-3 times their basal width. Microsculpture of six to nine low radial riblets between each major rib pair, with barely visible spiral riblets plus weak secondary spiral cords near umbilicus and sutures. Sutures moderately deep, whorls strongly rounded above suture, compressed above obtusely angulated periphery, evenly rounded and compressed below. Umbilicus widely open, saucer-shaped, contained 3.00 times in the diameter. Color light yellowish-white below with a slight reddish tinge above. Aperture subcircular, compressed laterally above and below periphery, inclined about 15° from shell axis. Parietal wall with 2 narrow barriers, extending about three-sixteenths of a whorl: upper high and bladelike, serrated on top, with rather sharp anterior descension, otherwise the same in shape. No columellar or palatal barriers. Height of holotype 0.99 mm., diameter 2.76 mm.

Holotype. — Society Islands: Tahiti, Station 870, small valley west of Aorai Trail at 5,000 ft. elevation. Collected by Donald Anderson on September 16, 1934. BPBM 145536.

Range. — Near Aorai Trail at 4,700-5,500 ft. elevation, Tahiti, Society Islands.

Paratypes. — BPBM 145536.

Material. — Tahiti: Aorai Trail (Stations 863, 870) at 4,700-5,500 ft. elevation (3 specimens, BPBM 145536).

Remarks. — The three known specimens of *Mautodontha aoraiensis* are subadult, but the numerous differences from any other Society Island species warrant their description as a new species. Despite the many obvious differences in form and barriers, I expect the *M. zimmermani* will be found to be the closest relative. Additional young specimens may be mixed with juveniles of *Libera bursatella,* which is sympatric.

Description of soft parts. — One fragmentary example available. Penis (fig. 64e, P) approximately 0.6 mm. long. Vas deferens (VD) inserting laterally well below head of penis. No trace of penial retractor left on specimen. Penis markedly tapering anteriorly, becoming quite narrow near junction with atrium. Penis sculptured internally with two longitudinal pilasters that merge above entrance of vas deferens and extend as a single lobe into penis head. Shaft of spermatheca and free oviduct joining just before union with penis to form atrium. No other features of anatomy observed.

(Based on a partially extracted animal from BPBM 145536.)

Subgenus **Garrettoconcha,** new subgenus

Shell with normally elevated spire, narrower umbilicus than in *Mautodontha* s.s., body whorl usually descending abruptly with the

TABLE LXVI. - RANGE OF VARIATION IN MAUTODONTHA (GARRETTOCONCHA)

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
consobrina (Garrett)	7	153.3(141-164)	1.89(1.78-1.97)	3.82(3.55-4.31)	0.497(0.458-0.532)	6 3/8+(5 3/4-7 1/4)	3.10(2.79-3.52)	4	1	4+3
saintjohni	23	123.3(109-136)	1.50(1.36-1.72)	2.84(2.65-3.05)	0.528(0.494-0.584)	5 1/8(4 7/8-5 5/8)	3.41(3.17-3.64)	4	1	4+4
maupiensis (Garrett)	24	OVER 200	1.75(1.50-1.97)	3.07(2.68-3.39)	0.567(0.510-0.607)	6+(5 1/4-6 1/2)	4.25(3.33-5.42)	4[1]	1	4+2-3-5
punctiperforata (Garrett)	10	139(136-143)	1.90(1.74-2.04)	3.36(3.13-3.59)	0.566(0.529-0.614)	5 1/2+(5 1/8-5 7/8)	11.2(8.5-14.3)	2-3+0, 4-6	1	3-4+0-4
imperforata (Pease)	31	OVER 200	2.04(1.81-2.60)	3.43(3.22-3.95)	0.592(0.539-0.658)	5 3/4(5 1/2-6 1/2)	CLOSED	3+6-7-9	0	4+4-6
parvidens (Pease)	59	138(104-180)	1.58(1.25-2.07)	3.19(2.80-3.95)	0.496(0.430-0.558)	5 1/8-(4 1/2-5 3/4)	3.81(3.09-4.55)	2-3-4	0	3-4-5
subtilis (Garrett)	8	75.7[2] (68-124)	1.61(1.49-1.85)	3.13(2.94-3.38)	0.513(0.484-0.553)	5 3/4+(5 1/2-6 1/2)	4.43(3.92-5.00)	2	0	4
rarotongensis (Pease)	12	130(118-137)	1.58(1.28-1.81)	3.01(2.76-3.26)	0.522(0.464-0.556)	4 7/8+(4 1/2-5 1/4)	5.47(4.67-6.14)	2-3	1	2-3
consimilis (Pease)	81	73.3(53-117)	2.02(1.68-2.34)	3.43(3.03-4.05)	0.588(0.523-0.666)	5 1/8+(4 5/8-5 5/8)	4.36(3.42-6.25)	1-2	0	0
acuticosta (Garrett)	58	80.95(59-106)	1.94(1.78-2.07)	4.01(3.42-4.90)	0.483(0.423-0.571)	5 1/16(4 5/8-5 3/8)	3.37(2.89-4.27)	1-2-3-5	0	0
unilamellata (Garrett)	5	82(78-87)	2.19(2.01-2.60)	3.96(3.68-4.28)	0.554(0.492-0.642)	5 1/8(5 -5 3/8)	3.61(3.31-4.10)	1+0-1	0	0

1. 2nd and 4th parietals reduced and shortened
2. of nongerontic specimens

TABLE LXVII. - LOCAL VARIATION IN MAUTODONTHA

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
boraborensis						
BPBM 3763 BPBM 170955	11	1.94±0.045 (1.76-2.19)	4.44±0.106 (3.94-5.00)	0.438±0.0081 (0.411-0.504)	7 1/8- (6 1/2-8)	2.60±0.063 (2.33-2.98)
daedalea						
Makatea BPBM 115738	14	1.27±0.026 (1.15-1.45)	3.09±0.04 (2.80-3.36)	0.412±0.0064 (0.376-0.452)	5 1/4+ (5-5 1/2)	3.09±0.045 (2.65-3.27)
Paris	8	1.44±0.050 (1.25-1.68)	3.38±0.052 (3.13-3.59)	0.425±0.0111 (0.375-0.481)	5 1/2+ (5 1/2-6 1/4)	3.01±0.073 (2.71-3.31)
Niau BPBM 118516	5	1.30±0.028 (1.22-1.32)	3.05±0.046 (2.90-3.13)	0.426±0.0098 (0.400-0.455)	5 1/4 (5-5 3/8)	3.34±0.089 (3.16-3.66)
Anaa BPBM 136519	3	1.38±0.098 (1.18-1.51)	3.27±0.154 (2.96-3.49)	0.421±0.0110 (0.400-0.434)	5 1/4 (5-5 1/2)	3.03±0.156 (2.77-3.31)
zimmermani	4	1.65±0.221 (1.41-1.91)	3.61±0.154 (3.22-3.95)	0.455±0.012 (0.434-0.483)	5+ (4 3/4-5 1/4)	5.13±0.540 (4.15-6.67)
zebrina						
ANSP 47799	4	1.98±0.184 (1.61-2.47)	3.92±0.245 (3.42-4.57)	0.502±0.016 (0.471-0.540)	4 3/4 (4 1/2-5 3/8)	6.16±0.270 (5.35-6.50)
saintjohni						
BPBM 152391	9	1.50±0.037 (1.36-1.72)	2.84±0.041 (2.65-3.05)	0.528±0.009 (0.499-0.580)	5 1/8 (4 7/8-5 5/8)	3.41±0.050 (3.17-3.64)
maupiensis						
BPBM 3358	4	1.85±0.063 (1.69-1.99)	3.34±0.037 (3.25-3.41)	0.553±0.016 (0.510-0.588)	6 1/4 (6-6 1/2)	4.55±0.480 (3.33-5.42)
ANSP 47791	5	1.73±0.070 (1.61-1.95)	3.09±0.084 (2.82-3.33)	0.555±0.012 (0.521-0.587)	6 1/8- (5 5/8-6 1/2)	3.90±0.107 (3.66-4.29)
imperforata						
BPBM	5	2.09±0.055 (1.95-2.19)	3.48±0.060 (3.31-3.64)	0.599±0.007 (0.578-0.617)	5 3/4+ (5 1/2-6)	CLOSED
parvidens						
Huahine	28	1.52±0.030 (1.18-1.84)	3.07±0.045 (2.40-3.49)	0.497±0.006 (0.438-0.558)	5- (4 1/8-5 1/4)	3.94±0.060 (3.46-4.55)
Moorea	15	1.61±0.052 (1.25-2.07)	3.27±0.070 (2.86-3.95)	0.492±0.009 (0.430-0.556)	5 1/8+ 4 5/8-5 3/4)	3.59±0.104 (3.09-4.53)
subtilis						
ANSP 47781	4	1.67±0.074 (1.52-1.85)	3.13±0.087 (2.98-3.38)	0.534±0.033 (0.511-0.553)	5 1/8- (4 7/8-5 3/8)	4.53±0.170 (4.18-5.00)
BPBM 2279 BPBM 170889	4	1.54±0.022 (1.49-1.59)	3.13±0.067 (2.95-3.25)	0.492±0.005 (0.484-0.505)	5- (4 3/4-5)	4.34±0.235 (3.92-4.95)
consimilis						
BPBM material	25	2.02±0.037 (1.69-2.38)	3.40±0.044 (3.05-4.07)	0.594±0.009 (0.530-0.666)	5 1/8- (4 3/4-5 1/2)	4.59±0.152 (3.56-6.25)
acuticosta						
BPBM material	29	1.98±0.038 (1.66-2.42)	4.06±0.063 (3.44-4.93)	0.488±0.008 (0.423-0.571)	5+ (4 5/8-5 1/2)	3.40±0.074 (2.89-4.27)
unilamellata						
BPBM 2339	2	2.37±0.248 (2.12-2.62)	4.19±0.116 (4.07-4.30)	0.567±0.075 (0.492-0.642)	5 1/4 (5 1/8-5 3/8)	3.76±0.339 (3.42-4.10)
ANSP 47799	3	2.07±0.040 (2.02-2.15)	3.81±0.069 (3.71-3.94)	0.546±0.019 (0.513-0.580)	5+ (5-5 1/4)	3.51±0.179 (3.31-3.86)

periphery laterally compressed or evenly rounded (only rarely, *M. imperforata*, weakly angulated). Apertural barriers reduced in size, one or more parietals and palatals absent or split into fine accessory traces.

Type species. – *Helix parvidens* Pease, 1861.

To a slight extent, *Mautodontha consobrina* and *M. saintjohni* tend toward the basic form of *Libera*, but I cannot say whether this has any direct phyletic significance. They and their obvious direct derivative, *M. maupiensis*, are most similar to *Mautodontha, s.s.* *M. punctiperforata, M. parvidens, M. subtilis,* and *M. rarotongensis* represent similar stages in barrier reduction with various specializations in form and sculpture (tables LXVI, LXVII). Probably *M. imperforata* should be viewed as an extreme variant within this grouping. Finally, *M. consimilis, M. acuticosta,* and *M. unilamellata* have reached an extreme stage of barrier reduction, are relatively large in size, and have prominent, widely spaced sculpture, whereas the other species tend to have crowded, very fine sculpture.

The average differences from *Mautodontha s.s.* are discussed above under that taxon. Unfortunately, no anatomical material of *Garrettoconcha* was available. Since the Mangarevan expedition of 1934 to Tahiti and Borabora failed to collect any of Garrett's species – I found no lowland endodontids in Tahiti during 1962 and 1974 collecting, and trips to Rarotonga in 1964 and 1965 failed to locate any endodontid species except the supra-littoral *Libera fratercula* – I have little doubt that *Garrettoconcha* is now extinct. The only possible exceptions might be *M. rarotongensis* from Atiu and *M. imperforata* from Aitutaki. A few examples of the latter were collected by Peter Buck in 1929, but no subsequent attempt at collecting on that island has been made.

Mautodontha (Garrettoconcha) consobrina (Garrett, 1884). Figure 75d-e.

Pitys consobrina Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9,** (1), p. 31, pl. 2, figs. 17, a,b,c. – Huahine, Society Islands.
Helix (Endodonta) consobrina (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 66, pl. 12, figs. 43-45.
Endodonta (Thaumatodon) consobrina (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Diagnosis. – Shell rather large, diameter 3.55-4.31 mm. (mean 3.82 mm.), with 5¾-7¼ rather tightly coiled whorls. Apex flattened or slightly depressed, last whorl descending moderately, H/D ratio 0.458-0.532 (mean 0.497). Umbilicus broadly U-shaped, regularly decoiling, contained 2.79-3.52 times (mean 3.10) in the diameter. Sculpture of fine, vertical radial ribs, 141-164 (mean 153.3) on the body whorl, whose interstices are about 2-4 times their width. Microsculpture of four to seven fine radial riblets between each pair of major ribs, crossed by barely visible spiral riblets. Sutures deep, strongly rounded above and on umbilical margin, evenly rounded on compressed outer margin. Aperture ovate, slightly compressed laterally and on basal margin, parallel to shell axis. Parietal barriers 4, extending three-sixteenths of a whorl: upper high and bladelike, posterior half serrated above, anterior half with very gradual descension; 2nd and 3rd with posterior quarter to third higher than 1st, serrated and weakly expanded above, anterior half to five-eighths threadlike; 4th with elevated posterior portion distinctly lower and shorter, anterior threadlike portion inconspicuous or partly absent. Columellar barrier a prominent raised ridge, rather broad, lying parallel to plane of coiling, recessed, continuing posteriorly beyond line of vision. Palatal barriers 4, prominent, extending one-eighth whorl, with three to four accessory traces: lower a short, bladelike lamella, expanded and serrated above, moderately recessed, with posterior descension; 2nd palatal much higher, longer, serrated on posterior half, gradually descending over anterior half; 3rd palatal slightly lower with very gradual anterior descension; 4th palatal supraperipheral, a moderately high threadlike ridge, deeply recessed within aperture, shorter than 3rd. Palatal traces located between palatals 1 and 2, 2 and 3, and 3 and 4, occasionally above 4th.

Mautodontha saintjohni from Borabora has one less whorl, is much smaller (mean diameter 2.84 mm.) and has the elevated portion of the parietal barriers much shorter. Otherwise the two species are very similar. The high whorl count of *M. consobrina* at once separates it from other *Garrettoconcha,* while the presence of palatal traces and sharply descending body whorl distinguish it from *Mautodontha s.s.*

Description. – Shell a little larger than average, with 5¾ relatively tightly coiled whorls. Apex barely emergent, whorls of spire gradually descending more rapidly, H/D ratio 0.532. Apical whorls 1⅜, sculpture of rather widely spaced, narrow radial ribs with a barely visible microsculpture between. Postnuclear whorls with crowded, V-shaped, vertically sinuated radial ribs, 164 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, crossed by very much finer and more crowded spiral riblets. Sutures moderately impressed, whorls evenly rounded on outer margin. Color light yellow horn with broad, frequent, zigzag, reddish flammulations. Umbilicus narrow, U-shaped, regularly decoiling, contained 3.52 times in the diameter. Aperture subcrescentic with evenly rounded outer margin, nearly parallel to shell axis. Parietal barriers 4, extending nearly one-quarter whorl: upper parietal high, bladelike, with gradual anterior descension, thickened and serrated above posteriorly; 2nd, 3rd, and 4th parietals equal in height to 1st, but with medial, sharp descension to a threadlike anterior portion which extends slightly further out of aperture. Columellar barrier a low, broadly rounded, deeply recessed ridge, extending beyond line of vision. Palatal barriers 4, extending about one-eighth whorl: lower palatal basal in position, a lamellar ridge moderately recessed within aperture; 2nd palatal a subcrescentic lamella, flattened and broadly expanded above; 3rd palatal a lamellar ridge with very gradual anterior descension; 4th palatal a long, low, lamellar ridge with very gradual anterior descension. Accessory traces located between 1st and 2nd, 2nd and 3rd, 3rd and 4th, and above 4th palatal barrier. Height of lectotype 1.91 mm., diameter 3.59 mm.

Lectotype. – Society Islands: Huahine. Collected by Andrew Garrett. ANSP 47777.

Range. – "Peculiar to one valley," Huahine Island, Society Islands.

Paratypes. – BPBM 2852, ANSP 290092.

Material. – Huahine (7 specimens, BPBM 2852, ANSP 47777, ANSP 290092, SMF 165433).

Remarks. – It was reported by Garrett (1884, p. 31) as "rare and peculiar to one valley." No later collections have been made.

The type is a small shell with somewhat unusual apertural barriers. It was selected because other members of the same set obviously were juvenile.

Mautodontha (Garrettoconcha) saintjohni, new species. Figure 75a-c.

Diagnosis. – Shell very small, diameter 2.64-3.03 mm. (mean 2.84 mm.), with 4⅞-5⅝ moderately tightly coiled whorls. Apex and spire flattened or barely elevated, spire descending slowly, last whorl more rapidly, H/D ratio 0.494-0.584 (mean 0.528). Umbilicus U-shaped, widely open, regularly decoiling, contained 3.17-3.64 times (mean 3.41) in the diameter. Sculpture of narrow, low, prominent, slightly protractively sinuated radial ribs, 109-136 (mean 123.3) on the body whorl, whose interstices are about 1½-2 times their width. Microsculpture of very fine radial riblets, four to seven between each pair of major ribs, crossed by distinctly finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above and on umbilical margin, with evenly rounded, very slightly compressed outer margin. Aperture ovate, with evenly rounded outer margin, inclined about 5° from the shell axis. Parietal barriers 4, extending a little more than three-sixteenths of a whorl: upper high and bladelike, posterior third serrated and weakly expanded above, anterior half reduced in height; 2nd and 3rd with posterior third equal to or slightly higher than 1st, anterior half threadlike, extending beyond edge of 1st; 4th with posterior portion lower and shorter, anterior threadlike section finer. Columellar barrier a deeply recessed, very low crescentic ridge. Palatal barriers 4, extending a little over one-eighth whorl, sometimes (22.2 per cent) with four accessory traces: lower small, bladelike, expanded and serrated above, with very gradual anterior descension; 2nd much higher and longer, identical in shape; 3rd slightly lower, with even more gradual descension, posterior expanded portion shorter; 4th a short, deeply recessed, supraperipheral V-shaped ridge. Accessory traces, when present, between palatals and above upper, all very short and threadlike.

The much larger (mean diameter 3.82 mm.) *Mautodontha consobrina* from Huahine has the same apertural barrier pattern, but the elevated posterior portion of the parietals is longer. In addition, *M. consobrina* has one more whorl. *M. maupiensis* has the 2nd and 4th parietals reduced in size, much finer and more crowded ribbing (over 200 ribs on the body whorl) and a narrower umbilicus (mean D/U ratio 4.25).

Description. – Shell small, with 5⅝ rather tightly coiled whorls. Apex and upper spire almost flat, lower whorls of spire descending rapidly, H/D ratio 0.554. Embryonic whorls 1¼, sculpture of widely spaced radial riblets crossing slightly lower and equally widely spaced spiral ribs, producing a latticed effect, plus very fine radials between the larger ones. Lower whorls with moderately prominent, rounded, slightly protractively sinuated radial ribs, 136 on the body whorl, whose interstices are 1½-2 times their width. Sutures moderately impressed, whorls strongly rounded above and in umbilicus, evenly rounded on outer margin. Umbilicus U-shaped, slightly and regularly decoiling, contained 3.42 times in the diameter. Color white with prominent zigzag, reddish flammulations that coalesce on base of shell. Aperture ovate, slightly compressed laterally. Parietal barriers 4, extending three-sixteenths of a whorl: upper parietal a high, bladelike lamella, serrated and weakly expanded posteriorly, anterior half slightly lower in height, with sharp descension at end; 2nd with posterior quarter equal in height to 1st lamella, expanded and thickened above, anterior two-thirds a threadlike ridge extending beyond anterior end of 1st parietal; 3rd and 4th nearly identical to 2nd, except 4th with posterior section slightly lower. Columellar barrier a deeply recessed, low crescentic ridge, parallel to plane of coiling. Palatal barriers 4, extending slightly more than one-eighth whorl: lower a low bladelike ridge, slightly recessed, with gradual anterior descension, expanded and serrated above; 2nd a high, bladelike lamella, with short flat posterior portion and very gradual anterior descension; 3rd slightly lower than 2nd, less expanded above, with very gradual anterior descension; 4th supraperipheral, a short, deeply recessed, V-shaped ridge. Height of holotype 1.71 mm., diameter 2.93 mm.

Holotype. – Society Islands: Borabora, Station 1093, south slope of Pahio-Temanu ridge at 800 ft. elevation. Collected by Clifford Gessler and Harold St. John on October 13, 1934. BPBM 152391.

Range. – Pahio-Temanu ridge at 800 ft. elevation, Borabora, Society Islands.

Paratypes. – BPBM 152391.

Material. – Borabora (23 specimens, same as list of types).

Remarks. – Unfortunately, no living specimens were collected, although several of the shells were quite fresh. About one-fifth of the shells had four accessory palatal traces, the remaining shells had only the 4 basic barriers. In the deepening of the umbilicus and sharp descension of the body whorl, there is a slight indication that both *M. consobrina* and *M. saintjohni* foreshadow the structures typified by *Libera.*

Great pleasure is taken in naming this species after its collector, Harold St. John, botanist of the Mangarevan Expedition.

Mautodontha (Garrettoconcha) maupiensis (Garrett, 1872). Figure 76a-b.

Pitys maupiensis Garrett, 1872, Proc. Calif. Acad. Sci., **1872**, p. 204 – Maupiti, Society Islands; Garrett, 1874, Proc. Acad. Nat. Sci., Philadelphia, **1873**, pp. 233-234, pl. 3, fig. 64; Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 31.

Patula maupitiensis Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 93 – unnecessary emendation.

Helix maupitiensis (Garrett), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 481.

Helix (*Endodonta*) *maupitiensis* (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 65, pl. 12, figs. 27-29.

Endodonta (*Thaumatodon*) *maupiensis* (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Endodonta maupiensis (Garrett), Gude, 1913, Proc. Malacol. Soc. London, **10**, (5), p. 330 – Fiji Islands (erroneous record).

Diagnosis. – Shell much smaller than average, diameter 2.68-3.39 mm. (mean 3.07 mm.), with 6-6½ relatively tightly coiled whorls. Apex flat to slightly elevated, lower whorls descending much more rapidly, H/D ratio 0.510-0.625 (mean 0.567). Umbilicus open, U-shaped, barely decoiling, contained 3.33-5.42 times (mean 4.25) in the diameter. Sculpture of extremely fine and crowded vertically sinuated radial ribs, many more than 200 on the body whorl, whose interstices are less than twice their width. Microsculpture of one or two fine radial riblets between each pair of major radials crossed by much finer and more crowded spirals. Sutures shallow, whorls evenly rounded except for lateral compression below periphery. Aperture ovate, compressed laterally, nearly parallel to shell axis. Parietal barriers 4, 2nd and 4th reduced in height, anterior portion absent, 1st and 3rd extending almost one-quarter whorl: upper a low lamellar ridge with gradual descension over anterior half; 2nd deeply recessed, lying along posterior third of upper, a higher lamellar blade with gradual anterior descension; 3rd with posterior quarter having same shape as 2nd parietal, anterior half a low threadlike ridge; 4th deeply recessed as 2nd, usually a low rounded ridge, occasionally as high as 2nd. Columellar wall with deeply recessed, low crescentic ridge, parallel to plane of coiling. Palatal wall with 4 moderately recessed lamellar ridges, extending a little more than one-eighth whorl, plus two to five (usually three), short, threadlike accessory traces: lower at baso-columellar margin, a raised lamellar ridge to bladelike barrier, slightly recessed, with gradual anterior descension; 2nd and

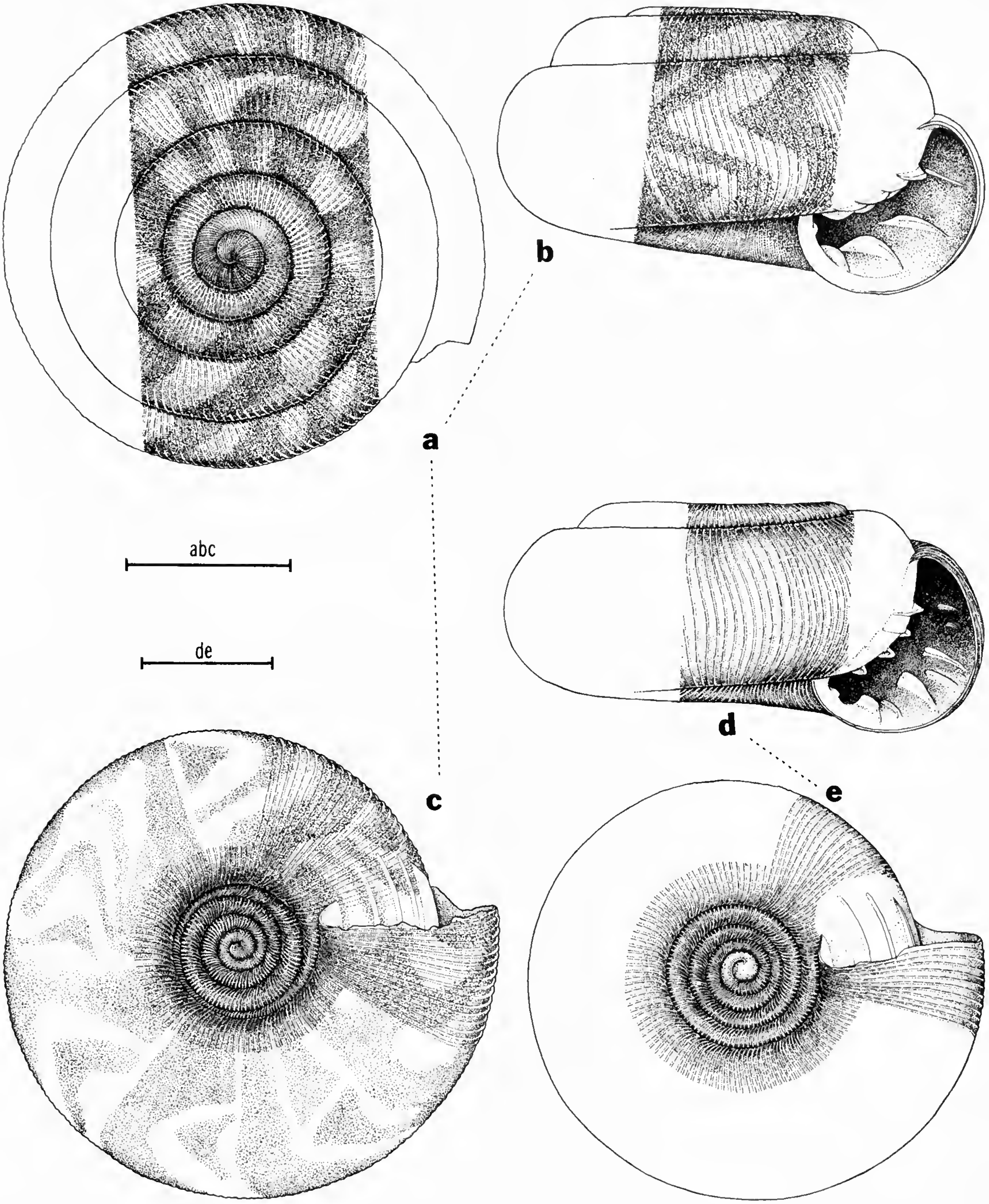

FIG. 75. **a-c**, *Mautodontha* (*Garrettoconcha*) *saintjohni*, new species. Station 1093, Borabora, Society Islands. Holotype. BPBM 152391; **d-e**, *Mautodontha* (*Garrettoconcha*) *consobrina* (Garrett). Huahine, Society Islands. Paratype. BPBM 2852. Scale lines equal 1 mm. (MM).

3rd higher, longer, more deeply recessed, with more gradual anterior descension; 4th very slightly supraperipheral, a shorter, threadlike ridge, quite deeply recessed. Accessory traces usually between 1st and 2nd, 2nd and 3rd, then 3rd and 4th palatals. Occasionally upper trace absent, or additional traces above 4th palatal.

The extremely fine and crowded ribbing of *Mautodontha maupiensis* is similar to the sculpture found in *M. imperforata* from the Cook Islands which differs in having a closed umbilicus and numerous parietal traces. The very small Cook Island *Minidonta rotellina* (diameter 1.96-2.19 mm.), differs in every feature but sculpture. The most closely related taxa, *M. consobrina* and *M. saintjohni,* do not have the 2nd and 4th parietals reduced in size; both have much less crowded sculpture.

Description. — Shell smaller than average, with slightly more than 6¼ tightly coiled whorls. Apex barely emergent, first postnuclear whorl flatly coiled, remaining whorls of spire gradually descending more rapidly until spire has a distinctly conical appearance, H/D ratio 0.587. Apical whorls 1⅜, sculpture of fine, crowded radial riblets with a barely distinguishable microsculpture of spiral and radial riblets. Postnuclear whorls with low, narrow, nearly vertically sinuated, very crowded radial ribs, about 280 on the body whorl, whose interstices are less than twice their width. Microsculpture of an occasional radial riblet visible between the crowded macroribs, with much finer spiral microribbing. Sutures moderately impressed, whorls almost evenly rounded on outer margin, more steeply rounded at shoulder and umbilicus. Color light yellow horn with vague, somewhat regularly spaced, reddish flammulations. Umbilicus narrowly U-shaped, barely decoiling, contained 3.94 times in the diameter. Aperture ovate, laterally compressed, evenly rounded on outer margins, inclined about 5° from shell axis. Parietal barriers 4, 2nd and 4th recessed: upper parietal long, bladelike, extending nearly one-fourth whorl, posterior two-thirds serrated and slightly expanded above; 2nd parietal with posterior one-third as in 1st, with sudden anterior descension to a threadlike appendage reaching only to midpoint of 1st parietal; 3rd parietal identical in shape to 2nd, but with threadlike anterior portion extending slightly beyond anterior edge of 1st parietal; 4th parietal slightly reduced in height, reaching only to midpoint of 3rd parietal. Columellar barrier deeply recessed, moderately prominent, crescentic, lying parallel to plane of coiling. Palatal barriers 4, with two accessory traces: 1st palatal near baso-columellar margin, moderately prominent, bladelike, extending one-eighth of a whorl; 2nd, 3rd, and 4th palatals evenly spaced up to periphery, moderately recessed, low and bladelike, extending slightly more than one-eighth whorl, 4th much lower than 3rd. Accessory traces threadlike, short, located between 1st and 2nd, 2nd and 3rd palatals. Height of lectotype 1.83 mm., diameter 3.11 mm.

Lectotype. — Society Islands: Maupiti. Collected by Andrew Garrett. ANSP 47791.

Range. — Maupiti Island.

Paratypes. — BPBM 3358, ANSP 290096.

Material. — Maupiti (21 specimens, BPBM 3358, BPBM 170956, ANSP 47791, ANSP 290096, SMF 165728, Zurich).

Remarks. — Although Garrett stated that there are only 2 or 3 parietal barriers, all specimens examined proved to have 4. Since the barriers are low and deeply recessed within the aperture, it is certain that the lower one was overlooked. Although only 21 specimens could be located, this species apparently was common on Maupiti Island. The subsequent record from Fiji by Gude (see above), is almost certainly based on a misidentification, although the specimens on which this record was based could not be located. It has been included above only for completeness of literature citations.

An obvious derivative of *M. consobrina, M. maupiensis* is somewhat intermediate to the *M. parvidens* complex.

Mautodontha (Garrettoconcha) punctiperforata (Garrett, 1884). Figure 76c-d.

Pitys punctiperforata Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 32, pl. 2, figs. 16a, b, c — Moorea, Society Islands.

Helix (Endodonta) punctiperforata (Garrett), Tryon, 1887, Man. Conchol., (2), **9**, p. 66, pl. 12, figs. 49-51.

Endodonta (Thaumatodon) punctiperforata (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Diagnosis. — Shell slightly less than average in size, diameter 3.13-3.59 mm. (mean 3.36 mm.,) with 5½-5⅞ normally coiled whorls. Apex flat or slightly elevated, lower whorls descending much more rapidly, H/D ratio 0.529-0.614 (mean 0.566). Umbilicus barely perforate, constricted by expansion of the columellar region, last whorl slightly decoiling, contained 8.50-14.3 times (mean 11.2) in the diameter. Sculpture of numerous, slightly protractively sinuated radial ribs, 136-143 (mean 139) on the body whorl, whose interstices are about 2-3 times their width. Microsculpture of very fine radial riblets, five to eight between each pair of major ribs, crossed by much finer and more crowded spiral riblets that are barely visible under 96× magnification. Sutures deep, whorls strongly rounded above, slightly compressed laterally above very weakly angled periphery, with evenly rounded, laterally compressed lower palatal and umbilical walls. Aperture elongate-ovate, with barely angled periphery, inclined about 5° from shell axis. Parietal barriers 2, extending about one-quarter whorl, with four to six accessory traces or sometimes (28.6 per cent) 3 parietals, the lower greatly reduced: upper high and bladelike, posterior half serrated and expanded above, anterior third descending gradually; 2nd lower, posterior third to half as in 1st, anterior half to third threadlike or a raised threadlike ridge. Accessory traces below 2nd parietal, shorter than parietals, often with an enlarged threadlike ridge in same position as 3rd parietal in related species. Columellar wall with a heavy callus surmounted by a broad, blunt crescentic barrier, moderately recessed within aperture. Palatal barriers 4, extending one-eighth whorl, upper reduced in size: lower at baso-columellar margin, rarely (14.3 per cent) shifted onto columellar wall, elongated and crescentic, slightly recessed with sharp anterior descension; 2nd and 3rd high, bladelike, longer, with progressively much more gradual anterior descension, posterior half to two-thirds serrated and expanded above; 4th slightly supraperipheral, a threadlike to V-shaped ridge, shorter and more deeply recessed than 3rd, sometimes absent. Accessory traces very low, short, threadlike traces, located between palatals and/or above 4th palatal.

The minute umbilicus at once separates *Mautodontha punctiperforata* from the other Society Island species. The Cook Island *M. imperforata* has much finer sculpture, a completely closed umbilicus, and much lower and longer palatal barriers. The minute (mean diameter 1.97 mm.) *Minidonta rotellina* from Aitutaki, Cook Islands has very fine sculpture and reduced palatal barriers.

Description. — Shell slightly smaller than average, with 5⅞ normally coiled whorls. Apex flat, whorls of spire gradually descending more rapidly, H/D ratio 0.614. Apical whorls 1⅜,

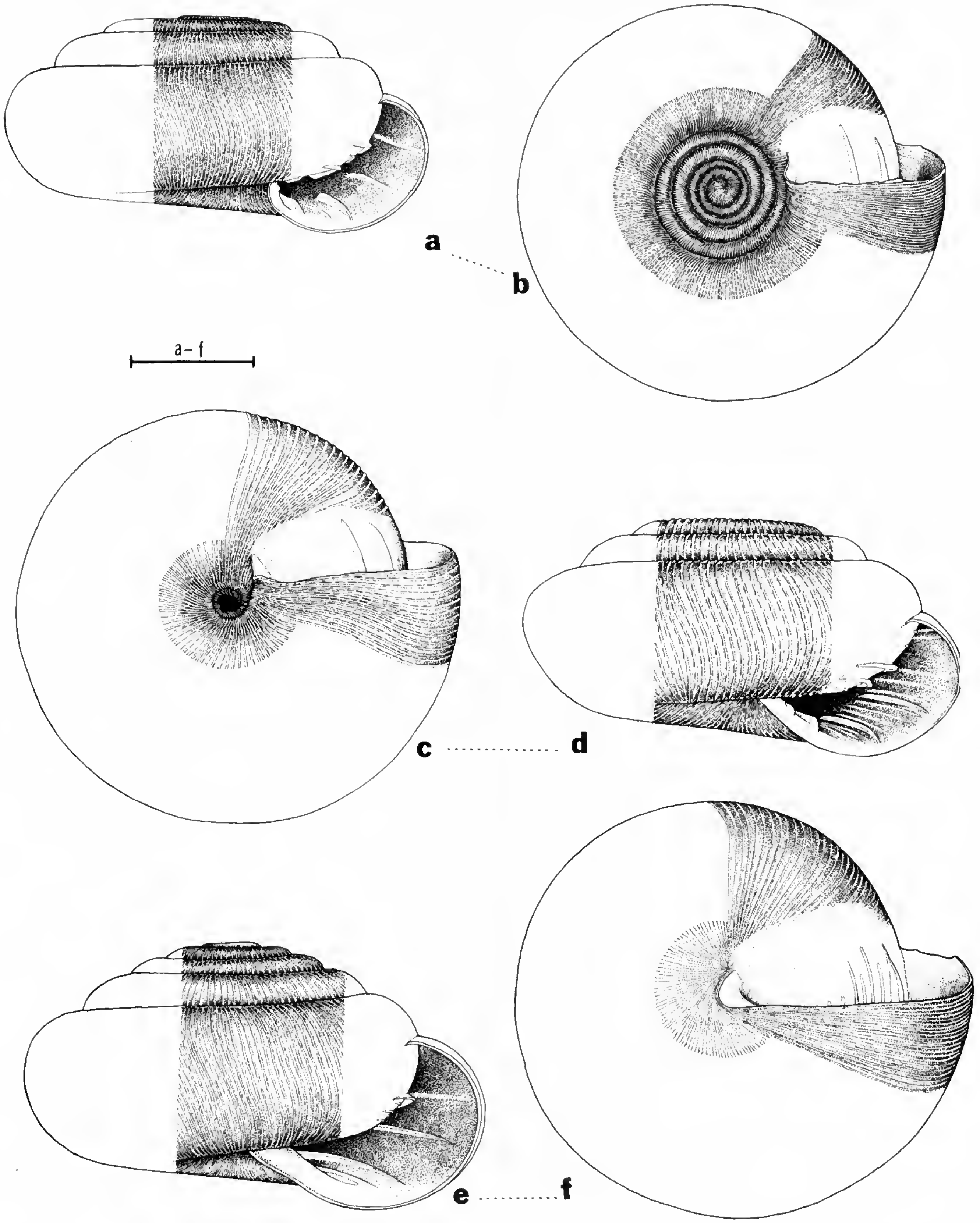

FIG. 76. **a-b**, *Mautodontha* (*Garrettoconcha*) *maupiensis* (Garrett). Maupiti, Society Islands. Paratype. BPBM 3358; **c-d**, *Mautodontha* (*Garrettoconcha*) *punctiperforata* (Garrett). Moorea, Society Islands. Paratype. BPBM 2857; **e-f**, *Mautodontha* (*Garrettoconcha*) *imperforata* (Pease). Aitutake, Cook Islands. Lectotype. BPBM 2322. Scale line equals 1 mm. (MM).

sculpture of narrow, crowded, radial ribs, microsculpture obscured. Postnuclear whorls with high, rounded, prominent, slightly protractively sinuated radial ribs, 138 on the body whorl, whose interstices are about twice their width. Microsculpture of relatively prominent radial riblets, crossed by extremely fine and crowded spiral riblets. Sutures moderately impressed, whorls strongly rounded on outer margin, slightly compressed basally. Color light yellow horn with prominent, reddish flammulations, broader above, becoming narrower on the body whorl, fading out on base of shell. Umbilicus barely perforate, constricted by extension of whorls, contained about 12.6 times in the diameter. Aperture subovate, slightly flattened basally, inclined about 10° from shell axis. Parietal barriers 2, low, threadlike, extending one-quarter whorl, with a faint, much shorter, lower trace. Columellar wall with a heavy callus surmounted by two slightly recessed threadlike ridges. Palatal barriers 2, low, threadlike, moderately recessed within aperture, extending about one-eighth whorl. Two accessory traces located between the barriers and several faint traces located above upper palatal barrier. Height of lectotype 2.04 mm., diameter 3.33 mm.

Lectotype. — Society Islands: Moorea. Collected by Andrew Garrett. ANSP 47780.

Range. — Moorea, Society Islands.

Paratypes. — BPBM 2857, ANSP 290094.

Material. — Moorea (10 specimens, BPBM 2857, BPBM 116093, BPBM 170890, ANSP 47780, ANSP 290094).

Remarks. — The lectotype has slightly aberrant apertural barriers, but was selected because of its good preservation. Garrett (1884, p. 32) reported that a "few examples were found" and that "one specimen is uniform pale horn-color." The latter specimen was not seen.

The angulation of the body whorl, great proliferation of secondary traces, height reduction of the major barriers, and great constriction of the umbilicus seem to be correlated changes that are carried much further in the Cook Island *M. imperforata*. In that species the umbilicus is closed, the major parietal barriers have the elevated portions deeply recessed, there are many more lamellar traces and extreme flattening of the basal margin, but the peripheral angulation is absent.

Mautodontha (Garrettoconcha) imperforata (Pease, 1870). Figure 76e-f.

Pithys imperforata Pease, 1870. Jour. de Conchyl., **18**, p. 394 — Aitutaki, Cook Islands.

Pitys imperforata Pease, 1871. Proc. Zool. Soc. London, **1871**, pp. 453, 474: Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, 8, (4), pp. 389-390.

Patula aitutakiana "Mousson" Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 94 — nude name.

Helix (*Endodonta*) *imperforata* (Pease), Tryon, 1887, Man. Conchol., (2), 3, p. 68.

Endodonta (*Thaumatodon*) *imperforata* (Pease), Pilsbry, 1893, *op. cit.*, (2), 9, p. 27.

Diagnosis. — Shell average in size, diameter 3.22-3.78 mm. (mean 3.43 mm.), with 5½-6½ moderately tightly coiled whorls. Apex and spire almost evenly elevated, slightly rounded above, last whorl descending more rapidly, H/D ratio 0.539-0.658 (mean 0.592). Umbilicus completely closed by expansion and reflection of columellar lip. Sculpture of extremely fine, slightly protractively sinuated radial ribs, more than 200 on the body whorl, whose interstices are about equal to their width. Microsculpture of two to four very fine radial riblets between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures shallow, whorls evenly rounded on outer margin, slightly compressed laterally below periphery, basal margin flatly extended to umbilical callus. Aperture elongately-ovate, laterally and basally compressed, inclined about 10° from shell axis. Parietal barriers extending more than one-quarter whorl, almost to or past limit of vision, 3 with elevated portion and six to nine threadlike traces: upper high, thin, bladelike, posterior two-thirds serrated and weakly expanded above, anterior third gradually descending; 2nd with posterior eighth weakly elevated, anterior three-quarters threadlike; 3rd with posterior eighth slightly lower and shorter than 2nd, anterior part identical. Usually two traces between 1st and 2nd parietals, one between 2nd and 3rd, and four traces below 3rd parietal. All traces threadlike and stopping well short of major parietals' anterior end. Columellar region covered by very thick callus. Palatal barriers 4, long and bladelike, extending nearly one-quarter whorl, with very short threadlike to crescentic traces between major palatals near anterior margin, plus one or two traces above 4th palatal: lower palatal reduced in height, hidden in frontal view by edge of umbilical callus, identical in shape to 2nd palatal; 2nd palatal prominent, bladelike, serrated and expanded above, with very gradual anterior descension; 3rd and 4th palatals equal in height and length to 2nd, with more gradual anterior descension, 4th peripheral in position.

The closed umbilicus, heavy columellar callus, and very fine sculpture immediately separate *Mautodontha imperforata* from the other Society and Cook Islands species. Only *M. punctiperforata* is apt to be confused, and that species' less crowded sculpture and narrowly open umbilicus are diagnostic differences.

Description. — Shell of average size, with 6 relatively loosely coiled whorls. Apex and spire almost evenly elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.608. Apical whorls 1⅝, with slight traces of fine radial sculpture remaining. Lower whorls with very fine, low, rounded, indistinct, slightly protractively sinuated radial ribs, more than 225 on the body whorl, whose interstices are about equal to their width. Microsculpture of fine radial riblets, two to three between each pair of major ribs, and minute, crowded spiral ribs. Sutures shallow, whorls somewhat flattened above, evenly rounded laterally and on compressed basal margin, slanting gradually toward closed umbilicus. Color yellowish-white with vague, irregular, reddish flammulations. Aperture elongate-ovate with sharp baso-columellar prolongation, inclined about 10° from shell axis. Columellar and inner basal walls with thick strong callus, becoming weaker on palatal wall. Parietal wall with 3 barriers and six traces extending posteriorly beyond line of vision: upper very narrow, high, bladelike, serrated and very slightly expanded above, with gradual anterior descension; 2nd with raised lamellar posterior portion barely visible from aperture, anterior segment threadlike; 3rd identical to 2nd, except elevated posterior portion slightly lower. Accessory traces threadlike, stopping short of major parietals' anterior end, located between 1st and 2nd, between 2nd and 3rd, and four below 3rd parietal. No columellar barrier. Palatal barriers 4, extending one-quarter whorl, upper greatly reduced: lower an inconspicuous lamellar ridge hidden behind columellar-basal callus in front view, serrated above with gradual anterior descension; 2nd and 3rd high and bladelike, with very gradual anterior descension; 4th a faint V-shaped peripheral ridge, distinctly shorter than 3rd palatal. Height of lectotype 2.20 mm., diameter 3.52 mm.

Lectotype. — Cook Islands: Aitutaki. Collected by Andrew Garrett. BPBM 2322.

Range. — Aitutaki, Cook Islands.

Paratypes. — BPBM 2322.

Material. — Cook Islands (8 specimens, FMNH 117044, BPBM 167426, BPBM 170886): Aitutaki (14 specimens, BPBM 2322, BPBM 170938, BPBM 167425); inland of Reureu at 100 ft. elevation (6 specimens, BPBM 95647-8). "Rarotonga" (3 specimens, SMF 165704).

Remarks. — In many specimens the lower palatal barrier is hidden from casual view, but can be seen by tilting the aperture. In most specimens the posterior elevated portions of the 2nd and 3rd parietals can be seen only by extreme tilting of the shell, since the elevated portions sometimes do not start until just before the limit of vision into the aperture.

The closure of the umbilicus and very heavy columellar callus are quite different from the characters found in the other Cook and Society Islands species.

Mautodontha (Garrettoconcha) parvidens (Pease, 1861). Figure 77a-b.

Helix parvidens Pease, 1861, Proc. Zool. Soc. London, **1861**, p. 243 — Tahiti, Society Islands; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 220; Pfeiffer, 1876, *op. cit.*, **7**, p. 257.

Pitys parvidens (Pease), Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 31, pl. 2, figs. 14,*a*,*b*,*c* — Tahiti, Moorea, Huahine, Society Islands.

Patula incerta "Mousson" Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 93 — nude name.

Endodonta incerta (Mousson), Binney, 1885, Ann. New York Acad. Sci., **3**, p. 88, pl. 2, fig. N — radula of Huahine Island specimens.

Helix (*Endodonta*) *parvidens* (Pease), Tryon, 1887, Man. Conchol., (2), **3**, p. 64, pl. 12, figs. 20-22.

Endodonta (*Thaumatodon*) *parvidens* (Pease), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 26.

Diagnosis. — Shell somewhat smaller than average, diameter 2.80-3.95 mm. (mean 3.19 mm.), with 4½ - 5¾ relatively loosely coiled whorls. Apex and spire roundly elevated, last whorl descending a little more rapidly, H/D ratio 0.430-0.558 (mean 0.496). Umbilicus broadly U-shaped, often almost V-shaped, contained 3.09-4.55 times (mean 3.81) in the diameter. Sculpture of very fine, closely spaced, almost vertically sinuated, radial ribs, 104-180 (mean 138) on pregerontic portion of body whorl, whose interstices are 2-3 times their width. Microsculpture of two to five radial riblets between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above and in umbilicus, evenly rounded on outer margins. Aperture subcircular, inclined about 5° from shell axis. Parietal barriers 2, rarely (7.1 per cent) 3 or with 2nd fragmented into traces (4.8 per cent), extending nearly one-quarter whorl: upper high and bladelike, posterior two-thirds serrated and weakly expanded above, anterior segment smooth, and sharply descending; 2nd distinctly lower, anterior third often threadlike; accessory traces, when present, threadlike, very crowded, equal in length to 2nd parietal. Columellar wall often with 1st palatal slightly elevated above baso-columellar margin. Palatal barriers 4, rarely (14 per cent) 3 or 5, short, extending one-eighth whorl: lower a very short, recessed, crescentic ridge at baso-columellar margin or elevated on columellar wall, rarely absent; 2nd high and bladelike, serrated above, nearly reaching lip margin, with gradual anterior descension; 3rd equal in height to 2nd, slightly longer, with more gradual anterior descension, nearly reaching lip margin; 4th a short supraperipheral threadlike trace, rather deeply recessed. Rarely (4.8 per cent) a 5th palatal present between numbers 1 and 2, accessory threadlike traces in a few examples.

Mautodontha subtilis from Huahine has a slightly more open umbilicus, but differs most obviously in the more widely spaced ribbing (fig. 77a, d), particularly on the upper spire. The only other species normally with only 2 parietals either lack palatal barriers or have a much narrower umbilicus (*M. rarotongensis*).

Description. — Shell of average size, with 5¼ normally coiled whorls. Apex and spire moderately elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.525. Embryonic whorls 1¼, with only traces of microradial and microspiral ribbing remaining. Lower whorls with quite closely spaced, slightly protractively sinuated radial ribs, about 170 on the body whorl, whose interstices are less than twice their width. On the last quarter whorl, gerontic growth prevents accurate counting of the ribs. Microsculpture of three or four fine radial riblets between each pair of major ribs. Sutures deep, whorls strongly rounded above, evenly rounded on outer margins. Umbilicus broadly U-shaped (nearly V-shaped), regularly decoiling, contained 3.52 times in the diameter. Color light yellowish-white with broad, protractively sinuate, reddish flammulations becoming faint or absent on base of shell. Aperture subcircular with flattened basal margin. Parietal barriers 2, extending about three-sixteenths of a whorl: upper a prominent lamellate ridge, posterior two-thirds serrated and weakly expanded, anteriorly with sharp descension; lower a high threadlike ridge for entire length. Palatal wall with 4 short barriers, extending about one-eighth whorl: lower a broad, low ridge, slightly recessed, at baso-columellar margin; 2nd and 3rd progressively narrower, much higher, with more gradual anterior descension, more deeply recessed, serrated above; upper reduced to a deeply recessed threadlike trace. Height of lectotype 1.71 mm., diameter 3.26 mm.

Lectotype. — Society Islands: Tahiti. Collected by Andrew Garrett. BPBM 170888 from the W. H. Pease collection.

Range. — Tahiti, Moorea, and Huahine Islands.

Material. — Huahine (40 specimens, BPBM 3225, BPBM 165092, FMNH 46598, FMNH 90620, SMF 165331, SMF 165735, ANSP 47793, ANSP 47758, Zurich). Moorea (18 specimens, BPBM 15393, BPBM 165093, AMS). Tahiti (1 specimen, BPBM 170888).

Remarks. — Garrett (1884, p. 31) reported *M. parvidens* as very common on Tahiti, Moorea and Huahine Islands. He stated that specimens from Huahine were slightly smaller and with a lighter colored base than those from Tahiti and Moorea. No specimens have been collected since Garrett's time, and all observations must be based upon an analysis of material in old collections. Only a single shell from Tahiti was seen, while comparisons of the Moorea and Huahine examples (table LXVII) showed that shells from Huahine were significantly smaller in diameter (with 41 df, "*t*" = 2.5039) and with a narrower umbilicus ("*t*" = 3.1127).

Most specimens had only 2 parietal barriers, but occasionally a 3rd one was present. Similarly, most specimens had only 4 palatals, but occasionally an additional palatal or several small traces are present. Binney (1885, p. 88, pl. 2, fig. N) examined the radula of Huahine specimens and reported (as *Endodonta incerta*) that they had four laterals and seven marginals in a half row.

Mautodontha (Garrettoconcha) subtilis (Garrett, 1884). Figure 77c-d.

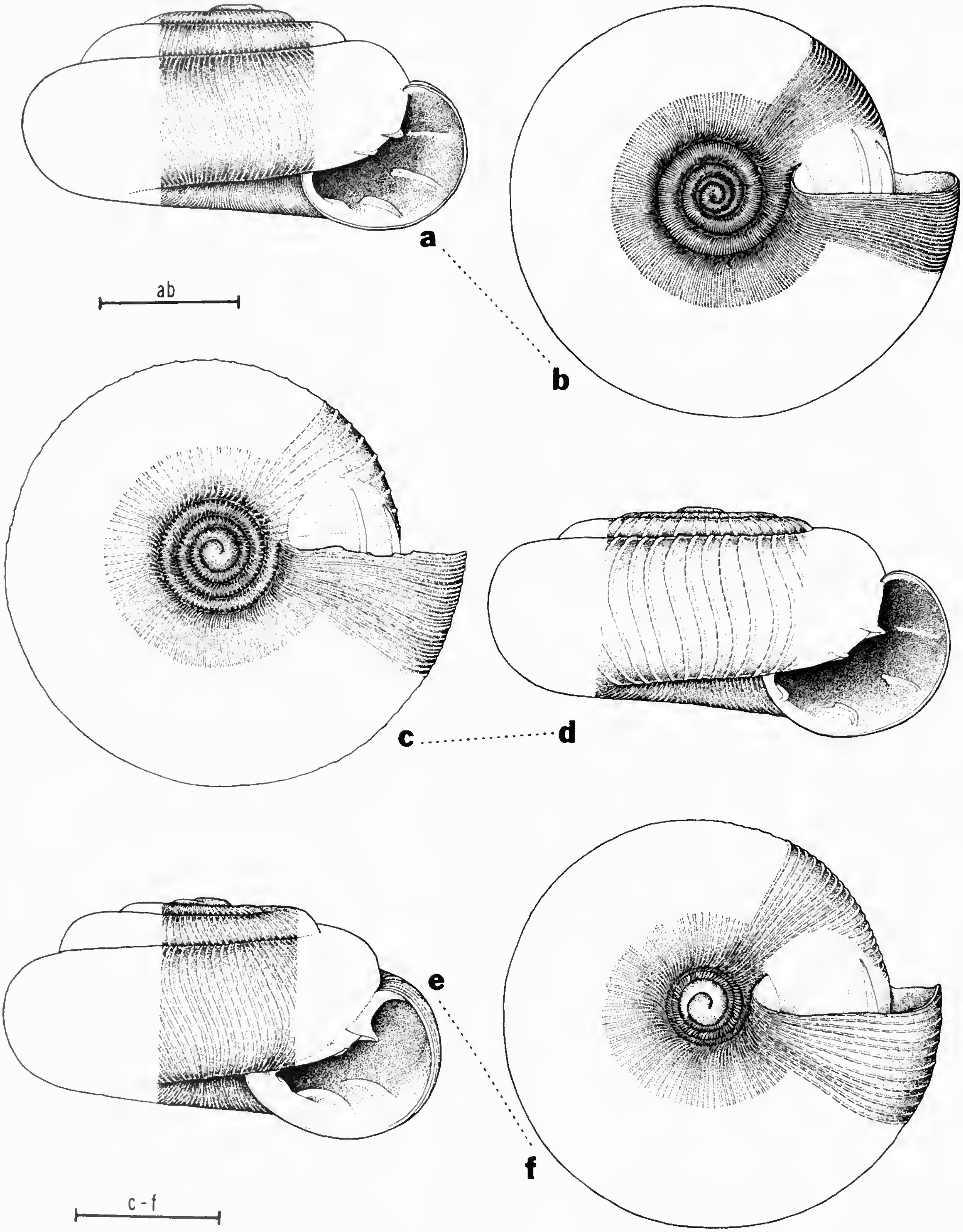

FIG. 77. **a-b**, *Mautodontha* (*Garrettoconcha*) *parvidens* (Pease). Tahiti, Society Islands. Lectotype. BPBM 170888; **c-d**, *Mautodontha* (*Garrettoconcha*) *subtilis* (Garrett). Huahine, Society Islands. Paratype. BPBM 2279, **e-f**, *Mautodontha* (*Garrettoconcha*) *rarotongensis* (Pease). Rarotonga (error), Cook Islands. Lectotype. BPBM 170885. Scale lines equal 1 mm. (MM).

Pitys subtilis Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), pp. 31-32 – Huahine, Society Islands.

Helix (Endodonta) subtilis (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 66, pl. 12, figs. 46-48.

Endodonta (Thaumatodon) subtilis (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 27.

Diagnosis. – Shell of less than average size, diameter 2.94-3.38 mm. (mean 3.13 mm.), with 4¾-5⅝ normally coiled whorls. Apex slightly elevated, lower whorls descending more rapidly, H/D ratio 0.484-0.553 (mean 0.513). Umbilicus U-shaped, slightly and regularly decoiling, open, contained 3.92-5.00 times (mean 4.43) in the diameter. Sculpture of narrow, rather widely spaced, vertically sinuated radial ribs, 68-124 (mean of nongerontic shells 75.7) on the body whorl, whose interstices are 3-5 times their width. Two gerontic shells had 103 and 124 ribs, the rest 68-86. Microsculpture of fine radial riblets, four to twelve between each pair of major ribs, crossed by very much finer and more crowded spiral riblets. Sutures deep whorls strongly rounded above and on umbilical margin, outer wall evenly rounded. Aperture ovate, inclined less than 5° from shell axis. Parietal barriers 2, extending about three-sixteenths of a whorl: upper bladelike, posterior half to two-thirds expanded and serrated above, with very gradual anterior descension; 2nd with posterior third to half expanded and serrated above, but much lower, anterior third to half threadlike, extending slightly beyond end of 1st parietal. No columellar barrier, although 25 per cent of specimens have 1st palatal moved up onto columellar wall. Palatal barriers 4, extending about one-eighth whorl: lower at baso-columellar margin (75 per cent) or on columellar wall (25 per cent), a slightly recessed, low lamellar ridge; 2nd and 3rd progressively higher, longer, more deeply recessed, with more gradual anterior descension; 4th supraperipheral, a deeply recessed, low to raised threadlike ridge, slightly shorter than 3rd palatal.

The nearest relative to *Mautodontha subtilis* is *M. parvidens*, which differs primarily in having much more crowded sculpture (mean body whorl rib count 138).

Description. – Shell of average size, with 4⅞ rather loosely coiled whorls. Apex and spire evenly elevated, body whorl descending a little more rapidly, H/D ratio 0.522. Apical whorls 1½, sculpture of fine, crowded, radial riblets, whose interstices are about 1½ times their width, with a microsculpture of co-equal radial and spiral riblets. Postnuclear whorls with prominent, rounded, rather widely spaced, vertically sinuated radial ribs, 68 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine radial riblets, eight to twelve between each major rib, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, with very slightly flattened basal margin. Color light yellow horn with evenly spaced, wide, slightly zigzag, reddish flammulations, fading out on base of shell. Umbilicus moderately open, U-shaped, slightly decoiling, contained 4.18 times in the diameter. Aperture ovate with strongly rounded margins, inclined less than 5° from shell axis. Parietal barriers 2, extending slightly more than three-sixteenths of a whorl: upper parietal high, bladelike, with sharp anterior descension, posterior half rounded above with fine, crystalline barbs; 2nd parietal slightly lower with more gradual anterior descension, becoming threadlike near end. Palatal barriers 4, extending one-eighth of a whorl: 1st a broadly rounded ridge located at columellar-basal margin, moderately recessed on strong callus; 2nd and 3rd prominent, bladelike, with more gradual anterior descension, slightly expanded and barbed above; 4th palatal lower, less expanded, nearly threadlike. Height of lectotype 1.58 mm., diameter 3.03 mm.

Lectotype. – Society Islands: Huahine. Collected by Andrew Garrett. ANSP 47781.

Range. – An unspecified valley on the north end of Huahine, Society Islands.

Paratypes. – BPBM 2279, ANSP 290095.

Material. – Huahine (8 specimens, same as list of types).

Remarks. – Garrett (1884, p. 32) reported that this was a somewhat rare species, confined to a valley on the north end of Huahine Island. No further information is available.

In younger specimens, the difference in sculpture between *M. subtilis* and *M. parvidens* is striking, but in the older specimens of *M. subtilis* the distinction becomes blurred because of gerontic growth. *M. parvidens* has the sculpture crowded on the spire whorls, while in *M. subtilis,* the sculpture is very widely spaced on the spire, although usually crowded on the body whorl. The lectotype is sub-adult, but is by far the best preserved of the type set, clearly showing details of the apical and microsculpture.

Possibly *M. parvidens* and *M. subtilis* are only subspecifically distinct. Available material showed no intergradation in sculpture and I prefer to accept Garrett's opinion that they are specifically distinct.

Mautodontha (Garrettoconcha) rarotongensis
(Pease, 1870). Figure 77e-f.

Pithys roratongensis (sic) Pease, 1870, Jour. de Conchyl., **18**, pp. 395-396 – Rarotonga, Cook Islands (error).

Pitys roratongensis (sic) Pease, 1871, Proc. Zool. Soc. London, **1871**, pp. 453, 474.

Helix (Pitys) roratongensis (sic) (Pease), Pfeiffer, 1876, Monog. helic. viv., 7, p. 257.

Pitys rarotongensis Pease, Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, 8, (4), p. 390 – Correction of Pease's misspelling of the name and of the locality to Atiu, Cook Islands.

Helix (Endodonta) rarotongensis (Pease), Tryon, 1887, Man. Conchol., (2), **3**, p. 64.

Endodonta (Thaumatodon) rarotongensis (Pease), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 27.

Diagnosis. – Shell rather small, diameter 2.76-3.26 mm. (mean 3.01 mm.), with 4½-5¼ relatively loosely coiled whorls. Apex flattened, spire moderately elevated, last whorl descending more rapidly, H/D ratio 0.464-0.556 (mean 0.522). Umbilicus U-shaped, narrow, slightly decoiling, contained 4.67-6.00 times (mean 5.47) in the diameter. Sculpture of narrow, relatively prominent, slightly protractively sinuated radial ribs, 118-137 (mean 130) on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by barely visible, crowded spiral riblets. Sutures impressed, whorls strongly rounded above with slight lateral compression below periphery. Aperture elongately-ovate, slightly compressed laterally below periphery, inclined about 10° from shell axis. Parietal barriers 2 (36.4 per cent) or 3 (63.6 per cent), extending about one-quarter whorl: upper high and bladelike, posterior half serrated and expanded, anterior half with gradual descension to just before end; 2nd with posterior quarter to third equal in height to 1st, serrated and expanded, anterior half to two-thirds threadlike, extending very slightly beyond anterior end of 1st; 3rd, when present, a short threadlike trace or V-shaped ridge lying along posterior half of 2nd parietal. Columellar and palatal wall with thick heavy callus. Columellar barrier deeply recessed, threadlike trace, angling slightly downward from plane of coiling. Palatal barriers 2 (66.7 per cent) or 3 (33.3 per cent) extending about one-eighth whorl: lower a low lamellar structure with gradual anterior descension; 2nd a distinctly higher bladelike ridge, slightly less recessed, with more gradual anterior descension; 3rd, when present, a short, weak, deeply recessed supraperipheral threadlike trace.

The presence of only 2 or 3 parietal and 2 or 3 palatal barriers effectively separates *Mautodontha rarotongensis* from any species except *M. parvidens.* The latter has a wider umbilicus, normally at least 4 palatals, and a more elevated spire.

Description. – Shell rather small, with 5 relatively loosely coiled whorls. Apex flat, whorls of spire descending moderately, last whorl more rapidly, H/D ratio 0.544. Embryonic whorls 1⅜, sculpture eroded. Remaining whorls with relatively closely spaced, slightly protractively sinuated, prominent radial ribs, about 130 on the body whorl, whose interstices are less than twice their width. Microsculpture of three to five fine radial riblets between each pair of major ribs, crossed by barely visible spiral ribs. Sutures moderately impressed, whorls rounded above and in umbilicus with slight basal flattening. Umbilicus narrow, U-shaped, slightly decoiling, contained 6.00 times in the diameter. Aperture ovate, slightly flattened basally, with moderately heavy columellar and palatal callus extending up past periphery of body whorl. Parietal barriers 2, extending almost one-quarter whorl: upper high and bladelike with very gradual anterior and posterior descension; lower a threadlike ridge for entire length. Columellar barrier reduced to a low swelling just posterior to heavy columellar callus. Palatal barriers 2, extending about one-eighth whorl, both moderately elevated, V-shaped ridges, lower almost lamellar. Height of lectotype 1.61 mm., diameter 2.96 mm.

Lectotype. – Cook Islands. BPBM 170885, ex W. H. Pease Collection.

Range. – Atiu, Cook Islands (on the authority of Garrett).

Paratypes. – BPBM 2314, BPBM 170885, BPBM 170922.

Material. – Cook Islands (6 specimens, BPBM 170885, BPBM 170922); Rarotonga (3 specimens, BPBM 2314); Atiu (3 specimens, BPBM 8545, SMF 165462).

Remarks. – Pease's original citation of Rarotonga as the locality was corrected to Atiu by Garrett (1881, p. 390). Pease originally spelled the specific name "*roratongensis*" which was also corrected by Garrett (*loc. cit.*) to the proper *rarotongensis.*

This would appear to be a derivative from a *parvidens* type ancestor with a smaller umbilicus and the palatal barriers reduced through expansion of the apertural callus.

Mautodontha (Garrettoconcha) consimilis (Pease, 1868). Figure 78a-c.

Helix consimilis Pease, 1868, Amer. Jour. Conchol., **3**, p. 227 – Tahiti, Society Islands (error); Pfeiffer, 1876, Monog. helic. viv., **7**, p. 262.

Patula societatus "Mousson" Schmeltz, 1874, Cat. Mus. Godeffroy, **4**, p. 73 – nude name.

Patula consimilis (Pease), Schmeltz, 1874, *op. cit.,* **5**, p. 207; Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia **9**, (1), p. 29, pl. 2, figs. 12, a, b – Raiatea, Society Islands.

Helix (Endodonta) consimilis Pease, Tryon, 1887, Man. Conchol., (2), **3**, p. 60, pl. 11, figs. 80-81.

Endodonta (Thaumatodon) consimilis (Pease), Pilsbry, 1893, *op. cit.,* (2), **9**, p. 26.

Diagnosis. – Shell about average in size, diameter 3.03-4.05 mm. (mean 3.43 mm.), with 4⅝-5⅝ rather tightly coiled whorls. Apex flattened or barely elevated, whorls of spire descending moderately, last whorl descending abruptly, H/D ratio 0.523-0.666 (mean 0.588). Umbilicus U-shaped, usually regularly decoiling, rarely broadly V-shaped, contained 3.56-6.19 times (mean 4.36) in the diameter. Body whorl with slightly protractive radial ribs, 53-117 (mean 75.3) on the body whorl, whose interstices are 3-4 times their width. Microsculpture of very fine and crowded radial riblets, nine to fourteen between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, with nearly evenly rounded or laterally compressed outer wall. Aperture nearly circular, sometimes compressed on outer margin, inclined about 5° from shell axis. Parietal barriers 1 (9.9 per cent) to 2 (90.1 per cent), extending about three-sixteenths of a whorl: upper a raised threadlike ridge about twice as wide as high, situated well above middle of parietal wall; 2nd, when present, a prominent to very inconspicuous threadlike ridge. No columellar or palatal barriers.

Mautodontha consimilis is apt to be confused with both *M. acuticosta* and *M. unilamellata.* The former is generally larger (mean diameter 4.01 mm.), more depressed (mean H/D ratio 0.483), with a wider, V-shaped umbilicus (mean D/U ratio 3.37), a greater number of ribs on the body whorl (mean rib count 81.0), and more frequently lacks the 2nd parietal. *M. unilamellata* is larger (mean diameter 3.96 mm.), similar in shape (mean H/D ratio 0.554) and umbilical width (mean D/U ratio 3.61), has more ribs on the body whorl (mean rib count 82.0), a rounded periphery, and usually lacks the 2nd parietal. The very small, flat-spired *M. aoraiensis* is the only other *Mautodontha* without palatal barriers.

Description. – Shell average in size, with slightly more than 5 rather tightly coiled whorls. Apex and spire slightly and evenly elevated, body whorl descending much more rapidly, H/D ratio 0.592. Apical whorls 1⅜, sculpture eroded on upper surface with traces of prominent micro and major radial ribbing present in sutures. Postnuclear whorls with prominent, narrowly rounded, slightly protractive radial ribs, about 84 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine, relatively crowded radial riblets crossed by much finer and more crowded spiral riblets. Sutures deep, whorls somewhat shouldered above, relatively compressed laterally with slightly flattened basal margin. Color light yellowish horn with regularly spaced zigzag, reddish flammulations, becoming less prominent on base of shell. Umbilicus U-shaped, regularly and slightly decoiling, contained 4.29 times in the diameter. Aperture ovate, compressed laterally, basal margin flattened, inclined less than 5° from shell axis. Parietal barriers 2, extending almost one-quarter whorl, low and threadlike, upper slightly more elevated and narrower. Columellar and basal lips with a moderately heavy white callus, without trace of barriers. Height of lectotype 2.01 mm., diameter 3.39 mm.

Lectotype. – Society Islands: Raiatea (erroneously reported by Pease as Tahiti). Collected by Andrew Garrett. BMNH 71.1.5.28 from the W. Harper Pease collection.

Range. – Raiatea, Society Islands (originally stated erroneously to come from Tahiti).

Paratype. – BMNH 71.1.5.28.

Material. – Raiatea (57 specimens, BPBM 3485, BPBM 170891, Zurich, FMNH 46396, FMNH 90637, FMNH 152017, ANSP 47786, ANSP 47784, ANSP 47787). Mislabelled material (24 specimens, BPBM

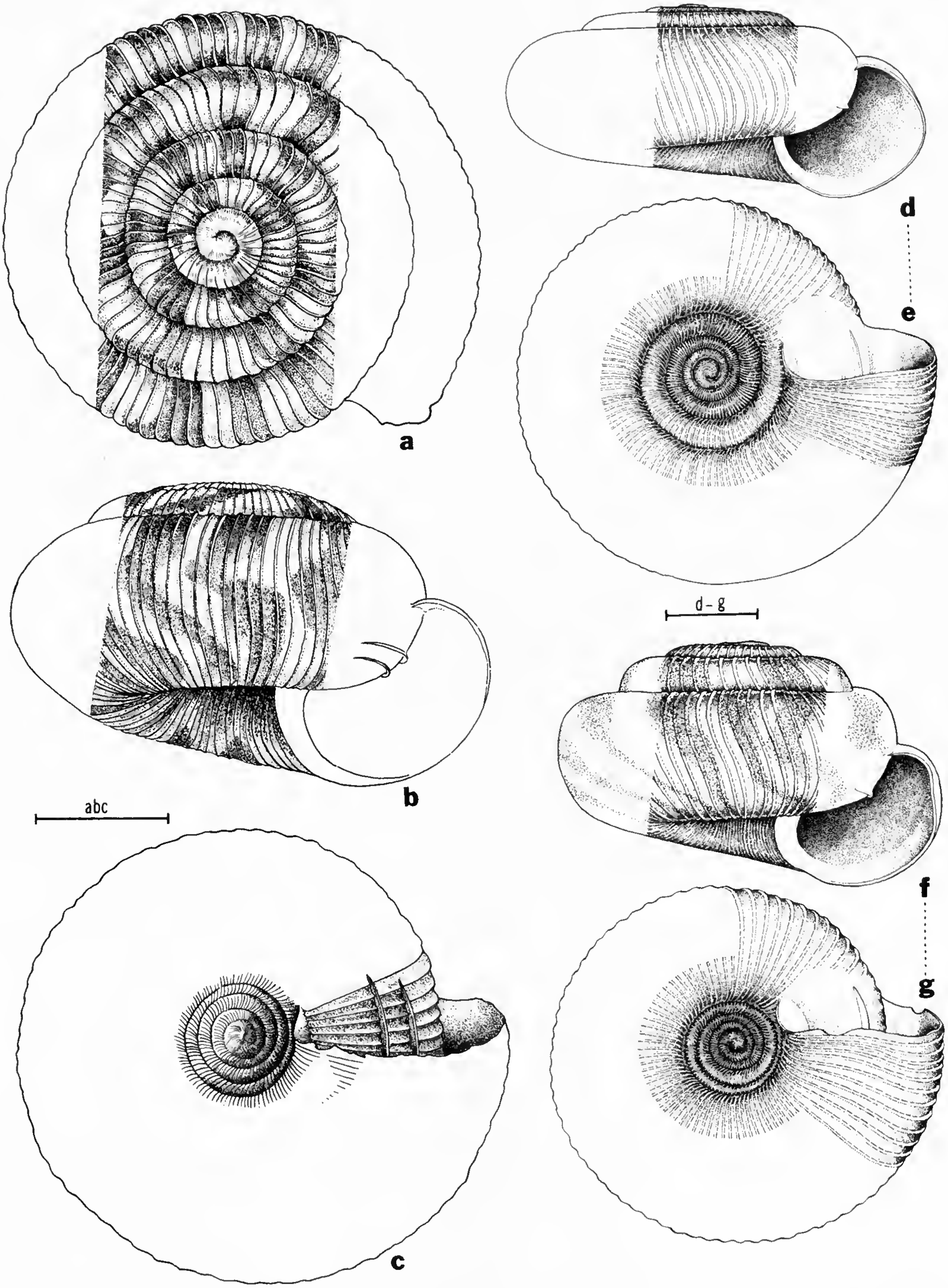

FIG. 78. **a-c**, *Mautodontha* (*Garrettoconcha*) *consimilis* (Pease). Raiatea, Society Islands. Paratype. BPBM 3485; **d-e**, *Mautodontha* (*Garrettoconcha*) *acuticosta* (Garrett). Raiatea, Society Islands. Paratype. BPBM 3392; **f-g**, *Mautodontha* (*Garrettoconcha*) *unilamellata* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2339. Scale lines equal 1 mm. (*d-g*, MM; *a-c*, SG).

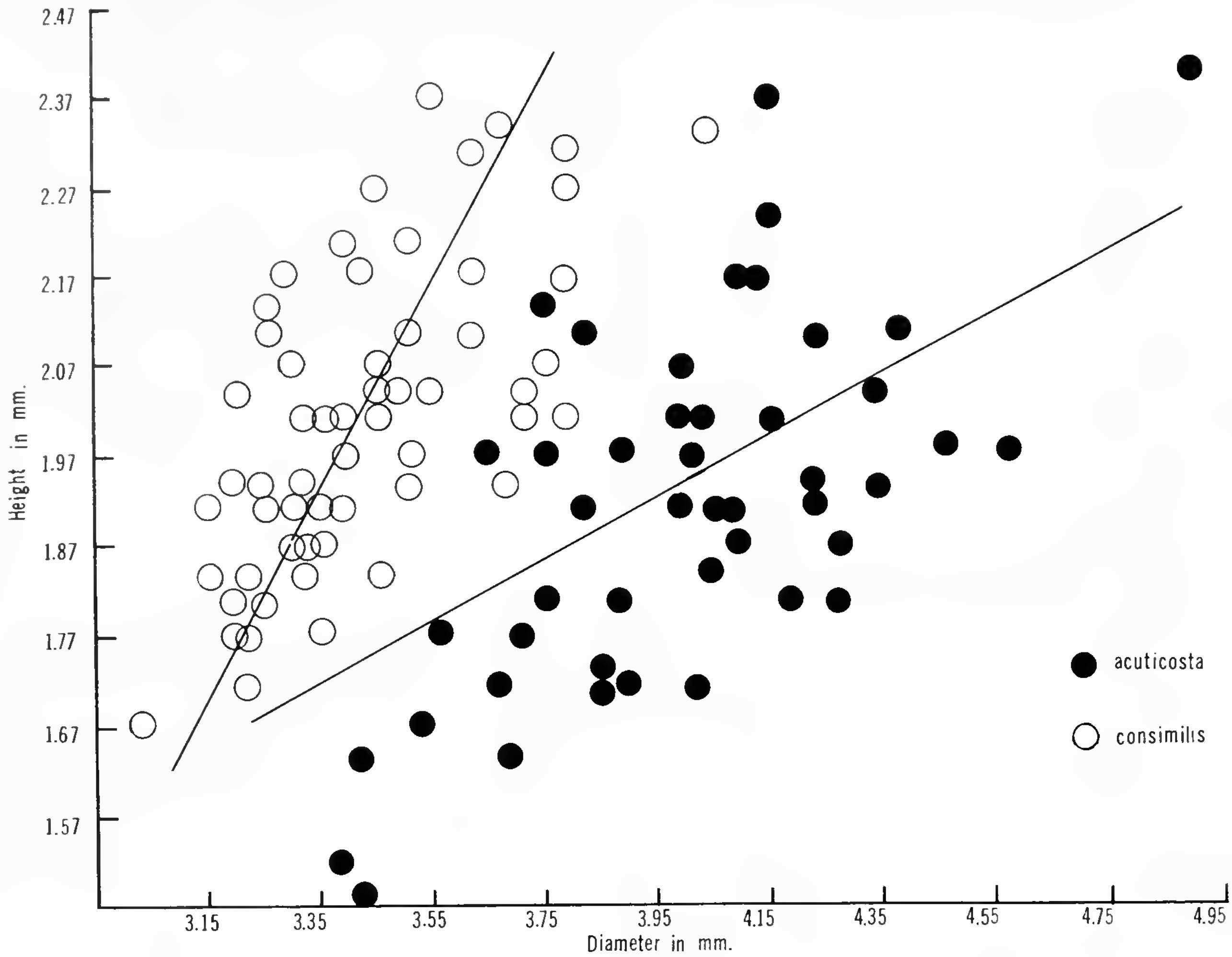

FIG. 79. Scatter diagram showing relationship of height to diameter in *Mautodontha consimilis* and *M. acuticosta*.

170891, BPBM 170895, FMNH 73186, FMNH 152020, BMNH 71.1.5.28).

Remarks. — Garrett (1884, p. 29) reported this as common and diffused throughout all the larger valleys of Raiatea, and that Pease's type examples (reported from Tahiti by Pease) were collected by him on Raiatea. The type set in the British Museum (Natural History) contained two specimens of *Mautodontha consimilis* and three specimens of *M. acuticosta*. Similar mixtures were seen in other old collections. Presumably all such sets labeled "Tahiti" originated through exchanges from Pease. The original description of *M. consimilis* perhaps better fits the form that Garrett subsequently named *M. acuticosta*, but selecting a widely umbilicated shell for the type of *M. consimilis* would have necessitated proposal of a new name for the narrowly umbilicated species. I preferred to avoid this and thus selected a narrowly umbilicated shell for the type of *Helix consimilis*, leaving *Patula acuticosta* Garrett, 1884, as the valid name for the widely umbilicated species from Raiatea.

While the average differences between *M. consimilis* and *M. acuticosta* are large (table LXVI), in respect to any one character there is considerable overlap. No specimen was seen that could not be assigned to one or the other species without any hesitation. Unfortunately, Garrett gave no indication as to whether the species were geographically isolated on Raiatea or found together. To test the hypothesis that these might be selected examples from a continuous range of variation, all measured individuals were plotted in respect to height and diameter (fig. 79), then for whorl count and diameter (fig. 80). The division into two separate clusters is obvious. Calculation of linear regressions of the height-diameter relationships for the two species by Bartlett's method produced obviously divergent lines. I consider that *M. consimilis* and *M. acuticosta* are distinct species.

Mautodontha (Garrettoconcha) acuticosta (Garrett, 1884). Figure 78d-e.

Patula acuticosta "Mousson" Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 93 — nude name; Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 30, pl. 2, figs. 13, a, b — Raiatea, Society Islands.

Helix (*Endodonta*) *acuticosta* (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 60, pl. 11, figs. 60-61.

Endodonta (*Thaumatodon*) *acuticosta* (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

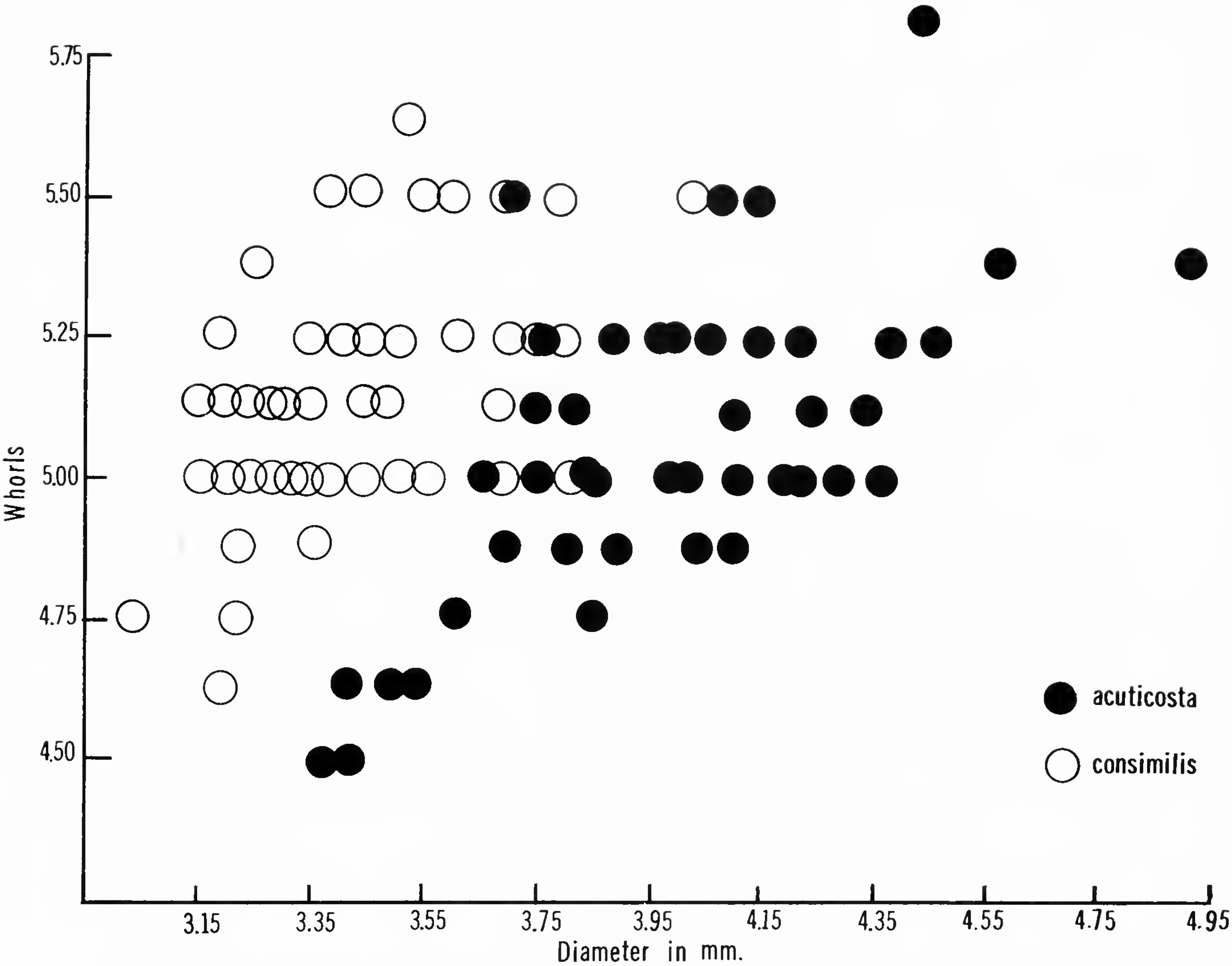

FIG. 80. Scatter diagram showing relationship of whorls to diameter in *Mautodontha consimilis* and *M. acuticosta*.

Diagnosis. — Shell large, diameter 3.42-4.90 mm. (mean 4.01 mm.), with 4⅝ - 5⅜ relatively loosely coiled whorls. Spire flattened or barely elevated, later whorls descending more rapidly, occasionally last whorls dropping sharply, H/D ratio 0.423-0.571 (mean 0.483). Umbilicus V-shaped (rarely U-shaped), widely open, decoiling regularly, contained 2.89-4.27 times (mean 3.37) in the diameter. Sculpture of relatively widely spaced, weakly protractive radial ribs, 59-106 (mean 80.95) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine, radial riblets, seven to eleven between each pair of major ribs, plus barely visible spiral riblets. Sutures deep, whorls strongly rounded above, slightly compressed laterally above and below rounded periphery. Aperture subcircular, generally flattened laterally above periphery, inclined about 5° from shell axis. Parietal barriers extending three-sixteenths of a whorl, usually 1 (23.4 per cent) or 2 (63.9 per cent) rarely (10.6 per cent) with lower split into two traces, or very rarely (2.1 per cent) with additional traces (four): upper a raised threadlike ridge about twice as high as wide, serrated on top, with gradual anterior descension, located well above middle of parietal wall; lower (when present) an inconspicuous threadlike ridge equal in length to 1st parietal. Accessory traces, one to four in number, identical in shape and length to 2nd parietal. No columellar or palatal barriers present.

Mautodontha consimilis and *M. unilamellata* are the most closely related species. *M. consimilis* is distinctly smaller (mean diameter 3.43 mm.), more elevated (mean H/D ratio 0.588), with a narrower umbilicus (mean D/U ratio 4.36), fewer major radial ribs (mean 73.3 on the body whorl), and only rarely (9.1 per cent) lacks the 2nd parietal. *M. unilamellata* is more elevated (mean H/D ratio 0.554) and usually has only 1 parietal, sometimes with an accessory trace. *M. aoraiensis* has 2 much larger parietals, a depressed spire, and is much smaller (diameter 2.60-2.76 mm.).

Description. — Shell rather large, with slightly more than 5 moderately tightly coiled whorls. Apex and upper spire flat, lower whorls descending gradually, H/D ratio 0.461. Apical whorls 1⅜, sculpture mostly eroded, with traces of moderately closely spaced radial ribs and a microsculpture of radial and spiral riblets persisting in the suture. Postnuclear whorls with high, prominent, rounded, almost vertically sinuated radial ribs, 86 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine, crowded radial riblets crossed by very much finer and more crowded spiral riblets. Sutures deep, whorls moderately shouldered above, slightly compressed laterally both above and below rounded periphery. Color light yellow horn without traces of darker markings. Umbilicus V-shaped, regularly decoiling, contained 2.91 times in the diameter, with slightly shouldered umbilical margin. Aperture subcircular, slightly compressed laterally above and below periphery, inclined about 5° from shell axis. Parietal barriers 3, extending slightly more than one-eighth whorl: upper high, bladelike, gradually descending anteriorly, slightly flattened above with lower threadlike bifid portion below: 2 lower parietals low and threadlike, extending slightly further anteriorly. Columellar and basal lips with moderately heavy callus but no trace of barriers. Height of lectotype 1.94 mm., diameter 4.21 mm.

Lectotype. — Society Islands: Raiatea. Collected by Andrew Garrett. ANSP 47774.

Range. — Raiatea.

Paratypes. — BPBM 3392, ANSP 290097.

Material. — Raiatea (28 specimens, BPBM 3392, BPBM 115290, BPBM 165095, BPBM 170898, BPBM 170936, BPBM 170967, ANSP 47774, FMNH 46413, FMNH 90623, FMNH 116996, FMNH 152019). Mislabelled material (30 specimens, BPBM 170891, BPBM 170895, BPBM 170903, FMNH 91090, FMNH 152018, BMNH).

Remarks. — Garrett (1884, p. 30) reported that this species was less abundant than *M. consimilis,* and confined to Raiatea. Of some 58 shells, two were a pure whitish horn color mutant that Garrett reported as very rare.

The set of types in the Academy of Natural Sciences Philadelphia consists of a juvenile, an albino, and two adult specimens. One adult is aberrant in having very few and widely separated ribs (64 on the body whorl) while the other has the upper parietal barrier bifid and the lower parietal split into two traces. Despite the aberration of the parietals, the specimen with more normal ribbing and form has been selected as lectotype.

Of the 47 specimens for which the parietal barrier number was recorded, 11 had 1 parietal; 30 had 2 parietals; 5 had the 2nd parietal split into two traces; and one shell had a single parietal and four traces.

Mautodontha (Garrettoconcha) unilamellata (Garrett, 1874) Figure 78f-g.

Pitys unilamellata Garrett, 1874, Proc. Acad. Nat. Sci., Philadelphia, **1873**, p. 234, pl. 3, fig. 67 — Rarotonga, Cook Islands.
Patula unilamellata (Garrett), Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, 8, (4), p. 388.
Helix (*Endodonta*) *unilamellata* (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 60, pl. 11, figs. 74-76.
Endodonta (*Thaumatodon*) *unilamellata* (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 27.

Diagnosis. — Shell rather large, diameter 3.68-4.28 mm. (mean 3.96 mm.), with 5-5⅜ normally coiled whorls. Apex moderately, spire strongly elevated, last whorl descending much more rapidly, H/D ratio 0.492-0.642 (mean 0.554). Umbilicus U- to V-shaped, regularly decoiling, rather widely open, contained 3.31-4.10 times (mean 3.61) in the diameter. Postnuclear whorls with prominent, slightly protractively sinuated radial ribs, 78-87 (mean 82) on the body whorl (149 in one gerontic shell), whose interstices are 2-3 times their width. Sutures deep, whorls strongly rounded above, flattened laterally, with slightly compressed basal margin, umbilical margin strongly rounded. Aperture subcircular, flattened laterally above periphery, inclined about 10° from shell axis. Parietal wall with single raised, threadlike barrier, extending less than three-sixteenths of a whorl, often (40 per cent) with a vague lower accessory trace present. No columellar or palatal barriers.

The open, regularly decoiling umbilicus, single parietal and absence of any palatal barriers at once separates *Mautodontha unilamellata* from the other Cook Island species. It is very similar to the Raiatean *M. consimilis* and *M. acuticosta,* differing most obviously in having the single parietal barrier and high spire.

Description. — Shell relatively large, with 5¼ rather loosely coiled whorls. Apex moderately elevated, whorls of spire descending gradually more rapidly, H/D ratio 0.513. Apical whorls 1⅜, sculpture eroded with traces of fine radial ribbing remaining in the suture. Postnuclear whorls with high, rounded, rather prominent, somewhat protractively sinuated radial ribs, 149 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of very fine radial riblets crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, slightly compressed laterally and on basal margin. Color light yellow horn with numerous, crowded zigzag, reddish flammulations. Umbilicus widely open, V-shaped, regularly decoiling, contained 3.31 times in the diameter. Aperture ovate, slightly compressed laterally and on basal margin, inclined about 15° from shell axis. Parietal wall with single, supramedial, threadlike barrier extending three-sixteenths of whorl, and a very faint, short, medial threadlike trace. Columellar and palatal walls without barriers. Height of lectotype 2.01 mm., diameter 3.91 mm.

Lectotype. — Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47798.

Range. — In mountain ravines on Rarotonga, Cook Islands.

Paratypes. — BPBM 2339, ANSP 290110.

Material. — Rarotonga (5 specimens, same as type material).

Remarks. — Garrett (1874, p. 235) stated this was "A rare species found under decayed vegetation in mountain ravines." The few known specimens exhibit considerable variation in sculpturing. Four of the five have 78-87 rather widely spaced ribs on the body whorl, but the type has much more crowded and numerous ribbing (149 ribs on the body whorl). Probably this species occurred in more than one place, and the ribbing types may have belonged to geographically separated populations.

Genus **Anceyodonta**, new genus

Generally large (except *A. ganhutuensis, A. subconica, A. constricta,* and probably *A. alternata*) and specialized Endodontidae in which the usually 4 parietal barriers extend at least one-quarter whorl, the V-shaped upper palatal lies opposite the upper parietal, there are normally four or more palatal traces, the mean H/D ratio is over 0.600, the umbilicus is contained more than 7 times in the diameter, and secondary spiral cording is present in most of the specimens. Except in the very small species, there are, on the average, more than 5⅝ whorls. Generally the ribbing is quite widely spaced, with fewer than 9 ribs per mm. Many species have the columellar barrier slanting downward or displaced onto the basal lip. Several species have a subsutural and/or a supraperipheral (*A. sexlamellata*) sulcus developed. Anatomy unknown.

Type species.—Anceyodonta difficilis, new species.

Anceyodonta represents a stage of evolutionary specialization that is obviously derived from the *simulata* group of *Minidonta.* Species of this complex show some characters that are present in most or all

Anceyodonta, but in most respects they are much more similar to the typical *Minidonta. Minidonta micra* also shows several strong similarities to *Anceyodonta,* but a greater number of differences. These species were close to the threshold of becoming *Anceyodonta,* but for various reasons have been classified in the less specialized genus.

Some 12 characters of size, shape, sculpture, and barriers generally present contrasting states in *Minidonta* and *Anceyodonta.* Scoring of these characters in Table LXVIII shows that nine of the 12 *Anceyodonta* have two-thirds or more of the advanced states, while 10 of the 12 characters are present in two-thirds or more of the species placed in *Anceyodonta.* For comparison, the five *Minidonta* that approach *Anceyodonta* in structure are included in the same table.

Three species, *A. ganhutuensis, A. constricta,* and *A. alternata,* are included in *Anceyodonta* despite showing relatively few of the specialized character states. In all three, the minute or small size drastically reduced the whorl count and thus eliminated two characters in one change. *A. ganhutuensis* has the strongly elevated spire, minute umbilicus, strong secondary spiral cording, and widely spaced ribs typical of *Anceyodonta.* The presence of only 3 parietals and three palatal traces can be correlated with the very small size. *A. alternata,* known from a single probably juvenile example, has the apertural barriers, rib spacing, and secondary spiral cording of *Anceyodonta.* Its departure from the *Anceyodonta* pattern in shape, umbilical width, whorl count, size, and spire depression can be viewed as secondary modifications possibly resulting from a single mutation that caused a radical change in coiling pattern, plus the potentially juvenile size. *A. constricta* has a very specialized umbilical pattern (fig. 82b) and lacks the shape and sculptural features typifying *Anceyodonta,* but the apertural barriers are so completely those of *Anceyodonta* that I prefer to keep it in that genus, despite its general similarity to *Minidonta.*

Both *Anceyodonta constricta* and *Minidonta taravensis* could be transferred to the other genus and such a placement defended. If additional material becomes available, a more critical assessment of their affinities may be possible. At present they can be recognized as species that are transitional in observable character states and whose generic placement must be arbitrarily decided.

While in many respects speciation in *Anceyodonta* is characterized by varying combinations of a few differing features (secondary cording, presence or absence of a sulcus, size of 1st palatal, position of columellar barrier), there are a few striking variations that require comment. The generic norm is a high, dome-shaped spire, rounded above, and without marked descension of the body whorl. In both *A. constricta* and *A. andersoni* the spire is only moderately and evenly elevated, while in *A. alternata* the spire is actually depressed. Depression of the spire normally is accompanied by widening of the umbilicus, and both *A. alternata* and *A. andersoni* have wide, regularly decoiling umbilici. *A. constricta,* however, has a very strangely narrowed umbilicus (fig. 82b). The only other *Anceyodonta* with a widely open umbilicus, *A. soror,* attained this by extremely rapid decoiling of the body whorl (fig. 83c). Other species have minute to closed umbilici, and only in *A. subconica* do even a few examples show slight umbilical decoiling (fig. 81c, f).

Sculpture in *Anceyodonta* generally is quite widely spaced (table LXIX). Calculation of the mean ribs per millimeter on the body whorl showed most species with 6.3-8.2 ribs/mm. *A. sexlamellata* with 9.5; *A. densicostata* with 11.1; *A. subconica* with 11.5; and *A. constricta* with 13.0 had considerably more crowded ribbing. In *A. densicostata* (fig. 87a) there is a clear increase in number of ribs, hence greater crowding (see table LXIX), but in *A. subconica* and *A. constricta* the number of ribs on the body whorl is the same as in much larger species.

The situation in *A. obesa* populations on Mangareva and Aukena offers data that bear on the importance of this crowding. Comparing sample populations (table LXX) from the two islands demonstrated that a 13.1 per cent change in diameter that is very highly significant (with 62 df, "*t*" = 5.8735) resulted in an insignificant change in rib count (with 24 df, "*t*" = 0.7910). Local dwarfing of one population apparently left the total rib count unaffected, but altered the spacing. The Mangareva shells of *A. obesa* averaged 8.81 ribs/mm., the Aukena specimens 8.11 ribs/mm. In view of this effect, it is tempting to suggest that the crowded ribbing of the very small *A. constricta* and *A. subconica* indicates that these species were derived from larger ancestors with the rib number remaining constant, rather than to consider that they are primitively small. Without stratigraphic data on species occurrence, any phylogenetic conclusions are premature. The above suggestion is offered at this time to emphasize the complexity of minor changes within *Anceyodonta.* A more detailed discussion of rib-diameter relationships is given above (pp. 44-47).

Variation in the barriers is relatively minor (table LXIX). Except in *A. labiosa* (fig. 87d, e), the parietals extend more than one-quarter whorl, generally with 4 parietals elevated. Only in *A. ganhutuensis* and *A. sexlamellata* are there normally only 3 elevated parietals; in *A. labiosa* slightly more than one-third the specimens have only 3 (the remainder have 4) and in *A. hamyana* an equal number of specimens have 3 and 4 parietals. *A. obesa, A. subconica, A. densicostata,* and *A. soror* normally have 5 major parietals, while in *A. difficilis* the 4th parietal is reduced to a threadlike trace without elevated posterior portion. *A. alternata* and *A. sexlamellata* normally have 2 columellar barriers, while a 2nd one is rarely seen in *A. constricta.* The normal endodontid pattern of the columellar barrier lying parallel to the plane of coiling

TABLE LXVIII. - CHARACTER STATES TYPIFYING ANCEYODONTA

	Mean diameter over 2.6 mm.	Mean H/D ratio over 0.600	Mean D/U ratio over 7.00	Mean whorl count over 5-5/8	Sulcus present	Secondary spiral cording present	Less than 9.0 ribs/mm.	4th P lying opposite 1st Pr	Pr (1/4 whorl) or longer	Columellar slanting or displaced	4 or more Pr	Four or more palatal traces	Number or characters	Per cent of characters present
Minidonta														
simulata	X												1	8.3
extraria	X						X						2	16.6
taunensis								X	X	X			3	25.0
micra		X						X	X			X	4	33.3
taravensis							X	X	X	X	X		5	41.7
TOTAL	2	1	0	0	0	0	2	3	3	2	1	1		
Anceyodonta														
constricta			X					X	X		X	X	5	41.7
alternata	?			?		X	X	X	X		X	X	6	50.0
ganhutuensis		X	X			X	X	X	X				6	50.0
andersoni	X			X		X	X	X	X		X	X	8	66.7
subconica		X	X		X	X		X	X	X	X	X	9	75.0
sexlamellata	X	X	X	X	X	X[1]		X	X	X		X	10	83.3
densicostata	X	X	X	X				X	X	X	X	X	9	75.0
obesa	X	X	X	X	X		X	X	X	X	X		10	83.3
labiosa	X	X	X	X		X	X	X		X	X[2]		9	75.0
hamyana	X	X	X	X		X[1]	X	X	X	X	X[3]		10	83.3
soror	X	X		X	X	X	X	X	X	X	X	X	11	91.7
difficilis	X	X	X	X	X	X	X	X	X	X	X		11	91.7
TOTAL	8	9	9	8	5	9	8	12	11	8	10	7		

1. Present or absent
2. One-third with 3, two-thirds with 4
3. 3 or 4 almost equally

TABLE LXIX. - RANGE OF VARIATION IN ANCEYODONTA

Name	Number of Specimens	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
ganhutuensis	6	40.3(34-54)	1.48(1.26-1.72)	1.87(1.69-2.19)	0.789(0.741-0.839)	5 1/8+(4 3/4-5 7/8)	15.8 (10.00-20.60)	3	1	4+3
subconica	104	79.7(58-94)	1.51(1.28-2.20)	2.20(1.94-2.50)	0.686(0.603-0.762)	5 1/2+(4 7/8-7)	7.67(4.47-14.75)	4-5-6+4-6	1	4+4 Traces
constricta	7	90.0(86-95)	1.22(1.16-1.29)	2.20(2.09-2.28)	0.553(0.507-0.576)	5 3/8(5 1/4-5 5/8)	12.8 (6.90-22.70)	4+0-2	1-2	4+5
andersoni	25	79.0(61-96)	1.86(1.71-2.14)	3.29(2.96-3.62)	0.570(0.547-0.625)	5 11/16(5 1/4-6)	3.34(2.95-3.96)	4+0-1	1-2	4+3-5
alternata	1	48	1.02	2.24	0.456	4 1/4	2.72	4+1	2	4+6
difficilis	26	68.8(53-84)	2.09(1.74-2.57)	2.93(2.57-3.49)	0.711(0.651-0.762)	6 3/8+(6-7 1/4)	19.1 (8.27-40.00)	4-5	1[1]	4-2-3-4
soror	19	65.0(53-74)	1.64(1.38-1.94)	2.61(2.24-3.09)	0.628(0.592-0.677)	5 5/8+(5-6 1/8)	4.25(2.96-7.83)	5+1	1[1]	4+4-6
sexlamellata	613	89.6(60-125)	2.21(1.45-2.99)	2.99(2.44-3.59)	0.743(0.634-0.929)	6 1/8+(5 1/4-7 1/2)	20.0 (6.20-46.00)	3+3-5	2	4+6-11
densicostata	31	104.4(95-114)	2.07(1.84-2.30)	3.00(2.73-3.19)	0.687(0.621-0.778)	6 1/4+(5 7/8-6 5/8)	15.1 (6.93-29.60)	3-5+0-1	1	4+4-5
obesa	416	79.6(47-106)	2.25(1.84-3.16)	3.14(2.63-4.01)	0.715(0.561-0.929)	6 3/8-(5 3/8-7 5/8)	20 - CLOSED	3-5+0-2	1	4+0-3-6
labiosa	27	91.0(78-100)	2.46(2.17-2.80)	3.55(3.06-4.05)	0.700(0.658-0.735)	6 1/2-(6-6 7/8)	7.24(5.48-9.80)	3-4+0-2	1[1]	4+0-2
hamyana	245	79.3(60-120)	2.66(1.91-3.45)	3.98(3.09-4.93)	0.667(0.557-0.773)	6+(5 1/4-7)	22.2 (7.31-64.00)	3-4	1	4

[1] Displaced onto basal lip

TABLE LXX. - LOCAL VARIATION IN ANCEYODONTA

Name	Number of Specimens	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
ganhutuensis All Specimens	6	40.3±4.73 (34-54)	1.48±0.081 (1.26-1.72)	1.87±0.082 (1.69-2.19)	0.789±0.0159 (0.741-0.839)	5 1/8+ (4 3/4-5 7/8)	15.83±1.883 (10.00-20.65)
subconica BPBM 9410 Aukena	18		1.48±0.031 (1.29-1.69)	2.19±0.028 (1.99-2.38)	0.675±0.0083 (0.609-0.762)	5 1/4+ (4 7/8-6 1/8)	7.06±0.358 (5.12-10.30)
BPBM 9662-3 Aukena	15		1.49±0.033 (1.29-1.76)	2.18±0.037 (1.95-2.52)	0.684±0.0088 (0.603-0.722)	5 1/2+ (5-6 1/4)	7.74±0.643 (4.47-14.75)
constricta BPBM 9660	4		1.22±0.034 (1.16-1.29)	2.20±0.044 (2.09-2.28)	0.553±0.0160 (0.507-0.576)	5 3/8 (5 1/4-5 5/8)	12.77±3.430 (6.90-22.70)
andersoni BPBM 138936	9		1.84±0.037 (1.72-2.05)	3.25±0.060 (2.98-3.64)	0.566±0.0063 (0.550-0.612)	5 5/8+ (5 1/4-6)	3.31±0.057 (3.04-3.63)
difficilis BPBM 141688	12		2.05±0.037 (1.76-2.22)	2.91±0.045 (2.58-3.15)	0.703±0.0953 (0.653-0.762)	6 3/8- (6-6 5/8)	18.22±2.720 (8.27-39.00)
soror BPBM 138965,-37	11		1.61±0.049 (1.39-1.92)	2.54±0.059 (2.25-2.91)	0.633±0.0042 (0.592-0.677)	5 1/2+ (5-6 1/8)	4.16±0.139 (3.56-4.80)
sexlamellata BPBM 141666, 9675 Mangareva	12		2.05±0.073 (1.66-2.48)	2.79±0.065 (2.45-3.18)	0.732±0.0133 (0.667-0.804)	5 7/8- (5 1/4-6 5/8)	PERFORATE
BPBM 138704 Aukena	11		2.37±0.106 (1.76-2.85)	3.02±0.108 (2.45-3.61)	0.788±0.0262 (0.694-0.923)	6 3/8 (5 1/2-7 1/4)	PERFORATE
BPBM 138850 Akamaru	10		2.50±0.090 (2.12-3.01)	3.15±0.092 (2.72-3.51)	0.795±0.0183 (0.705-0.929)	6 1/2+ (6-7 1/2)	31.84±6.212 (15.85-46.00)
BPBM 138882 Taravai	5		2.01±0.071 (1.82-2.22)	2.95±0.069 (2.72-3.08)	0.683±0.0143 (0.645-0.720)	5 7/8+ (5 1/2-6 3/8)	12.37±1.355 (9.00-16.40)

TABLE LXX, CONTINUED

BPBM 138900, -896 Agakauitai	16		2.03±0.027 (1.79-2.19)	2.92±0.039 (2.65-3.21)	0.697±0.0058 (0.652-0.730)	6 1/8- (5 3/4-6 5/8)	13.36±1.425 (7.75-28.40)
British Museum 1962702/18	7	83.6±3.05 (75-98)	2.29±0.047 (2.09-2.42)	3.02±0.050 (2.88-3.21)	0.759±0.0083 (0.725-0.797)	6 1/8+ (6-6 3/8)	25.31±1.614 (19.20-29.66)
densicostata							
BPBM 138975	18		2.08±0.033 (1.89-2.32)	3.00±0.032 (2.75-3.21)	0.692±0.0101 (0.621-0.778)	6 1/4+ (5 7/8-6 3/4)	15.67±1.230 (10.62-29.60)
obesa							
BPBM 138974, -43 Mangareva	30	80.8±3.12 (56-96)	2.14±0.030 (1.85-2.55)	2.92±0.035 (2.65-3.58)	0.732±0.0049 (0.683-0.785)	6 3/8+ (5 7/8-7 3/8)	CLOSED
BPBM 138706 Aukena	34	84.1±2.63 (73-98)	2.31±0.049 (1.85-3.18)	3.30±0.053 (2.81-4.04)	0.698±0.0074 (0.561-0.787)	6 1/4+ (5 3/8-7 5/8)	CLOSED
labiosa							
BPBM 9413, -14	18		2.48±0.041 (2.19-2.81)	3.55±0.051 (3.08-4.07)	0.700±0.0078 (0.658-0.766)	6 1/2- (6-6 7/8)	7.24±0.309 (5.48-9.80)
hamyana							
BPBM 138966 Mangareva	13		2.42±0.059 (2.05-2.95)	3.63±0.060 (3.21-4.04)	0.667±0.0097 (0.614-0.730)	6 5/8+ (5 1/4-6 1/4)	26.80±2.823 (19.20-41.00)
BPBM 138939, -67 Mangareva	14		2.74±0.047 (2.42-3.15)	4.00±0.064 (3.71-4.57)	0.685±0.0056 (0.652-0.732)	6 1/8+ (5 3/4-6 5/8)	25.36±2.602 (16.60-34.50)
BPBM 138700 Aukena	17		2.64±0.038 (2.38-3.01)	4.18±0.045 (3.87-4.44)	0.631±0.0061 (0.582-0.680)	6+ (5 7/8-6 3/8)	11.59±0.790 (7.31-19.15)
BPBM 138699 Aukena	18		2.76±0.057 (2.28-3.18)	4.01±0.062 (3.48-4.44)	0.687±0.0083 (0.613-0.746)	6 1/8+ (5 5/8-6 1/2)	23.12±4.111 (11.50-64.00)
BPBM 138897 Agakauitai	6	77.0±6.16 (62-91)	3.12±0.084 (2.95-3.38)	4.36±0.102 (3.97-4.74)	0.716±0.014 (0.664-0.742)	6 3/8+ (6-6 5/8)	32.32±3.193 (19.15-43.00)

is found in four species (*A. ganhutuensis, A. constricta, A. andersoni,* and *A. alternata*); it slants downward across the columellar callus in five species (*A. subconica, A. sexlamellata, A. densicostata, A. obesa,* and *A. hamyana*); and is displaced onto the basal lip in three species (*A. soror, A. difficilis,* and *A. labiosa*).

Although all species have 4 major palatals, in only five *Anceyodonta* is the 1st palatal equal or nearly equal in size to the 2nd (*A. subconica, A. ganhutuensis, A. alternata, A. andersoni,* and *A. hamyana,* see fig. 82). The other species have the 1st palatal greatly reduced in size, although it remains larger than the *adjacent* palatal traces. In some specimens (for example, fig. 89f) the 1st palatal is smaller than the palatal trace located between the 2nd and 3rd palatals. *Gambiodonta* species have this reduction carried much further. In both *G. grandis* and *G. mirabilis* the lower palatal cannot be distinguished from the accessory traces. There is little correlation between position of the columellar barrier and proportionate size of the 1st palatal, and none between shell diameter and proportionate size. No specimens with a displaced columellar have a large 1st palatal, but species with a slanted columellar (*A. subconica* and *A. hamyana*) have a large 1st palatal although others (*A. densicostata* and *A. obesa*) do not.

The two largest *Anceyodonta, A. hamyana* and *A. labiosa,* have, respectively, none or zero to two palatal traces. *A. sexlamellata* has the greatest number (normally up to 11) and most species have more than four. Utilizing the term "traces" is somewhat misleading, since in certain species (figs. 81d; 83a, c, e; 89f) the traces between the middle palatals are elevated and expanded miniature replicas of the major palatals. If not clearly marked by their position as being homologous to the reduced traces normally seen (figs. 82a, d, e; 83f; and 86a, c-e) and remaining distinctly smaller than the major palatals, they would be considered fully developed barriers. This very strong development of accessory barriers is unique to the Mangarevan taxa.

Two other shell features require comment. The development of secondary spiral cording, usually most clearly visible below the periphery, is one of the most characteristic features of *Anceyodonta.* Cording is absent only in *A. constricta, A. densicostata,* and *A. obesa;* present or absent on an individual basis in *A. sexlamellata* and *A. hamyana;* and always present on the other seven species. Unless the sculpture is so worn that even major ribs are not clearly marked, the cording can be seen without difficulty. Several species have a strong subsutural sulcus (*A. subconica, A. soror, A. difficilis, A. sexlamellata,* and *A. obesa*) and normally there is a prominent supraperipheral sulcus in *A. sexlamellata* (fig. 86e). In some specimens (fig. 89d) the sulcus may be very weak and detectable only as a flattening of the rib contour, but usually (fig. 88a, c) it is quite prominent.

While three pairs of closely related species can be recognized, no general hierarchial arrangement could be devised. *A. alternata* and *A. andersoni,* both restricted to Mangareva Islet, agree in the wide umbilicus, low spire, presence or occasional presence of 2 columellar barriers, absence of a subsutural sulcus, presence of spiral cording and spacing of the ribbing. The small recorded size of *A. alternata* is caused by the single specimen being subadult. *A. soror* and *A. difficilis* differ most obviously in umbilical width (fig. 83b, d), but also show minor differences in size, H/D ratio, and barriers (figs. 84, 85). They agree in all details of sculpture, have the columellar barrier deflected onto the basal lip, and show only minor changes in palatal and parietal barriers. Occurring essentially at the same stations, they may be chronologically separated species. *A. obesa* and *A. densicostata* are even more closely related, differing primarily in the rib spacing and the subsutural sulcus. The other species cannot be separated in pairs and none of the three pairs outlined above show strong similarities to other species.

Geographic distribution yields almost no information on relationships. Two of the three species pairs cited above are restricted to Mangareva Islet. *A. obesa* is found on four islets (table LXXI) and *A. densicostata* is restricted to Mangareva Islet. Derivation of *densicostata* from *obesa* is a distinct possibility. Of the 12 *Anceyodonta,* two (*A. hamyana* and *A. sexlamellata*) were found on five islets; one (*A. obesa*) on four islets; one (*A. subconica*) on three; two (*A. labiosa* and *A. densicostata*) on two islets; and the remaining six species are known only from a single islet. Of these six, *A. constricta* was found on Aukena and the other five solely on Mangareva. Taravai Islet, from which only 18 *Anceyodonta* were collected, had three species; Agakauitai and Akamaru, from which 61 and 215 specimens, respectively, were collected each had four species; Aukena Islet, from which the fossil beds yielded 857 specimens, had six species; and Mangareva Islet, where 332 *Anceyodonta* were collected, had 10 species.

Collecting effort on the islets was not equivalent, with much more effort being invested in the collections from Mangareva and Aukena Islets, and very little time spent on Taravai and Agakauitai.

As in the collections of *Gambiodonta* (pp. 432-434), there were instances where collecting stations were taken within very close proximity of each other: 1) on the same day and by the same people (Stations 88 and 102 on Aukena); 2) by the same people on different days (Stations 187 and 189 near Rikitea, Mangareva); or 3) by different people on different days (Stations 142 and 277 near Ganhutu on Mangareva). On a large scale map, these stations are not separable (see Part II), but were at least 100-300 ft. apart. If the proportion of species collected at each station is expressed as a per cent of the entire sample (table LXXII), it is obvious that the relative abundance

TABLE LXXI. - GEOGRAPHIC DISTRIBUTION AND RELATIVE ABUNDANCE OF MANGAREVAN ENDODONTIDAE

	Total Specimens	Agakauitai	Akamaru	Aukena	Mangareva	Taravai	Tauna	Number of Records
Anceyodonta								
ganhutuensis	6				6			1
subconica	104	2		94	8			3
constricta	7			7				1
andersoni	25				25			1
alternata	1				1			1
difficilis	26				26			1
soror	19				19			1
sexlamellata	577	47	208	265	44	13		5
densicostata	31				30	1		2
obesa	416	4	3	302	107			4
labiosa	27		2	25				2
hamyana	244	8	2	164	66	4		5
Rikitea								
insolens	1				1			1
Minidonta								
micra	228			228				1
simulata	32	1		30	1			3
taunensis	2						2	1
taravensis	2					2		1
extraria	3			1	1	1		3
Gambiodonta								
agakauitaiana	17	17						1
p. pilsbryi	88				88			1
p. aukenensis	79			79				1
mangarevana	6				6			1
mirabilis	41			4	37			2
tumida	33				33			1
grandis	259	32		227				2
TOTALS	2,274	111	215	1,426	499	21	2	

TABLE LXXII. - PERCENTAGE SPECIES COMPOSITION OF MANGAREVAN ANCEYODONTA IN SELECTED SAMPLES

	Aukena		Mangareva			
			Rikitea		Ganhutu	
	Station 88	Station 102	Station 187	Station 189	Station 142	Station 277
ganhutuensis			2.6		2.5	2.0
subconica	7.3	22.1				4.1
andersoni			5.3	4.7	22.5	6.2
difficilis			15.8	20.3	7.5	2.0
soror				4.7	7.5	6.2
sexlamellata	28.8	46.5	39.4	23.4		4.8
densicostata					2.5	17.9
obesa	50.4	24.2	23.7	34.4	25.0	35.3
labiosa	4.6					
hamyana	8.9	7.2	13.2	12.5	32.5	21.5
Number of specimens	434	275	38	64	40	145

varied greatly within each pair of stations. Since the size range of these specimens is rather small, and the collectors could not have been aware that such a diversity of forms was involved, I am confident that these differences reflect stratigraphic differences in the deposits.

The disparity between islets in collecting effort and gross differences between adjacent stations in species composition prevent any meaningful comparisons of faunal differences. Available data do suggest that attempts to make stratigraphic collections on at least Mangareva and Aukena might provide considerable information concerning temporal variations in species abundance, and possibly might yield data on phylogeny within both *Anceyodonta* and *Gambiodonta.*

The species sequence adopted below goes roughly from the smallest to the largest in size, deviating only when necessary to place pairs of species together.

KEY TO THE GENUS *Anceyodonta*

1. Apex and spire markedly elevated; umbilicus usually very narrow; if widely open last whorl decoiling more rapidly 2
   Apex and spire flat or slightly depressed; umbilicus widely open, regularly decoiling, contained less than 3.00 times in the diameter.............................*Anceyodonta alternata*, new species
2. Columellar barrier displaced onto basal lip (fig. 83e)....................3
   Columellar barrier parallel to plane of coiling (fig. 81a) or slanted downward (fig. 89d)..5
3. Subsutural sulcus present (fig. 89a); parietals 4 or 5; palatal traces two to six...4
   Subsutural sulcus absent (fig. 90a); parietals 3 or 4; palatal traces zero to two.................*Anceyodonta labiosa*, new species
4. D/U ratio less than 5.00...............*Anceyodonta soror*, new species
   D/U ratio more than 7.00.
   Anceyodonta difficilis, new species
5. Lower palatal barrier much smaller than 2nd (fig. 87e)...............6
   Lower palatal barrier equal to or slightly larger than 2nd (fig. 90d)...9
6. No subsutural or supraperipheral sulcus..7
   Distinct subsutural or supraperipheral sulcus present (fig. 86c). 8
7. Diameter less than 2.4 mm.; H/D ratio less than 0.600.
   Anceyodonta constricta, new species
   Diameter more than 2.6 mm.; H/D ratio more than 0.600.
   Anceyodonta densicostata, new species
8. Only 1 columellar barrier, 5 major parietals; never a supraperipheral sulcus...........................*Anceyodonta obesa,* new species
   Always 2 columellar barriers, 3 major parietals; usually a supraperipheral sulcus present.
   Anceyodonta sexlamellata (Pfeiffer, 1845)
9. Columellar barrier parallel to plane of coiling (fig. 81a)............10
   Columellar barrier slanting downward across columellar callus (fig. 89d)...11
10. Diameter less than 2.3 mm.; 3 parietals.
    Anceyodonta ganhutuensis, new species
    Diameter more than 2.8 mm.; 4 parietals.
    Anceyodonta andersoni, new species
11. Diameter less than 2.6 mm.; parietal and palatal traces present.
    Anceyodonta subconica, new species
    Diameter usually much more than 3.0 mm.; no parietal or palatal traces....................*Anceyodonta hamyana* (Ancey, 1889)

Anceyodonta ganhutuensis, new species (Cooke & Solem). Figures 81a-b.

Diagnosis. — Shell minute, diameter 1.69-2.19 mm. (mean 1.87 mm.), with 4¾-5⅞ very tightly coiled whorls. Apex and spire very strongly elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.741-0.839 (mean 0.789). Umbilicus

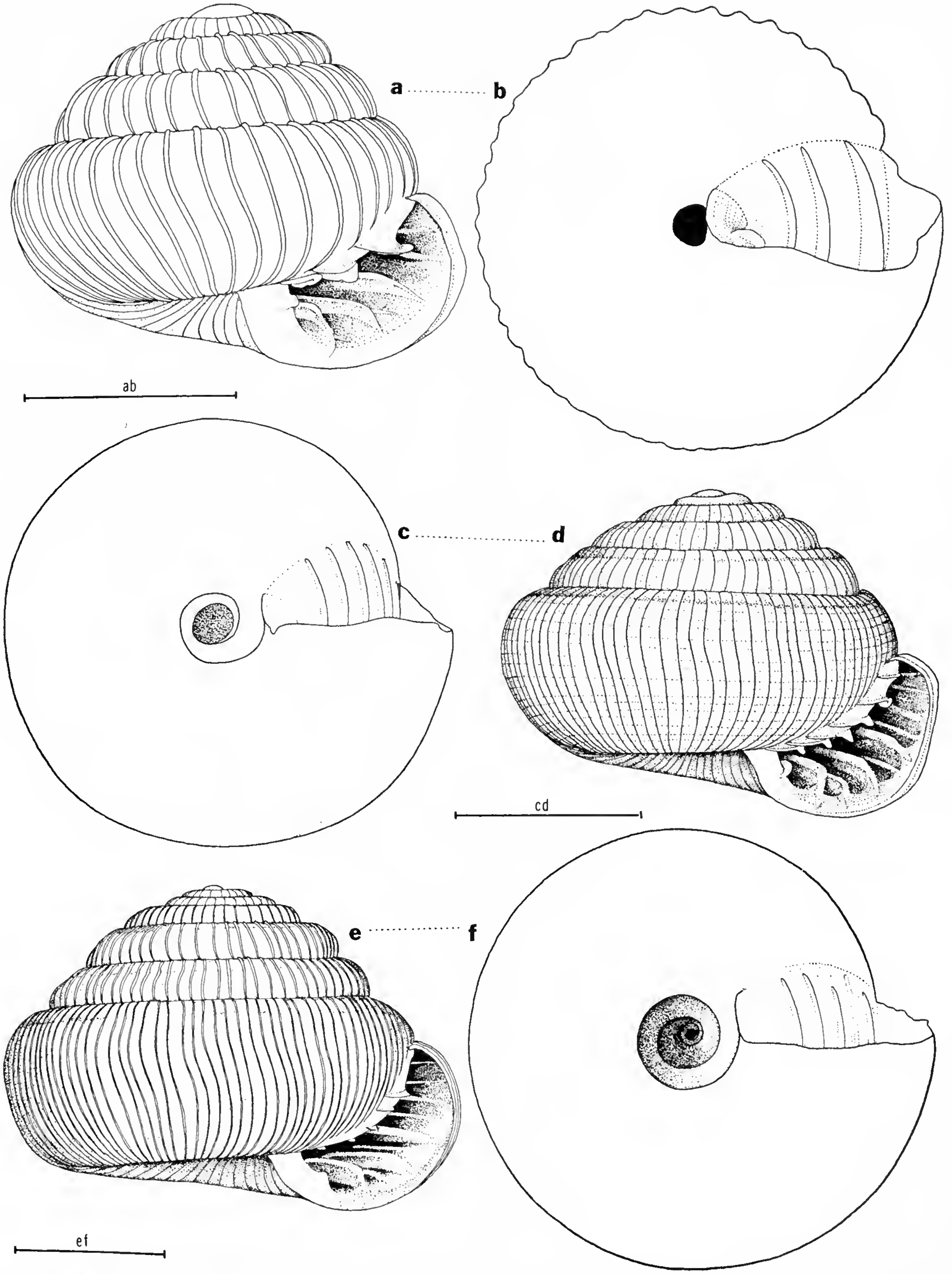

FIG. 81. **a-b**, *Anceyodonta ganhutuensis*, new species. Station 142, Ganhutu, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 9638; **c-f**, *Anceyodonta subconica*, new species. *c-d,* Station 102, Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 9662; *e-f,* Station 88, Aukena Islet, Mangareva, Gambier Islands. Paratype. BPBM 9411. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

minute, partly covered by reflected umbilical lip, contained 10-20.6 times (mean 15.8) in the diameter. Postnuclear sculpture of very large, prominent, protractively sinuated radial ribs, 34-54 (mean 40.3) on the body whorl, whose interstices are 2-3 times their width. Microsculpture a lattice of very fine radial riblets, five to nine between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets, plus a secondary sculpture of low, broadly rounded spiral cords, visible mainly on base of shell. Sutures impressed, whorls evenly rounded, slightly compressed laterally below periphery. No sulcus present. Aperture ovate, inclined about 10° from shell axis. Parietal barriers 3, extending posteriorly beyond line of vision: upper a high, slender blade with gradual descension over visible anterior third, posterior section expanded and serrated; 2nd equally high posteriorly, anterior visible half threadlike; 3rd with posterior portion reduced in height, threadlike portion slightly longer, more gradual descension from elevated portion. Columellar wall with very thick heavy callus extending onto basal margin, which is surmounted by a raised threadlike ridge, expanded and serrated posteriorly, anteriorly narrowing and sinuately twisting across callus, stopping well short of lip edge. Palatal barriers 4, extending posteriorly beyond line of vision, plus three very fine, threadlike traces: lower moderately recessed, bladelike, weakly expanded above with gradual anterior descension; 2nd equal in height, a trifle slenderer, more deeply recessed and with sharper anterior descension; 3rd same as 2nd, but a little more recessed; 4th greatly reduced in height, lying opposite 1st parietal, a narrow V-shaped ridge, less deeply recessed than lower palatals. Accessory traces short, very fine, located between 1st and 2nd, 2nd and 3rd, and above 4th palatals.

The extremely elevated spire, minute size and presence of only 3 parietals immediately separate *Anceyodonta ganhutuensis* from other species of the genus. The only species that even approaches it in size, *A. constricta, A. subconica* and *A. alternata,* have 4 or more parietals, are much more depressed (*A. alternata* and *A. constricta*), and have much more crowded ribbing (*A. subconica* and *A. constricta*).

Description. — Shell minute, with 5½ tightly coiled whorls. Apex and spire very strongly elevated, last whorl descending a little more rapidly, H/D ratio 0.788. Embryonic whorls 1½, sculpture eroded. Lower whorls with slightly protractive, wide, prominent, radial ribs, 54 on the body whorl, whose interstices are approximately twice their width. Microsculpture a lattice of extremely fine radial riblets, five to nine between each pair of major ribs, and slightly finer and more crowded spiral riblets, plus a secondary sculpture of low, broadly rounded spiral cords, visible mainly on base of shell. Sutures barely perforate, contained 13.2 times in the diameter. Color light yellow-brown except where leached from shell. Aperture ovate, somewhat flattened below periphery, inclined about 10° from the shell axis. Parietal barriers 3, extending beyond line of vision: upper a high blade, descending gradually over anterior third, posterior elevated portion serrated and slightly expanded above; 2nd with posterior section the same as 1st, anterior visible half threadlike; 3rd with posterior section reduced in height, threadlike portion longer, with less sharp descension from elevated portion. Columellar barrier lying on very heavy callus, a low ridge parallel to plane of coiling, elevated and serrated above posteriorly, anteriorly angling across callus, stopping well short of lip edge. Palatal barriers 4, extending beyond line of vision, bladelike ridges, plus three low accessory traces: lower nearly reaching lip edge, with rather gradual anterior descension; 2nd equal in height, slightly recessed, with sharper anterior descension; 3rd identical to 2nd; 4th greatly reduced in height, a narrow V-shaped ridge, less deeply recessed. Accessory traces short, narrow threadlike ridges between 1st and 2nd, 2nd and 3rd, and above 4th palatals. Height of holotype 1.71 mm., diameter 2.17 mm.

Holotype. — Gambier Islands: Mangareva, Station 142, inland 150 ft. from Ganhutu Bay at 6 ft. elevation. Collected by Yoshio Kondo and C. M. Cooke, Jr. on June 3, 1934. BPBM 9638.

Range. — Known as subfossil material from two localities on Mangareva Islet, Gambier Islands.

Paratypes. — Sames as list of material.

Material. — Mangareva Islet: near Ganhutu (Stations 139, 142, 277) on flat ground near sea level (5 specimens, BPBM 9638, BPBM 138972, BPBM 141272); in the north part of Rikitea (Station 187), a subfossil deposit at 6 ft. elevation (1 specimen, BPBM 9647).

Remarks. — The type is unusual only in having the ribbing more numerous and crowded than in the other examples. No variation was noted in the barriers.

Although reaching the size range of *Minidonta* (tables LXIII, LXIX) and having only 3 parietals, the very elevated spire, secondary spiral cording, quite narrow umbilicus, and V-shaped upper palatal lying opposite the 1st parietal relate *ganhutuensis* more to *Anceyodonta.*

Anceyodonta subconica, new species (Solem & Cooke). Figure 81c-f.

Diagnosis. — Shell very small, diameter 1.94-2.50 mm. (mean 2.20 mm.), with 4⅞-7 tightly coiled whorls. Apex and spire very strongly elevated, slightly rounded above, last whorl not descending more rapidly, H/D ratio 0.603-0.762 (mean 0.686). Umbilicus moderately open to very small, last whorl decoiling more rapidly, contained 4.47-14.8 times (mean 7.67) in the diameter. Postnuclear sculpture of narrow, prominent, rather crowded radial ribs, 58-94 (mean 79.7) on the body whorl, whose interstices are less than twice their width. Microsculpture a lattice of very fine radial riblets, four to seven between each pair of major ribs, crossed by finer and more crowded spiral riblets, with a secondary sculpture of low, rounded spiral cords, whose size and spacing is about equal to that of the major radial ribs, and which are generally absent or reduced near periphery. Sutures shallow, whorls strongly rounded above and on umbilical margin, slightly compressed laterally, with a weak subsutural sulcus present. Aperture ovate, inclined less than 5° from shell axis. Parietal barriers 5, rarely 4 or 6, extending posteriorly beyond line of vision, with four to six slender low traces: 1st and 3rd parietals more elevated than 2nd, 4th and 5th; all parietals low and bladelike, visible posterior half expanded and serrated above, anterior 3rd low and threadlike, first 3 parietals extending progressively further anteriorly, 4th and 5th very slightly recessed from anterior end of 3rd. Upper parietal trace slender, prominent, located just below parietal-palatal margin; remaining three to five traces lower, broader, located between major parietals, not extending anteriorly to end of threadlike portions. Columellar barrier a low, bladelike ridge, twisted slightly downward just before reaching edge of heavy columellar callus and terminating. Palatal barriers 4, extending posteriorly about three-eighths of a whorl, slightly reduced in height from bottom to top, normally with five, rarely six, much lower palatal traces. Palatal traces located between 1st and 2nd, 2nd and 3rd, 3rd and 4th, and above 4th palatal, rarely a very faint palatal trace between columellar and 1st palatal tooth.

Anceyodonta subconica is most readily recognized by having the palatal barriers regularly decreasing in size from bottom to top and its small size. Other *Anceyodonta* have the 1st palatal distinctly smaller than the 2nd, or if equal in size are very large (*A. hamyana* and *A. andersoni*), with a depressed apex (*A. alternata*), or with an extremely high spire and widely spaced ribbing (*A. ganhutuensis*).

Description. — Shell very small, with 6¼ relatively tightly coiled whorls. Apex and spire strongly elevated, last whorl not descending more rapidly, H/D ratio 0.722. Embryonic whorls 1⅜, sculpture eroded. Postnuclear whorls with narrow, prominent, crowded, almost vertical radial ribs, 85 on the body whorl, whose interstices are 1-2 times their width. Microsculpture eroded, faint traces of secondary spiral cording occasionally visible. Sutures shallow, whorls with a slight subsutural sulcus, somewhat laterally compressed, strongly rounded on basal margin. Umbilicus very narrowly open internally, becoming slightly more widely open on last whorl, contained 6.00 times in the diameter. All color leached from shell. Aperture ovate, somewhat compressed laterally, inclined less than 5° from shell axis. Parietal barriers 5, extending posteriorly beyond line of vision, with three indistinct parietal traces: major parietals with anterior visible third threadlike, posterior portions distinctly raised, expanded and serrated above; 1st and 3rd parietals larger than 2nd, 4th and 5th; upper parietal trace slender, prominent, located just below parietal-palatal margin, remaining faint traces between 1st and 2nd, 2nd and 3rd parietals. Columellar barrier a small threadlike ridge reaching top of columellar callus, only slightly declined anteriorly from plane of coiling. Major palatal barriers 4, extending posteriorly three-eighths of a whorl, lower 3 strongly elevated, rounded and serrated above, descending gradually to front edge of apertural callus, progressively reduced in height from bottom to top; upper palatal a lamellar ridge lying opposite and pointing toward the upper parietal. Accessory palatal traces located between the major palatal teeth with two additional ones above the upper. Palatal traces progressively reduced in size from bottom to top, lower trace with form of major palatals. Height of holotype 1.71 mm., diameter 2.37 mm.

Holotype. — Gambier Islands: Mangareva, Station 102, Aukena Islet, first cave east of gap. Collected by Donald Anderson on May 28, 1934. BPBM number 9662.

Range. — Agakauitai, Mangareva and Aukena Islets, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Aukena Islet (Stations 88, 102, 103) near the gap (94 specimens, BPBM 9410-1, BPBM 9662-3, BPBM 138798); Agakauitai Islet, northwest side (Station 195), 100 ft. inland (2 specimens, BPBM 9673); Mangareva Islet, 100-200 yd. inland, Ganhutu (Station 277) at northeast end (6 specimens, BPBM 9644); Mangareva Islet, vicinity (Stations 187, 189) of Rikitea (2 specimens, BPBM).

Remarks. — In possessing nearly equal parietal barriers, and in having the major palatals progressively reduced in size from bottom to top, *Anceyodonta subconica* departs from the usual pattern of Mangarevan shells. In most other Mangarevan species there are distinct differences in size of the various barriers, and the lower palatal normally is greatly reduced in size. In the above respects, *A. subconica* resembles more closely some of the Austral Island *Minidonta*. The presence of so many *Anceyodonta* characteristics in *A. subconica* (table LXVIII) unquestionably places it in the latter genus. *A. subconica* was a relatively common species on Aukena, and only sparsely represented on Mangareva and Agakauitai Islets. The rather crowded radial ribbing (fig. 81d, e), averaging 11.5 ribs per mm., is unusual for the *Anceyodonta,* where the average of eight species with "normal" ribbing is only 7.41 ribs per mm. As indicated above, it is possible that *A. subconica* is secondarily reduced in size rather than being primitively small.

A large specimen of *subconica,* diameter 3.03 mm., from Aukena (BPBM 9411) has the parietal barriers reduced in size (fig. 81f) and some of the palatals smaller than in the normal specimens. I consider that it is a gerontic individual.

Anceyodonta constricta, new species (Cooke & Solem. Figure 82a-b.

Diagnosis. — Shell very small, diameter 2.09-2.28 mm. (mean 2.20 mm.), with 5½ - 5⅝ rather tightly coiled whorls. Apex flat, spire moderately elevated, last whorl descending only slightly more rapidly, H/D ratio 0.507-0.576 (mean 0.553). Umbilicus strongly constricted with a weak basal sulcus, very narrow, U-shaped, last whorl decoiling more rapidly, contained 6.90-22.7 times (mean 12.8) in the diameter. Postnuclear whorls with narrow, crowded, slightly protractively sinuated radial ribs, 86-95 (mean 90) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by distinctly finer and more crowded spiral riblets. Sutures shallow, whorls strongly flattened laterally and on inward extending basal margin. Aperture compressedly ovate, lengthened basally, inclined less than 10° from shell axis. Parietal barriers 4, extending slightly more than one-quarter whorl, almost always with two accessory traces: upper a high lamellar ridge, expanded and serrated above on posterior two-thirds, anterior quarter a raised threadlike ridge; 2nd lower than 1st, threadlike portion a little longer, with more gradual descension from elevated portion; 3rd higher than 1st posteriorly, expanded edge slightly twisted upward; 4th slightly to greatly lower than 3rd posteriorly, threadlike anterior portion longer. Accessory traces located above 1st and between 1st and 2nd parietals. Columellar barrier a low, rounded threadlike trace parallel to plane of coiling, partly crossing thick columellar callus. Rarely a narrow superior columellar barrier present. Palatal barriers 4, extending nearly one-quarter whorl, plus usually five accessory traces: lower basal in position, reduced in height, with rather sharp anterior descension, slightly recessed; 2nd much higher, lying opposite 3rd parietal, less recessed, with a little more gradual anterior descension; 3rd equal in height to 2nd, lying opposite 2nd parietal; 4th a much lower, V-shaped, high ridge lying opposite 1st parietal. Accessory traces located between each pair of palatals and two above upper palatal. Latter occasionally absent.

Anceyodonta constricta is unique within the genus for its umbilical configuration. Constriction of the opening has produced a weak basal sulcus (fig. 82b) very like that of the Rapan *Rhysoconcha variumbilicata* (fig. 112b). The small size and relatively low spire of *constricta* combine with the basal sulcus to separate it from other *Anceyodonta.*

Description. — Shell small, with 5¼ tightly coiled whorls. Apex flattened, spire moderately and evenly elevated, H/D ratio 0.576. Embryonic whorls 1⅜ with only faint traces of microradial ribbing. Postnuclear whorls with closely set, slightly protractively sinuate radial ribs, 95 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets crossed by finer and more crowded spiral riblets. Sutures relatively shallow, whorls rounded above, strongly flattened laterally and on base. Color white with irregular, zigzagged, reddish flammulations. Umbilicus closed by a flattening and extension of the basal shell margin, contained 11 times in the diameter. Umbilical margin shouldered with a basal concavity above. Parietal barriers 4, extending beyond line of vision, with two accessory traces: upper medium sized, anterior quarter threadlike, becoming elevated, rounded and minutely serrated above posteriorly; 2nd parietal much lower with only weakly expanded upper portion; 3rd parietal much higher with expanded top slightly twisted upwards; 4th parietal with more broadly expanded top and

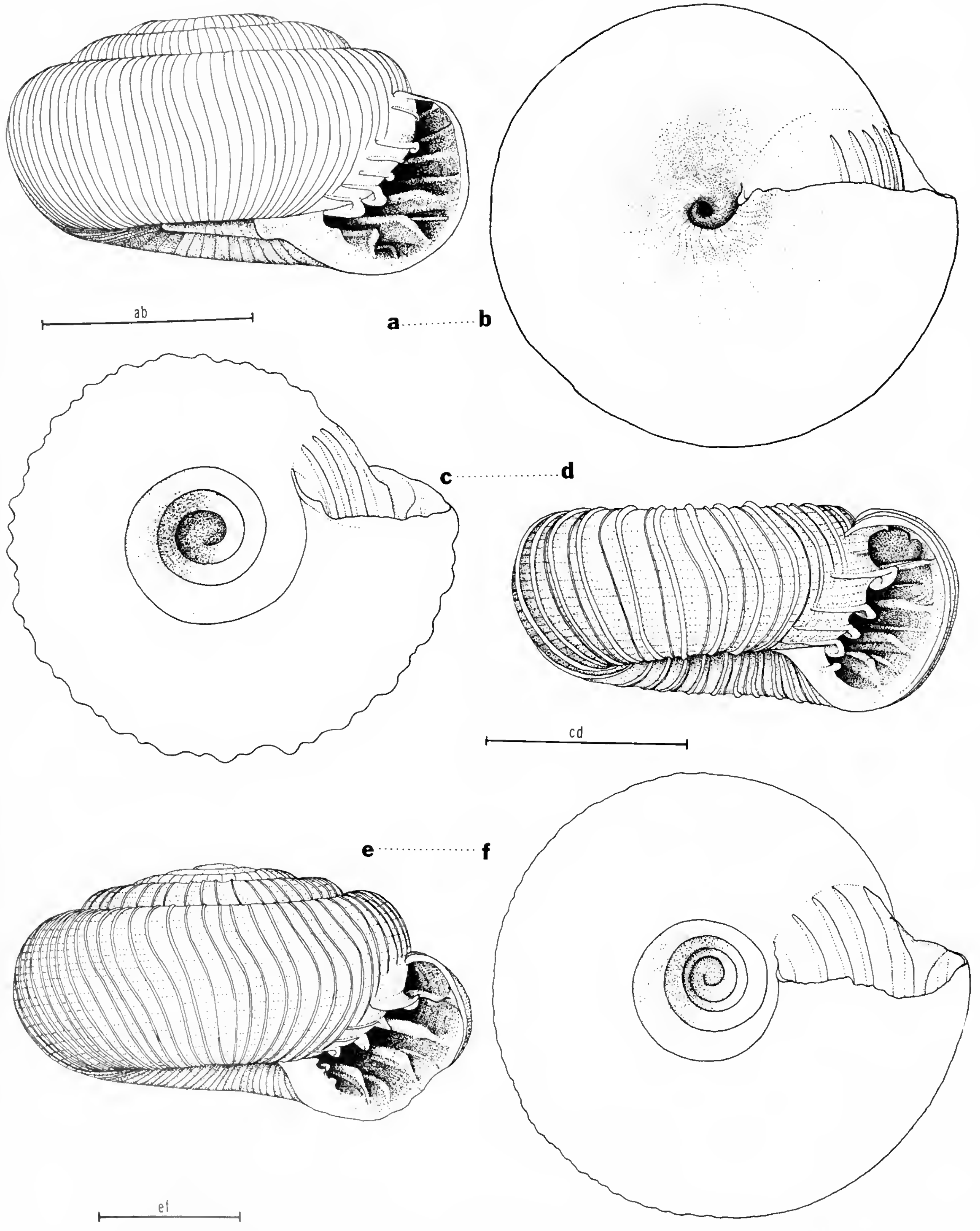

FIG. 82. **a-b**, *Anceyodonta constricta*, new species. Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 9660; **c-d**, *Anceyodonta alternata*, new species. Station 187, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 141661; **e-f**, *Anceyodonta andersoni*, new species. Station 142, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 138936. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

twisted more sharply upward. Accessory traces located above 1st and between 1st and 2nd lamellae. Columellar barrier a low threadlike ridge, parallel to plane of coiling, partly crossing columellar callus. Palatal barriers 4, extending one-quarter whorl, plus five accessory traces: lower reduced in height with very gradual anterior descension; 2nd very high, lying opposite 3rd parietal, long and bladelike, expanded and serrated above, with sharper anterior descension; 3rd same as 2nd, with more gradual anterior descension; 4th a prominent, V-shaped ridge lying opposite 1st palatal, much lower than 3rd palatal. Accessory traces located between each pair of major palatals and two above 4th palatal. Height of holotype 1.25 mm., diameter 2.17 mm.

Holotype. — Gambier Islands: Mangareva, Aukena Islet. Collected during Mangarevan Expedition. BPBM 9660.

Range. — Known only from the type collection.

Paratypes. — BPBM 9660.

Remarks. — One of the seven examples had the two upper parietal traces absent. Otherwise the barriers showed no significant variations.

Unfortunately, the station number was not available, so we do not know exactly where on Aukena the specimens were collected. The constricted umbilicus is diagnostic and at once separates *Anceyodonta constricta* from the other Mangarevan endodontids.

In having a low spire, few whorls, very crowded ribs, no sulcus or secondary spiral cording, and being quite small in size, *A. constricta* differs considerably from the other *Anceyodonta*. Its inclusion in *Anceyodonta* rather than *Minidonta* has been based on the apertural barriers, since it comes closest to being transitional between the two genera.

Anceyodonta andersoni, new species (Cooke & Solem). Figure 82e, f.

Diagnosis. — Shell of average size, diameter 2.96-3.62 mm. (mean 3.29 mm.), with 5¼-6 normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.547-0.625 (mean 0.570). Umbilicus widely open, V-shaped, later whorls decoiling more rapidly, contained 2.95-3.96 times (mean 3.34) in the diameter. Postnuclear whorls with high, prominent, slightly protractively sinuated radial ribs, 61-96 (mean 79.0) on the body whorl, whose interstices are 2 - 3 times their width. Microsculpture a lattice of very fine radial riblets crossed by slightly finer and more crowded spiral riblets, plus prominent secondary spiral cords. Sutures deep, whorls strongly rounded. Aperture ovate, inclined about 10° from shell axis. Parietal barriers 4, extending more than one-quarter whorl, usually with a recessed, threadlike trace above upper parietal: upper high and bladelike, gradually descending over anterior fourth, posterior two-thirds with downward pointing bifid section, joined with top of regular section by a heavy callus pad; 2nd with posterior visible half equal in height to 1st, weakly expanded posteriorly, with anterior third threadlike; 3rd same as 2nd, except posterior elevated portion a little shorter and with more gradual anterior descension; 4th with same form as 2nd, but greatly reduced in height posteriorly. Columellar wall with a low, recessed, threadlike ridge, lying parallel to plane of coiling, rarely (14.2 per cent) with a 2nd columellar barrier above. Palatal barriers 4, extending beyond line of vision, with three to five accessory traces: lower high and bladelike, with rather sharp anterior descension; 2nd slightly higher with more gradual anterior descension; 3rd more broadly expanded above, equal in height to 2nd; 4th a lower bladelike ridge, only weakly expanded above, with abrupt anterior descension, situated opposite 1st parietal. Accessory traces between 1st and 2nd plus 2nd and 3rd palatals are prominent threadlike ridges, extending to anterior palatal barrier margins; two smaller and rather inconspicuous recessed threadlike traces usually located above 4th palatal; and often a broad, low inconspicuous recessed trace located between columellar and 1st palatal.

The widely open umbilicus and relatively low spire of *Anceyodonta andersoni* immediately separate it from all species of *Anceyodonta* except *A. alternata* and *A. soror*. The former has a depressed apex, extremely wide umbilicus, alternating high and low ribbing and is much smaller (diameter 2.24 mm.). *A. soror* has 5 parietals, the columellar barrier deflected onto the basal lip, and is generally much smaller (mean diameter 2.61 mm.), while *A. andersoni* has 4 parietals, the columellar barrier parallel to the plane of coiling, and is generally much larger (mean diameter 3.29 mm.).

Description. — Shell of average size, with 5¼ normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.550. Apical whorls 1⅝, sculpture eroded. Postnuclear whorls with prominent, high, slightly protractively sinuated radial ribs, 77 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of numerous very fine radial riblets, eight to twelve between each pair of major ribs, crossed by even finer spiral riblets, plus a secondary sculpture of prominent spiral cords. Sutures deep, whorls strongly rounded, slightly flattened above and below periphery. Color mostly leached from shell, a few irregular, reddish flammulations remaining. Umbilicus broadly open, V-shaped, last whorls decoiling more rapidly, contained 3.45 times in the diameter. Aperture ovate, compressed laterally above and below periphery, inclined about 10° from shell axis. Parietal barriers 4, extending at least one-quarter whorl, well beyond line of vision: upper a high lamellar blade, becoming bifidly flattened above posteriorly, bifid portion hooked sharply downward; 2nd and 3rd with threadlike anterior third, becoming high lamellae posteriorly, slightly expanded above and turned moderately downward; 4th with threadlike anterior portion, becoming less high and lamellate posteriorly. Columellar barrier a low, deeply recessed thread lying parallel to the plane of coiling with a vague accessory lump at the umbilical-parietal margin. Palatal barriers 4, with four additional traces, extending beyond line of vision: lower three high and lamellate, rather expanded on top, the bottom one slightly lower than the next two, all gradually descending anteriorly to lip margin; upper palatal a thin lamellar ridge lying opposite the upper parietal tooth and abruptly descending anteriorly, much lower than 3rd palatal. Palatal traces lying between the columellar and bottom palatal, 1st and 2nd palatal, 2nd and 3rd palatal and above the upper palatal. Of these, the trace between the 1st and 2nd palatal is by far the largest. Height of holotype 1.81 mm., diameter 3.29 mm.

Holotype. — Gambier Islands: Mangareva, Station 142, Mangareva Islet, inland from Ganhutu. Collected by Y. Kondo and C. M. Cooke, Jr. on June 3, 1934. BPBM 138936.

Range. — Mangareva Islet, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Mangareva Islet, vicinity of Ganhutu (Stations 142, 277) on flat land (18 specimens, BPBM 138936, BPBM 138964); vicinity of Rikitea (Stations 187, 189) in gardens and on flat land (5 specimens, BPBM 141660, BPBM 141686-7); northeast of Vaituatai Bay (Station 197) on flat land (2 specimens, BPBM 139009).

Remarks. – The holotype is unusual in lacking the minor parietal trace and in having a weak 2nd columellar barrier. Only two of 14 adults had the additional columellar. Although the low spire and wide umbilicus give a quite different appearance to *A. andersoni,* the great majority of the shell features conform to the *Anceyodonta* pattern (table LXVIII). Similar changes in growth pattern followed by greatly increased size probably provided the means for *Gambiodonta* to evolve from *Anceyodonta.*

Great pleasure is taken in naming this species after Donald Anderson, malacological assistant on the Mangarevan Expedition.

Anceyodonta alternata, new species (Cooke & Solem). Figure 82c-d.

Diagnosis. – Shell very small, diameter 2.24 mm., with 4¼ planulately coiled whorls. Apex and spire depressed below level of body whorl, H/D ratio 0.456. Umbilicus broadly V-shaped, regularly decoiling, contained 2.72 times in the diameter. Postnuclear whorls with an alternation of major and minor slightly protractively sinuated radial ribs, 48 on the body whorl, whose interstices are about 2-3 times their width. Microsculpture of fine radial riblets, six to eight between each pair of major ribs, crossing very fine and crowded spiral riblets, with a secondary sculpture of low, rounded spiral cords. Sutures deep, whorls strongly rounded, flattened laterally. Aperture flatly ovate, inclined about 5° from shell axis. Parietal barriers 4, extending beyond line of vision, with one accessory trace, as in *Anceyodonta andersoni,* except lower parietal less reduced in height. Columellar and palatal barriers as in *andersoni.*

The depressed spire, very wide umbilicus, and striking alternation of large and small major ribs immediately separate *Anceyodonta alternata* from the other *Anceyodonta.*

Description. – Shell small, with slightly more than 4¼ planulately coiled whorls. Apex and spire depressed, body whorl strongly rounded above and below with flattened sides, H/D ratio 0.456. Embryonic whorls 1¼ with faint traces of microradial ribbing remaining. Lower whorls with pairs of larger and smaller radial ribs, the larger twice the height of the smaller and separated from it by the width of the smaller. Each pair is then separated by about the width of the larger from tbe next pair. Microsculpture of six to eight radial riblets between each pair of major ribs. Microradial riblets crossing low, rounded spiral cords on the mid-sections of the whorls and the basal portion. and barely visible crowded spiral riblets. Sutures moderately impressed, whorls rounded above, flattened laterally. Umbilicus widely opened. contained 2.72 times in the diameter. with slightly shouldered margins. Aperture ovate, strongly rounded above and below, inclined about 5° from shell axis. Parietal barriers 4, extending past the line of vision: lower 3 with visible anterior third low and threadlike, becoming lamellate and slightly expanded above posteriorly: upper parietal with much shorter anterior portion becoming quite high and lamellate with a sharply downwardly hooked lamellate bifidity posteriorly. Between the upper parietal and the lip margin is a slender accessory ridge. Columellar barrier a threadlike ridge, parallel to plane of coiling, extending partway across columellar callus. Deeply recessed within the aperture is a trace of a 2nd columellar barrier located above the one shown in the type figure. Major palatal barriers 4, with six accessory traces: first 3 bladelike, expanded and serrated above with gradual anterior descension; 1st palatal equal in size to 2nd; upper palatal more nearly ridgelike, with quite sharp anterior descension. Accessory palatal traces located between major palatals 1 and 2, 2 and 3 and above 4 are quite prominent with the ones on the upper lip margin, between palatals 3 and 4 and between the columellar and 1st palatal barrier, relatively small and insignificant. Height of holotype 1.02 mm., diameter 2.24 mm.

Holotype. – Gambier Islands: Mangareva, Mangareva Islet, Station 187, north part of Rikitea. Collected on open ground by Yoshio Kondo on June 7, 1934. BPBM 141661.

Remarks. – The single specimen cannot be mistaken for any other Mangarevan shell. The unique double ribbing of alternating large and small radial ribs and depressed spire combine with the very widely open umbilicus and downwardly hooked bifid upper parietal barrier to distinguish *A. alternata. Anceyodonta andersoni,* also from Mangareva Islet, has essentially identical apertural barriers, differing only in having the 4th parietal much reduced in height and the 2nd columellar and lowest palatal trace less deeply recessed.

Possibly *A. alternata* may be based on a teratological juvenile individual of *A. andersoni,* but the differences are so gross that I consider this unlikely. There is no trace of repaired damage on the specimen. If the alternating ribbing was not present, I would be less certain of its distinctiveness.

Anceyodonta difficilis, new species. Figure 83a, b.

Diagnosis. – Shell of average size, diameter 2.57-3.49 mm. (mean 2.93 mm.), with 6-7¼ tightly coiled whorls. Apex and spire strongly elevated, usually rounded above, H/D ratio 0.651-0.762 (mean 0.711). Umbilicus very small to minute or barely perforate, contained 8.27-40.0 times (mean 19.1) in the diameter. Postnuclear sculpture of narrow, prominent, slightly protractively sinuated radial ribs, 53-84 (mean 68.8) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by finer and much more crowded spiral riblets, with a secondary sculpture of low, rounded, prominent spiral cords. Sutures shallow, whorls slightly compressed laterally and on basal margin, a narrow prominent subsutural sulcus present. Aperture ovate, slightly compressed laterally and on basal margin, a narrow prominent subsutural sulcus present. Aperture ovate, slightly compressed laterally and on basal margin, inclined about 5° from shell axis. Parietal barriers 4 or 5, extending more than one-quarter whorl: upper parietal a high bladelike ridge, with gradual anterior descension, posteriorly bulbously expanded and serrated, deflecting downward laterally; 2nd parietal a low indistinct, threadlike ridge, absent or very reduced in most specimens; 3rd and 5th parietals with anterior visible two-thirds low and threadlike, becoming abruptly elevated, expanded and serrated posteriorly; 4th parietal a low and threadlike ridge for entire length. Columellar barrier a high bladelike ridge, deflected down onto basal margin, with sharp anterior descension to left margin, followed by a sinuated rise to flattened bladelike portion. Palatal barriers 4, extending one-quarter whorl, high and bladelike, with three to six accessory traces: lower palatal greatly reduced in height, a low ridge; 2nd and 3rd palatals high, similar in descension to columellar; 4th palatal a lower, V-shaped ridge, lying opposite 1st parietal. Accessory palatal traces lying between 1st and 2nd, 2nd and 3rd, rarely between 3rd and 4th, with two or three traces present above 4th palatal.

The quite small umbilicus is the most obvious character separating *Anceyodonta difficilis* from *A. soror,* which is found at the same localities. The former also is much more elevated. Some specimens of *A. difficilis* may be confused with *A. obesa,* but the

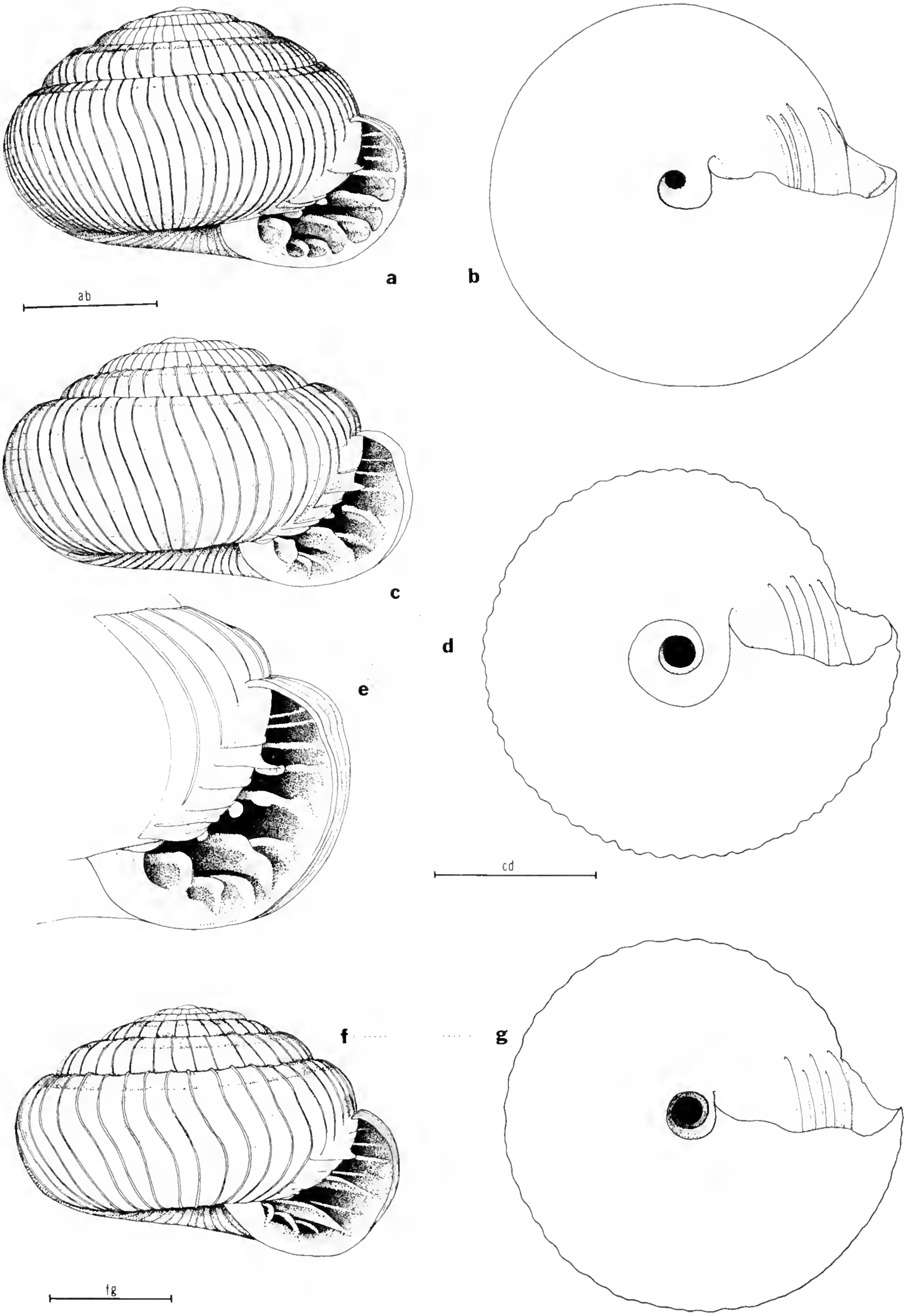

FIG. 83. **a-b**, *Anceyodonta difficilis,* new species. Station 189, Rikitea, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 141686; **c-g**, *Anceyodonta soror,* new species. *c-e,* Station 277, Ganhutu, Mangareva Islet, Mangareva,. Gambier Islands. Holotype. BPBM 138965; *f-g,* Station 189, Rikitea, Mangareva Islet, Mangareva, Gambier Islands. Paratype. BPBM 9657. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

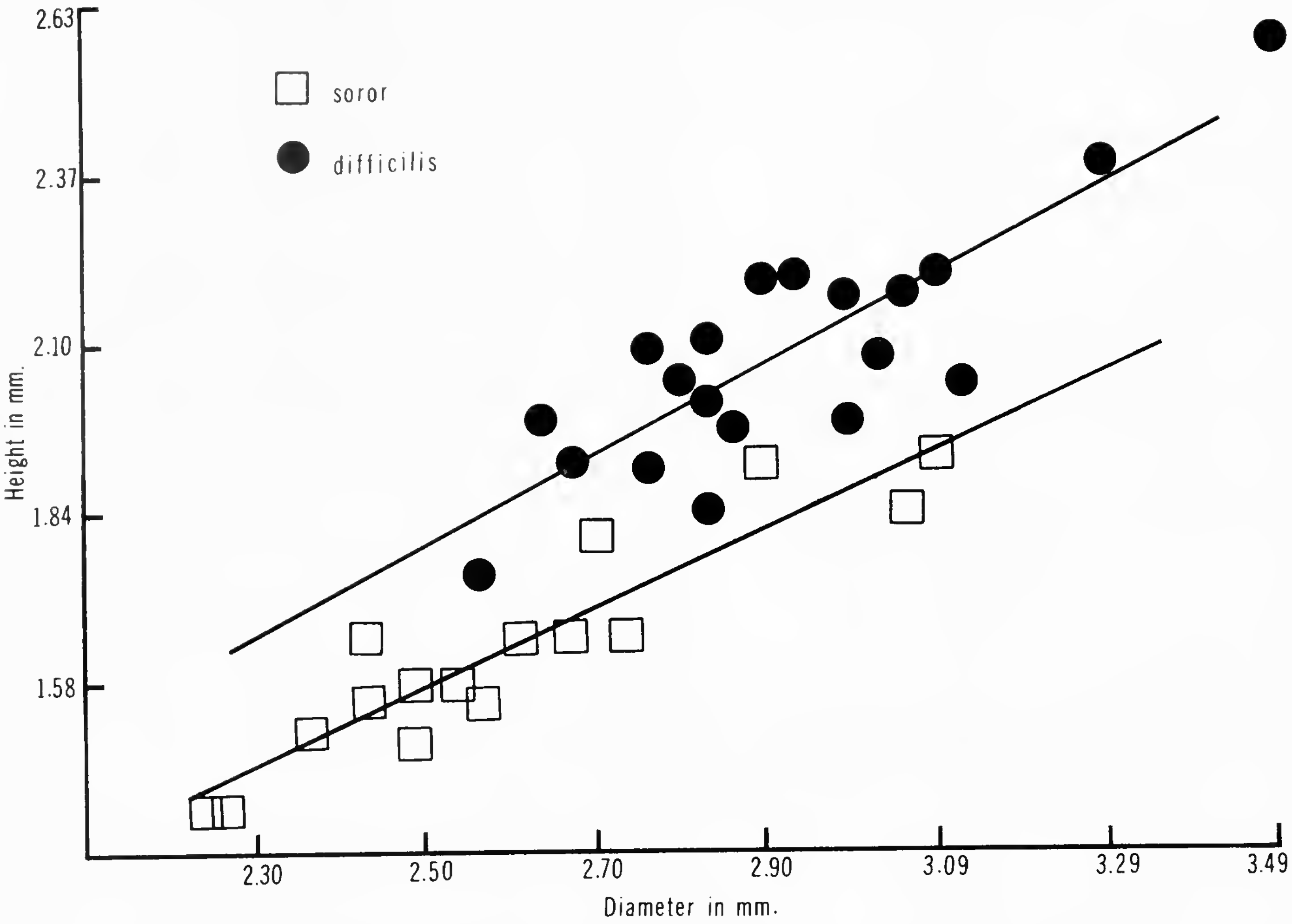

FIG. 84. Scatter diagram showing relationship for height to diameter in *Anceyodonta soror* and *A. difficilis*.

latter can easily be distinguished by having the columellar barrier on the columellar wall or at most slanting downward across the columellar callus, while in *A. difficilis* it is on the basal margin.

Description. – Shell a little larger than average, with 6⅜ relatively tightly coiled whorls. Spire markedly elevated, with apex slightly rounded, last whorl not descending more rapidly, H/D ratio 0.660. Embryonic whorls 1⅜, sculpture eroded. Postnuclear whorls with broad, prominent, slightly protractively sinuated radial ribs, 84 on the body whorl, whose interstices are 2 - 6 times their width. Microsculpture of numerous fine radial riblets, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of strong spiral cords. Sutures shallow, whorls slightly flattened above, with prominent sulcus below suture. Umbilicus constricted internally, last whorl decoiling, narrowly open, contained 8.27 times in the diameter. Color absent, except for faint remnants of reddish flammulation. Aperture constricted with evenly rounded outer margin and slightly flattened base. Parietal barriers 4, extending past line of vision: upper a narrow, high lamella with sharp anterior descension, pointing toward upper palatal tooth; 2nd and 4th palatals with visible anterior two-thirds a low thread, posteriorly becoming moderately high and almost bulbously expanded above; 3rd parietal a threadlike trace for its entire length. Columellar barrier higher than parietals, displaced onto basal lip and reaching apertural margin. Major palatals 4, extending about one-quarter whorl: basal a low ridge; 2nd and 3rd moderately high and lamellate, expanded and serrated above with gradual anterior descension; 4th a low, V-shaped ridge with sharp anterior descension, lying opposite the upper parietal. Palatal traces present between palatals 1 and 2, 2 and 3 very large, almost equal in size to 1st palatal; other three traces above upper palatal tooth small and threadlike. All palatal barriers and traces reaching edge of apertural callus. Height of holotype 1.98 mm., diameter 2.99 mm.

Holotype. – Gambier Islands: Mangareva, Station 189, Mangareva Islet, north end of Rikitea. Collected on open ground by C. M. Cooke, Jr. and Y. Kondo on June 8, 1934. BPBM 141686.

Range. – Mangareva Islet, Mangareva, Gambier Islands.

Paratypes. – Same as list of material.

Material. – Mangareva: Mangareva Islet (Stations 142, 277) vicinity of Ganhutu, on open ground (6 specimens, BPBM 9636, BPBM 9642); Mangareva Islet (Stations 187, 189) north end of Rikitea on open ground (19 specimens, BPBM 141668, BPBM 141688); Mangareva Islet, Rikitea (1 specimen, BPBM 9646).

Remarks. – In only two of the 26 specimens was the subsutural sulcus absent. Most shells showed a broad white area between the upper and second parietal that in three shells had become a recognizable 5th parietal barrier. The holotype is a relatively depressed individual with comparatively wide umbilicus, but is in better condition than most other specimens.

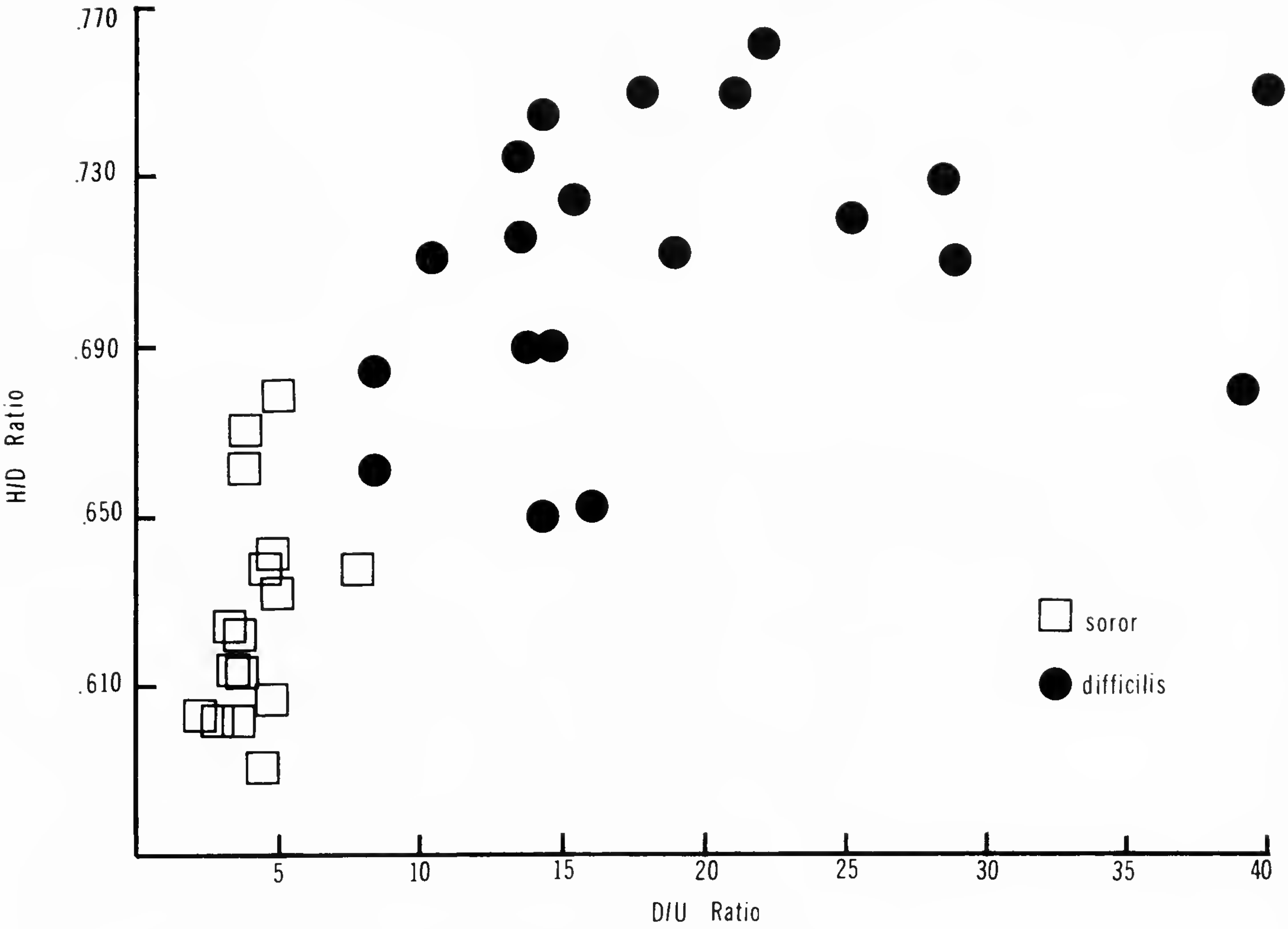

FIG. 85. Scatter diagram showing relationship of H/D ratio to D/U ratio in *Anceyodonta soror* and *A. difficilis.*

While the differences in parietal barriers and umbilical size at once separate *A. soror* from *A. difficilis,* there are subtle differences in relative height and size that are equally significant. Scatter diagrams of the height and diameter (fig. 84) and H/D and D/U ratios (fig. 85) show that, despite moderate overlap, there are distinct differences in size and proportions. Calculation of regression lines for the height and diameter by Bartlett's method yielded lines that diverge insignificantly, although being quite separated on the diagram. The differences in H/D and D/U ratios are much more dramatic, although even here there is some overlap for an individual character. Similar charts were prepared for the *A. obesa - A. densicostata* pair, but are not published because these two species have more obvious differentiating features.

Anceyodonta soror, new species. Figure 83c-g.

Diagnosis. — Shell slightly smaller than average, diameter 2.24-3.09 mm. (mean 2.61 mm.), with 5 to 6⅛ normally coiled whorls. Apex and spire moderately and evenly elevated, slightly rounded above, last whorl not descending more rapidly, H/D ratio 0.592-0.677 (mean 0.628). Umbilicus widely open, narrowed internally, last whorl decoiling more rapidly, contained 2.96-4.80 times (mean 4.25) in the diameter. Postnuclear sculpture of prominent, narrow, slightly protractively sinuated radial ribs, 53-74 (mean 65.0) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of low, rather widely spaced spiral cords that are most prominent on shell base. Sutures impressed, whorls strongly rounded above, slightly compressed laterally and on basal margin, very slight indication of a subsutural sulcus. Aperture ovate, slightly compressed laterally, inclined a little more than 5° from shell axis. Parietal barriers 5, extending more than one-quarter whorl, numbers 2 and 4 reduced, with a single superior parietal trace: upper high and lamellate, posteriorly expanded and serrated above, with gradual anterior descension; 2nd a faint threadlike trace for entire length; 3rd and 5th parietals with anterior visible two-thirds threadlike, posteriorly elevated, expanded and serrated above, slightly lower than 1st parietal; 4th parietal a prominent threadlike trace, expanded and serrated on top, equal in height to threadlike portions of 3rd and 5th parietals. Parietal trace situated above upper parietal, about one-third of way to parietal-palatal margin. Columellar barrier very large, twisted downward onto basal margin, with sinuated anterior descension. Major palatal barriers 4, with four to six accessory traces: lower palatal greatly reduced in height, scarcely larger than first palatal trace; 2nd and 3rd palatals similar in height and structure to columellar, extending posteriorly beyond line of vision; 4th palatal a low V-shaped ridge, lying opposite 1st parietal, equal in height to 1st palatal. Palatal traces large, reduced in size from bottom to top, present between 1st and 2nd, 2nd and 3rd, and two present above 4th palatal. Some specimens have a second trace present between palatals 2 and 3, plus a sixth trace between palatals 3 and 4. Rarely a second trace between 3rd and 4th, with two or three traces present above 4th palatal.

The widely open umbilicus is the most obvious character separating *Anceyodonta soror* from *A. difficilis*. *A. soror* generally is smaller, less elevated and invariably has the 5th parietal present, while in *A. difficilis* there may be only 4 parietals.

Description. — Shell relatively small, with 5½ loosely coiled whorls. Apex and spire distinctly elevated, last whorl not descending more rapidly, H/D ratio 0.624. Apical whorls 1⅜, sculpture eroded. Postnuclear whorls with low, relatively wide, somewhat protractively sinuated radial ribs, 61 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of eight to twelve radial riblets between each pair of major ribs, with a secondary sculpture of indistinct, low, broadly rounded spiral cords. Sutures shallow, whorls relatively flattened above with very slight subsutural sulcus, body whorl very slightly flattened laterally. Umbilicus narrowly open internally, 1st whorl decoiling rapidly, contained 3.85 times in the diameter. Aperture ovate, slightly compressed laterally and on basal margin, inclined less than 10° from shell axis. Parietal barriers 5, with one superior threadlike trace: upper high and bladelike, extending beyond the line of vision, thickened on lower edge and hooked downward with the thickened portion flattened, anterior descension gradual with very short threadlike portion; 2nd parietal a low threadlike ridge narrowly flattened above and serrated posteriorly, anterior visible third threadlike; 3rd parietal threadlike for anterior visible two-thirds, becoming high and bulbously expanded with minute serrations on posterior third, which is partly deflected down; 4th parietal a low threadlike ridge slightly higher and wider than 2nd, minutely serrated posteriorly; 5th parietal threadlike for anterior two-thirds, becoming bulbously expanded and serrated posteriorly, but smaller in size than 3rd parietal. Columellar barrier high, roundly expanded and serrated posteriorly, twisting parallel to shell axis, displaced onto basal lip and gradually descending across callus almost to apertural margin. Outer margin of columellar barrier flattened and serrated, inner rounded above. Apertural callus relatively low and wide. Palatal barriers 4, extending posteriorly almost one-quarter whorl, with six accessory traces: lower palatal greatly reduced in height, an elevated ridge, flattened above and sharply descending onto apertural margin; 2nd palatal high, broadly expanded above, with minute serrations; 3rd palatal somewhat lower, bulbously expanded above with minute serrations, gradually descending anteriorly; 4th palatal a V-shaped ridge situated opposite upper parietal, sharply descending to the apertural callus. Two low, threadlike palatal traces located above the upper palatal; one between palatals 3 and 4; two between palatals 2 and 3; and one between palatals 1 and 2: lower two palatal traces are the largest, the lowest almost equal in size to lower palatal. Height of holotype 1.58 mm., diameter 2.54 mm.

Holotype. — Gambier Islands: Mangareva, Station 277, Ganhutu, northeast end of Mangareva Islet. Collected on open ground by Donald Anderson on June 26, 1934. BPBM 138965.

Range. — Mangareva Islet, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Mangareva Islet (Stations 139, 142, 277) vicinity of Ganhutu on open ground (14 specimens, BPBM 138937, BPBM 138965, BPBM 141270); Mangareva Islet (Stations 155, 189), vicinity of Rikitea on open ground (4 specimens, BPBM 9657, BPBM 9679, BPBM 139001).

Remarks. — The number of palatal traces is variable in *Anceyodonta soror*, with only a few specimens having six, most possessing five. One gerontic individual from Rikitea (BPBM 9657) had the barriers somewhat reduced (fig. 83g), very widely spaced ribbing (53 on the body whorl), and the umbilicus narrower (contained 7.83 times in the diameter) than the other shells. Also the columellar barrier is only partly displaced from the columellar lip. Similar gerontic specimens are known in *Minidonta simulata* and *A. subconica,* so that this variation is not considered to be significant.

The wider opening of the umbilicus in *A. soror* is caused by rapid decoiling during the last whorl of growth, and thus differs greatly in form from the wide openings found in *A. andersoni* and *A. alternata*. The latter two have the more typical umbilical decoiling, while the umbilicus in *A. soror* is a modification of the typical *Minidonta-Anceyodonta* pattern.

Anceyodonta sexlamellata (Pfeiffer, 1845). Figure 86a-e.

Helix sexlamellata Pfeiffer, 1845, Zeits. Malak., **2,** p. 85—Gambier Islands; Pfeiffer, 1848, Monog. helic. viv., **1,** p. 186; Pfeiffer, 1852, Syst. Conchyl., Cab., I **12,** (2), p. 200, pl. 100, figs. 44-48 (plate issued in 1850); Pfeiffer, 1853, Monog. helic. viv., **3,** p. 144; Pfeiffer, 1859, *loc. cit.,* **4,** p. 155; Pfeiffer, 1869, *loc. cit.,* **5,** p. 221; Pfeiffer, 1876, *loc. cit.,* **7,** p. 259.

Pitys sexlamellata (Pfeiffer), Pease, 1871, Proc. Zool. Soc. London, **1871,** p. 474—Mangareva, Gambier Islands; Ancey, 1889, Le Naturaliste, **3,** p. 118.

Helix (Endodonta) sexlamellata (Pfeiffer), Tryon, 1887, Man. Conchol., (2), **3,** p. 63, pl. 12, figs. 11-13 (copied from Syst. Conchyl. Cab.).

Patula (Endodonta) perarmata Smith, 1892, Conchologist, **2,** (7), p. 165, figs.—St. Helena (error).

Endodonta (Thaumatodon) sexlamellata (Pfeiffer), Pilsbry, 1893, Man. Conchol., (2), **9,** p. 17.

Diagnosis. — Shell slightly larger than average, diameter 2.44-3.59 mm. (mean 2.99 mm.), with 5¼-7½ moderately tightly to very tightly coiled whorls. Apex and spire normally very strongly elevated, slightly rounded above, last whorl not descending more rapidly, H/D ratio 0.634-0.929 (mean 0.743). Umbilicus minute, occasionally moderately open, contained 6.93-29.6 times (mean 15.1) in the diameter. Postnuclear sculpture of prominent, narrow to broad, very slightly protractively sinuated radial ribs, 60-125 (mean 89.6) on the body whorl, whose interstices are usually less than twice their width. Microsculpture of very fine radial riblets, seven to twelve between each pair of major ribs, crossed by barely visible, extremely crowded spiral riblets, many specimens with a secondary sculpture of low rounded spiral cords. Sutures impressed, whorls strongly rounded above, somewhat compressed on basal margin, with inward extension of columellar wall, normally with a weak to very strong supraperipheral sulcus, many examples with a subsutural sulcus also present. Aperture ovate, strongly inwardly extended basally, inclined less than 5° from shell axis. Parietal barriers 3, extending more than one-quarter whorl posteriorly, usually with three to five accessory traces: upper parietal high and bladelike, expanded and serrated above on posterior two-thirds, with very gradual anterior descension; 2nd parietal with posterior visible half elevated slightly higher than 1st parietal, very broadly expanded and serrated above, anterior visible third low and threadlike; 3rd parietal identical in structure to 2nd, except less broadly expanded above posteriorly. Accessory parietal traces: two between upper parietal and parietal-palatal margin, with second less conspicuous; between 1st and 2nd parietal; between 2nd and 3rd parietal; below 3rd parietal. All parietal traces deeply recessed and inconspicuous, intraparietal traces often reduced or absent. Columellar barriers 2, high and bladelike, 2nd slightly lower, gradually descending across inward edge of very thick columellar callus. Palatal barriers 4, extending almost one-quarter whorl, with six to eleven accessory

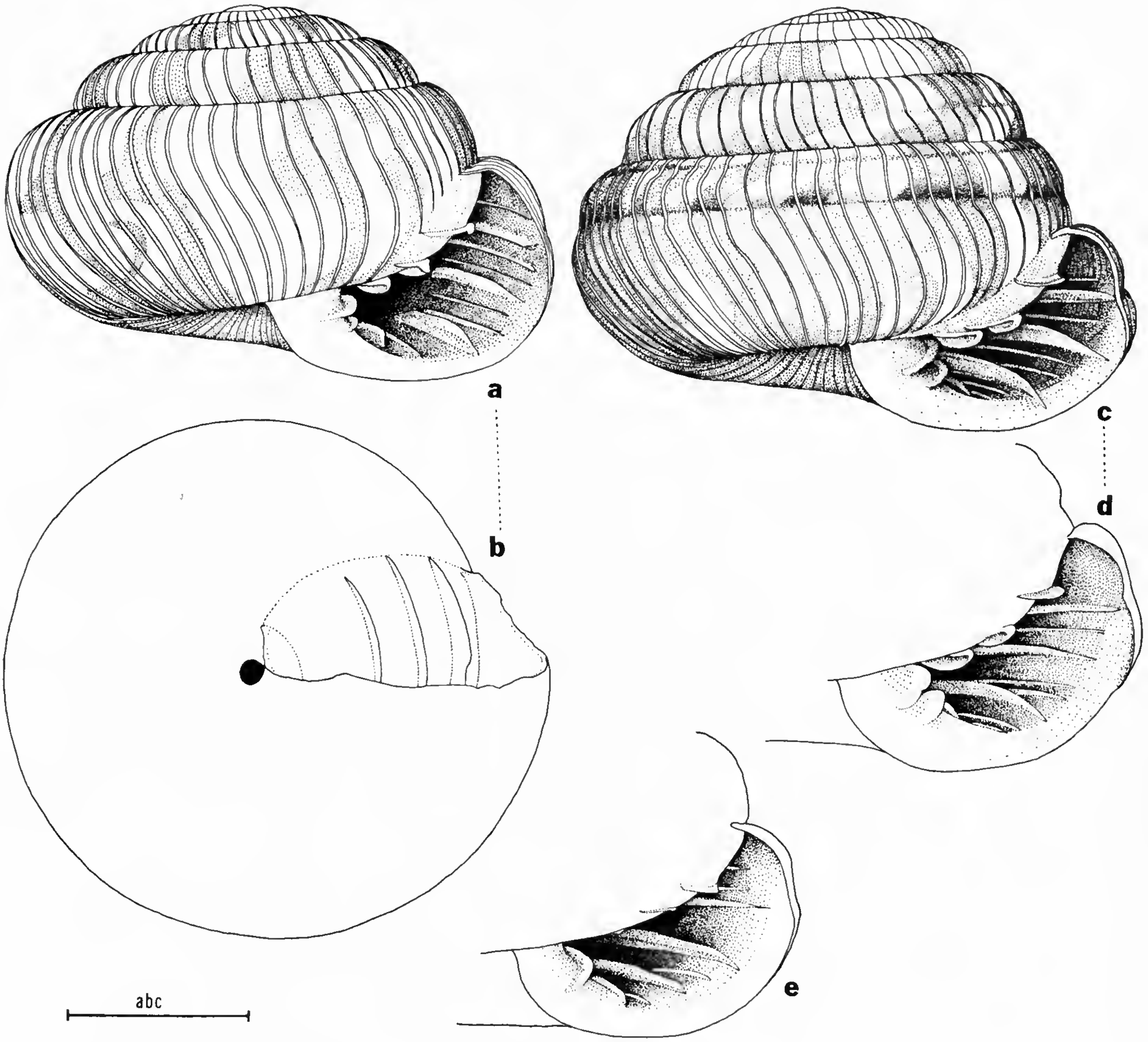

FIG. 86. *Anceyodonta sexlamellata* (Pfeiffer): **a-b**, Gambier Islands. BPBM 106237 ex W. F. Webb, Gude; **c-d**, Station 187, Rikitea, Mangareva Islet, Mangareva, Gambier Islands. BPBM 141666; **e**, Station 197, Vaituatai Bay, Mangareva Islet, Mangareva, Gambier Islands. BPBM 139012. Scale lines equal 1 mm. Figures *d* and *e* greatly enlarged. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

traces: lower palatal very slightly lower than 2nd, high and bladelike, expanded and serrated above posteriorly, with gradual anterior descension to middle of columellar basal callus; 2nd and 3rd palatals slightly higher, equally expanded and serrated above, with longer and more gradual descension, slightly more deeply recessed within aperture; 4th palatal reduced in height, a relatively high, V-shaped ridge lying opposite upper parietal. Palatal traces normally distributed as follows: three above upper palatal; two between 3rd and 4th palatal; three between 2nd and 3rd palatal; and three between 1st and 2nd palatal. Of the palatal traces between the lower 3 barriers, the central of each trio normally is largest. Reduction of palatal traces normally involves the smaller ones between the lower barriers and one or two of the smaller traces above upper palatal.

The 2 slanted columellar barriers, only 3 elevated parietals, very high spire, large number of palatal and parietal traces, plus the presence of a supraperipheral sulcus in many specimens separate *A. sexlamellata* from the other *Anceyodonta*. The only other species that have 3 parietals, even occasionally, are minute (*A. ganhutuensis*) or differ greatly in their barrier length and number of palatal traces and are very large (*A. labiosa* and *A. hamyana*). *A. obesa* and *A. densicostata* normally have 5 parietals and rarely have only 3.

Description. – Shell relatively large, with slightly more than 6⅜ tightly coiled whorls. Apex and spire strongly elevated, rounded above, last whorl descending a little more rapidly, H/D ratio 0.753. Apical whorls 1½, sculpture of prominent, moderately widely spaced radial ribs with a microsculpture of two or three radial riblets between each pair of major ribs and a barely visible faint spiral microsculpture. Postnuclear whorls with prominent, broadly rounded, sinuately protractive radial ribs, 87 on the body whorl, whose interstices are less than 3 times their width. Microsculpture a lattice of prominent, somewhat irregular radial riblets crossed by barely visible, much more crowded spiral riblets. Sutures deep, whorls somewhat shouldered above moderately prominent subsutural sulcus, basal margin elongated and flattened. Umbilicus minute, barely perforate, contained 24.3 times in the diameter. Color light yellowish horn with narrow to broad, irregularly spaced zigzag radial streaks more or less coalescing on base of shell. Aperture elongately ovate with flattened basal margin and fairly prominent subsutural sulcus, lip badly broken. Parietal barriers 3, extending slightly more than one-quarter whorl: upper parietal high, ridgelike, broadly rounded above with gradual anterior descension, posterior two-thirds minutely barbed on top and sides; 2nd parietal higher, less broadly rounded, with anterior quarter low, smooth, threadlike, becoming slightly higher posteriorly with coarser, more prominent barbing; 3rd parietal intermediate in height and breadth, anterior third very low and threadlike, somewhat less prominently barbed above posteriorly. Columellar and basal margins with heavy callus, occupying on columellar wall almost one-fourth width of aperture. Columellar barriers 2: upper a narrow, smooth ridge parallel to the plane of coiling and reaching just across inner face of callus; lower a much smaller threadlike ridge, slightly recessed and less prominent. Palatal barriers 4, extending nearly one-quarter whorl, with eleven accessory traces: lower palatal basal in position, an inconspicuous ridge with gradual anterior descension, partially affected by heavy callus; 2nd palatal near palatal-basal margin, a high lamellar ridge with gradual anterior descension, posterior two-thirds minutely barbed above and on sides; 3rd palatal opposite middle parietal, equal in height to 2nd but with slightly sharper anterior descension, relatively broadly rounded above with minute serrations extending to anterior quarter; upper palatal situated opposite 1st parietal, a lower, ridgelike barrier slightly expanded above with fine serrations present over most of length and relatively sharp anterior descension. Palatal traces low, all relatively inconspicuous, located as follows: three between 1st and 2nd palatals; three between 2nd and 3rd palatals; two between 3rd and 4th palatals, and three between upper palatal and the palatal-parietal margin. Height of lectotype 2.40 mm., diameter 3.19 mm.

Lectotype. – Gambier Islands. Collector unknown. BMNH 1962702/1 (ex-Hugh Cuming).

Range. – Agakauitai, Akamaru, Aukena, Mangareva and Taravai Islets, Mangareva, Gambier Islands.

Paratypes. – Gambier Islands (7 specimens, BMNH 1962702/2-8).

Material. – Gambier Islands (9 specimens, BPBM 106237, BMNH 1962702/1-8): Mangareva (27 specimens, BPBM 167414, BPBM 115402, FMNH 46445); Mangareva Islet, north end (Stations 155, 187, 189) and gardens of Rikitea (31 specimens, BPBM 9675, BPBM 9705, BPBM 139003, BPBM 141666, BPBM 141691); Mangareva Islet, northeast (Station 197) of Vaituatai Bay (5 specimens, BPBM 139012); Mangareva Islet, vicinity (Stations 139, 277) of Ganhutu (8 specimens, BPBM 138977, BPBM 141271); Aukena Islet, along trail near gap and caves (Stations 88, 102, 103) east of gap (257 specimens, BPBM 9661, BPBM 138704, BPBM 138754, BPBM 138756, BPBM 138796); Aukena Islet, west (Stations 79, 82, 92) end (8 specimens, BPBM 138667, BPBM 140841, BPBM 140853); Aukena Islet, north (Station 104) side (1 specimen, BPBM 138815); Akamaru Islet, in wave (Station 107) cutting (190 specimens, BPBM 138850); Akamaru Islet, northwest (Station 97) side (18 specimens, BPBM 138826, BPBM 138828); Agakauitai Islet, northwest (Station 195) side (47 specimens, BPBM 9672, BPBM 138896, BPBM 138899-900, BPBM 138902); Taravai Islet, in sand (Station 126) sweepings (13 specimens, BPBM 138882).

Remarks. – Specimens referable to *Anceyodonta sexlamellata* were collected on five islets. Further study of local variation is needed, since time did not permit full study of the 613 specimens. In several sets the umbilical width was not measured and only a few individuals had rib counts made. Only part of the adults from Stations 88 and 107 were utilized. There are obvious differences between populations (table LXX). Shells from Mangareva are much smaller than those from the other islets or the original Cuming material. The sets from Taravai and Agakauitai are quite depressed and have much wider umbilici than shells from Aukena and Akamaru. There is considerable variation in ribbing, the contrast between Aukena shells (Stations 88 and 102) and those from Akamaru (Station 107) being particularly large. Using just material available in Chicago, rib variations for four stations were:

Station	Mean	Range	SEM	Number of specimens
88	80.3	60-98	4.91	7
102	76.0	62-105	5.71	7
107	97.9	73-125	3.42	20
"Cuming material"	89.3	75-116	3.54	13

Some of these differences are statistically significant, but their biological significance is uncertain. Comparing Stations 102 and 107, with 25 df, "*t*" = 3.2628, and in comparing the "Cuming" material with Station 107, with 31 df, "*t*" = 1.6755. Other comparisons are less significant: between "Cuming material" and Station 88, with 18 df, "*t*" = 1.4946; and between Stations 88 and 102 there is no difference (with 12 df, "*t*" = 0.5689). Subspecific differentiation of at least the Taravai and Agakauitai shells from those found on Aukena and Akamaru may be justified when the material available is fully analyzed, but without more detailed study I prefer to withhold nomenclatural recognition.

The most significant variation was seen in the set from Vaituatai, about 1 mile north of Rikitea, Mangareva Islet (Station 197). In these shells (fig. 86e) the parietal barriers are reduced in size; there are no parietal traces; there is only a single columellar barrier; only four to six weak accessory palatals; and the characteristic sulci are reduced to absent. The very heavy columellar callus and position of the barriers are the same as in normal shells of *A. sexlamellata* and this seems to be only an extreme variant.

More specimens from old collections tended to have the sulci reduced (fig. 86a) than in material from the Mangarevan Expedition, but such small numbers are involved that sampling error may be responsible rather than morphological change. The prominence of the sulci is a highly variable character.

Description of *Patula* (*Endodonta*) *perarmata* Smith (1893, p. 165, figs.) from "St. Helena" is a matter of mislabelled specimens. The tablet on which the specimens were pasted contained one example of the European *Discus rotundatus* (Müller, 1774) and two specimens of *Anceyodonta sexlamellata*. I have selected the upper of the two specimens figured by Smith (*loc. cit.*) as lectotype and thus *Patula perarmata* Smith, 1893 becomes a synonym of *Anceyodonta sexlamellata*. I am not prepared to guess as to which islet the type material of *perarmata* came from and doubt that this name should be used for any eventually recognized subspecies in view of the complete absence of locality data.

Anceyodonta densicostata, new species (Cooke & Solem). Figure 87a-b.

Diagnosis. — Shell slightly larger than average, diameter 2.73-3.19 mm. (mean 3.00 mm.), with 5⅞-6⅝ relatively tightly coiled whorls. Apex and spire strongly elevated, rounded above, last whorl not descending more rapidly, H/D ratio 0.621-0.778 (mean 0.687). Umbilicus minute, last whorl barely or not decoiling, contained 6.93-29.6 times (mean 15.1) in the diameter. Postnuclear sculpture of fine, narrow, very crowded, protractively sinuated radial ribs, 95-114 (mean 104.4) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of very fine radial riblets, five to nine between each pair of major ribs, crossed by much finer and more crowded spiral riblets. No secondary spiral cording present. Sutures impressed, whorls strongly rounded above, slightly flattened basally. Aperture ovate, slightly flattened basally, inclined less than 10° from shell axis. Parietal barriers usually 5, often (15 per cent) 3, extending posteriorly beyond line of vision, with (50 per cent) or without (50 per cent) a superior accessory trace: upper parietal high and bladelike, weakly expanded above, with very gradual anterior descension; 2nd parietal, when present, a low threadlike trace for entire length; 3rd and 5th parietals with visible posterior quarter elevated, expanded and serrated on top, anterior three-quarters low and threadlike; 4th parietal, when present, low and threadlike for entire length. Parietal trace, when present, located just below parietal-palatal margin. Columellar barrier moderately recessed, elevated posteriorly and expanded above, with sinuated anterior descension to middle of columellar callus. Palatal barriers 4, extending slightly more than one-quarter whorl, with four to five accessory traces present: lower palatal equal in height to columellar, weakly expanded and serrated above, anterior descension simple; 2nd and 3rd palatals much higher, more broadly expanded above, with weakly sinuated anterior descension, reaching almost to left margin; 4th palatal reduced in height, a V-shaped ridge lying opposite 1st parietal. Palatal traces located between 1st and 2nd, 2nd and 3rd, 3rd and 4th with two traces above 4th palatal. Occasionally trace between 3rd and 4th palatals greatly reduced or absent.

Anceyodonta densicostata is closely related to *A. obesa,* apparently bearing the same relation to it that *A. soror* appears to have to *A. difficilis.* The absence of a subsutural sulcus, the very fine and crowded ribbing and the more open umbilicus are the main characters separating *A. densicostata* from *A. obesa.* The former normally has traces between the lower palatals, while the latter rarely does. Other species of similar size either have much more widely open umbilici (*A. andersoni* and *A. labiosa*) or 2 columellar barriers and many palatal traces (*A. sexlamellata*).

Description. — Shell larger than average, with 6¼ relatively tightly coiled whorls. Spire strongly elevated, rounded above, H/D ratio 0.677. Embryonic whorls 1⅜, with traces of microradial sculpture remaining. Postnuclear whorls with narrow, crowded, strongly protractively sinuated radial ribs, 95 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of extremely fine radial riblets, with traces of much finer and more crowded spiral riblets. Color light yellowish white with prominent, irregular, reddish-brown flammulations. Sutures moderately impressed, whorls strongly rounded above, slightly compressed laterally. Umbilicus minutely open, last whorl barely or not decoiling, contained 11.6 times in the diameter. Aperture ovate, somewhat compressed on basal margin, inclined about 10° from shell axis. Parietal barriers 5, extending posteriorly beyond line of vision, plus a deeply recessed spiral thread just below the upper parietal margin: 1st parietal high, gradually descending anteriorly, with rounded upper margin, pointing toward upper palatal; 2nd parietal very low and threadlike; 3rd parietal with anterior three-sixteenths whorl low and threadlike, becoming high, broadly expanded and minutely serrated posteriorly; 4th parietal a broadly rounded very low thread; 5th parietal similar in structure to 3rd with expanded portion and serrations slightly higher. Parietal trace located just below parietal-palatal margin. Apertural callus relatively weak, becoming stronger on columellar wall. Columellar barrier equal in height to 1st palatal, barely reaching past middle of umbilical callus, slanted slightly downward. Palatal barriers 4, with five accessory traces, extending beyond line of vision: 1st palatal moderately elevated with rounded and serrated top, reaching to middle of apertural callus; 2nd and 3rd palatals much higher, broadly rounded and minutely serrated on top, with sinuated anterior descension; 4th palatal a V-shaped ridge, much lower than 3rd, lying opposite upper parietal. Accessory palatal traces low and threadlike, located between 1st and 2nd, 2nd and 3rd, 3rd and 4th and two above 4th palatal. Height of holotype 2.07 mm., diameter 3.06 mm.

Holotype. — Gambier Islands: Mangareva, Station 277, Mangareva Islet, vicinity of Ganhutu. Collected by Donald Anderson on June 26, 1934. BPBM 138975.

Range. — Mangareva and Taravai Islets, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Mangareva Islet (Stations 142, 277), vicinity of Ganhutu (29 specimens, BPBM 9637, BPBM 138975); Taravai Islet (Station 126), in sand (1 specimen, BPBM 138883).

Remarks. — There was considerable variation in the number and prominence of the various parietal barriers. Of 20 adult or nearly adult specimens, 17 had 5 parietals and three had 3 parietals, with numbers 2 and 4 absent. Ten specimens had an accessory parietal trace, 10 lacked the trace. Nearly all specimens of *Anceyodonta densicostata* were found in fossil deposits near Ganhutu on Mangareva Islet. Surprisingly enough, a single specimen was recovered from sand on Taravai Islet (BPBM 138883). This specimen has a relatively wide umbilicus, contained 6.9 times in the diameter, and there are only 3 parietals. Since this reduction also was observed in Ganhutu shells, it is not deemed significant.

Specimens of *A. obesa* and *A. densicostata* on Mangareva are extremely similar in size, shape, and barriers. All individuals could be separated on the basis of the subsutural sulcus and less crowded sculpture in *A. obesa.* It is quite possible stratigraphic collections would demonstrate that *A. densicostata* is a local derivative of *A. obesa.*

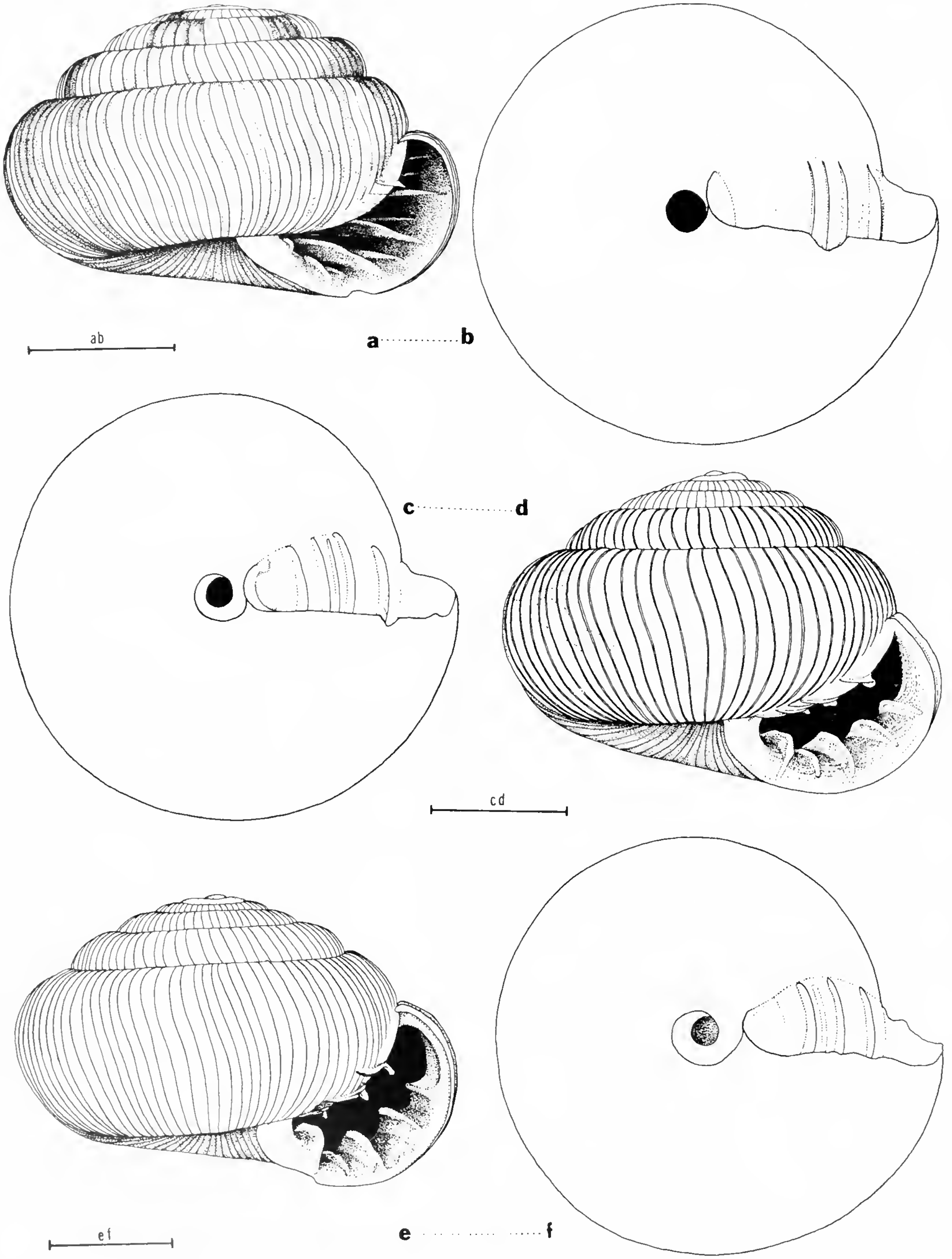

FIG. 87. **a-b**, *Anceyodonta densicostata*, new species. Station 277, Ganhutu, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 138975; **c-f**, *Anceyodonta labiosa*, new species. *c-d*, Station 88, Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 9414; *e-f*, Station 88, Aukena Islet, Mangareva, Gambier Islands. Form with 3 parietals. Paratype. BPBM 9413. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

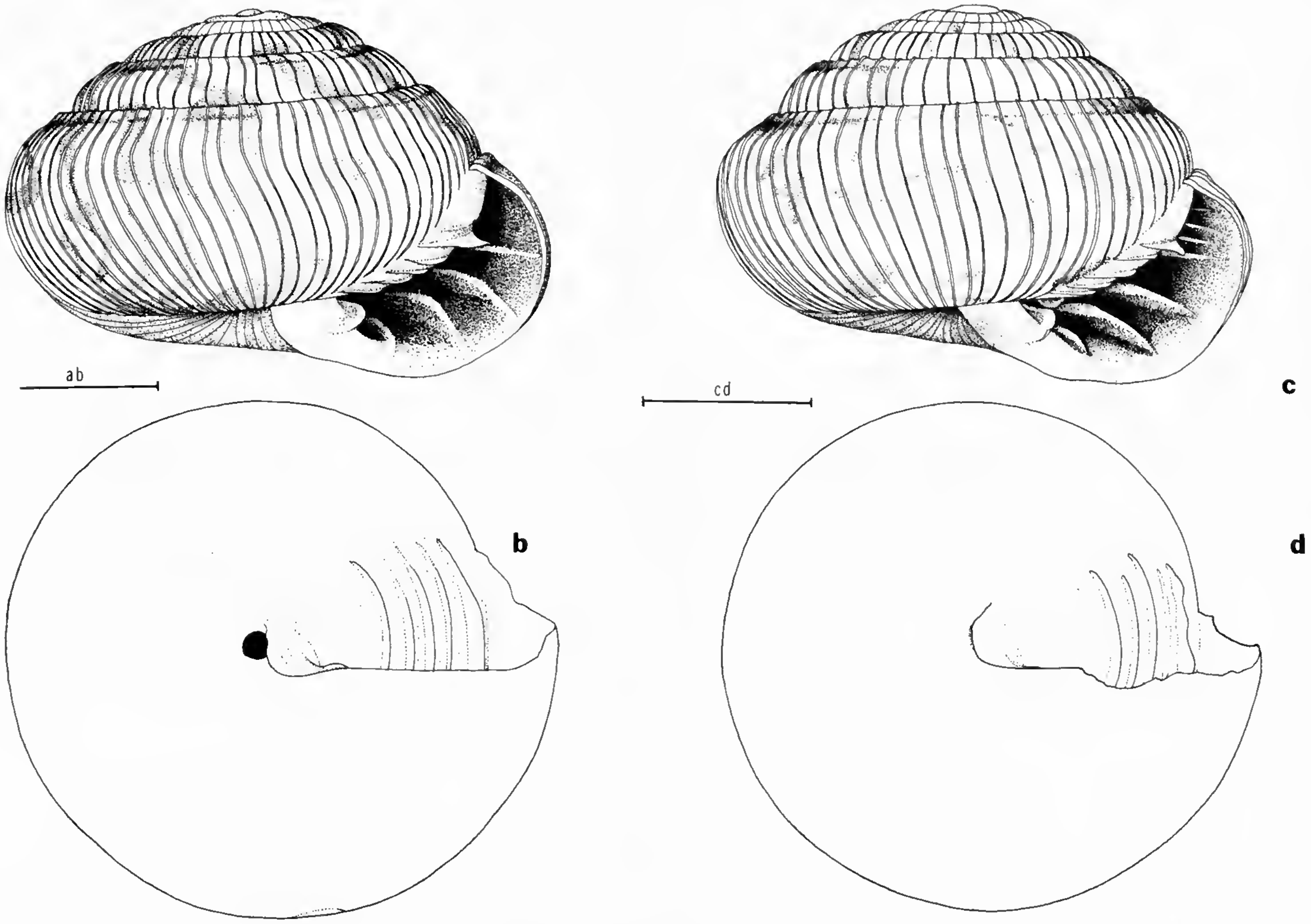

FIG. 88. *Anceyodonta obesa,* new species: **a-b**, Station 88, Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 138706; **c-d**, Station 142, Ganhutu, Mangareva Islet, Mangareva, Gambier Islands. Paratype. BPBM 138941; Palatal traces omitted from figure of holotype. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Anceyodonta obesa, new species. Figures 88a-d; 89a-f.

Diagnosis. – Shell larger than average, diameter 2.63-4.01 mm. (mean 3.14 mm.), with 5⅜-7⅝ normally to rather tightly coiled whorls. Apex and spire moderately to strongly elevated, normally rounded above, last whorl not descending more rapidly, H/D ratio 0.561-0.805 (mean 0.715). Umbilicus minute (contained more than 15 times in the diameter) to imperforate, normally closed or too narrow to measure. Postnuclear sculpture of narrow, widely spaced to crowded, almost vertically sinuated radial ribs, 47-106 (mean 79.6) on the body whorl, whose interstices are 2-7 times their width. Microsculpture of extremely fine radial riblets, four to ten between each pair of major ribs, crossed by much finer and more crowded spiral riblets. No secondary spiral cording present. Sutures shallow, whorls strongly rounded on basal margin, slightly compressed laterally and basally, a weak to usually prominent subsutural sulcus present. Aperture ovate, slightly compressed laterally and basally, inclined about 5° from shell axis. Parietal barriers normally 5, rarely reduced to 3 in number by loss of 2nd and 4th parietals, occasionally with one or more accessory parietal traces, extending posteriorly beyond line of vision: upper parietal high, slender, bladelike, with gradual descension over anterior visible third; 2nd parietal a low, often reduced, threadlike trace; 3rd and 5th parietals with anterior visible two-thirds raised threadlike ridges, posterior portion elevated to height of 1st parietal, expanded and serrated above on visible posterior quarter; 4th parietal, when present, a reduced threadlike trace equal in size to 2nd. Parietal traces, when present, situated above upper parietal near parietal-palatal margin. Columellar barrier a prominent, crescentic ridge located on columellar wall, angling slightly downward across columellar callus, stopping short of lip margin. Palatal barriers 4, extending about three-sixteenths of a whorl, with zero to six accessory traces: lower palatal greatly reduced in height, an elevated threadlike ridge stopping well short of apertural margin; 2nd and 3rd parietals elevated, weakly expanded and flattened above posteriorly with very gradual descension over anterior half, somewhat recessed within aperture; 4th palatal a much lower V-shaped ridge, less recessed within aperture, lying opposite upper parietal. Palatal traces highly variable in number, many specimens with no traces, others with two or three present above 4th palatal, some with one or two present between various lower palatals, and a few with large palatal traces present between each major palatal and three above 4th palatal.

Anceyodonta obesa differs from the generally much larger *A. hamyana* in having 5 parietal barriers (rarely only 3), usually is with a strong subsutural sulcus and has more closely spaced radial ribs (about 8/mm. in *obesa,* 6.34/mm. in *hamyana*). The specimens of *A. obesa* with accessory palatal traces can easily be confused with *A. difficilis* and *A. densicostata.* In *A. difficilis* the columellar barrier twists distinctly onto the basal lip and is removed from the umbilical wall for the entire line of vision, while *A. obesa* has a moderately low columellar ridge that, at most, slants downward across the umbilical wall toward the basal lip. *A. densicostata* lacks a subsutur-

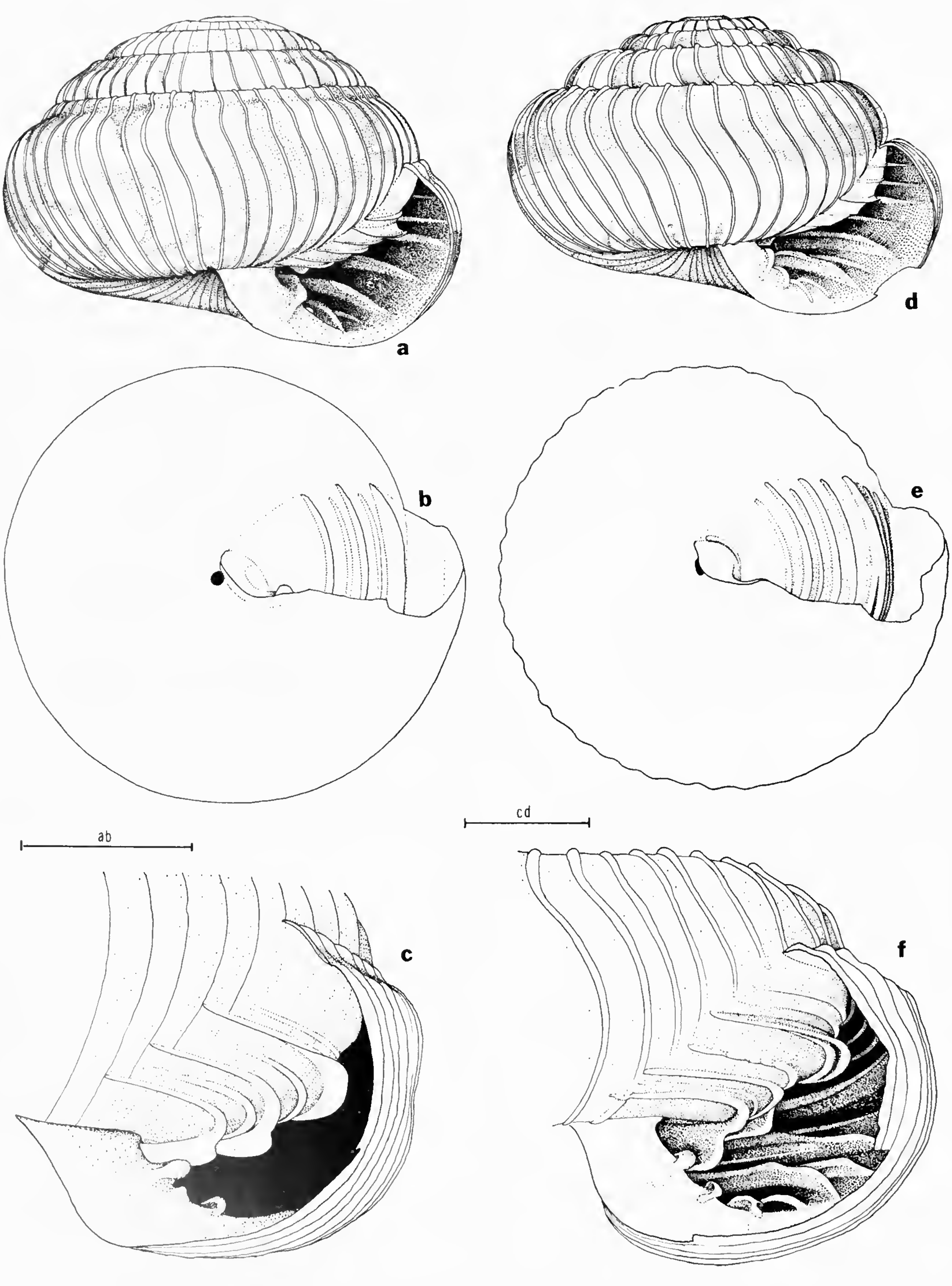

FIG. 89. *Anceyodonta obesa,* new species: **a-c,** Station 142, Ganhutu, Mangareva Islet, Mangareva, Gambier Islands. Paratype. BPBM 138943; **d-f,** Station 189, north end of Rikitea, Mangareva Islet, Mangareva, Gambier Islands. Paratype. BPBM 141692. Extreme development of palatal traces and ribbing. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

al sulcus and averages 11.1 ribs/mm. on the body whorl.

Description. – Shell quite large with slightly more than 6¼ relatively loosely coiled whorls. Spire and apex strongly elevated, obtusely rounded above, H/D ratio 0.680. Embryonic whorls 1⅜, sculpture eroded. Remaining whorls with relatively wide, protractively sinuated radial ribs, 78 on the body whorl, whose interstices are 2-3 times their width. Microsculpture consisting of fine radial riblets, six to ten between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures relatively shallow, whorls somewhat flattened above with a distinct subsutural sulcus. Umbilicus nearly closed by reflection of columellar lip, contained 25.7 times in the diameter. Aperture compressedly ovate, basal margin flattened and somewhat flattened subperipheral margin. Callus extremely heavy on columellar lip, gradually reduced in size and absent from above periphery of body whorl. Parietal barriers 5, extending more than one-quarter whorl, with one small superior trace: upper parietal quite high, bladelike, very slightly rounded above, with very gradual anterior descension; 2nd parietal a low threadlike ridge, extending beyond the line of vision; 3rd parietal threadlike for one-eighth whorl, becoming a high bladelike lamella posteriorly; 4th parietal a low, threadlike ridge for its visible length; 5th parietal threadlike for first one-eighth whorl, becoming moderately high and lamellate posteriorly with rounded and slightly expanded top. Parietal trace located just above upper parietal. Columellar barrier as high as lower palatal, a broadly rounded ridge reaching across the columellar callus and twisted slightly downwards. Palatal barriers 4, extending about three-sixteenths of a whorl, with three faint accessory traces above the upper palatal: lower palatal a threadlike raised ridge almost as high as columellar barrier; 2nd palatal very high and bladelike, slightly expanded above, gradually descending over anterior third to apertural callus; 3rd palatal similar in form to 2nd but a little lower in height; 4th palatal a lower V-shaped ridge opposite the upper parietal with the raised portion extending nearer the aperture. Height of holotype 2.30 mm., diameter 3.39 mm.

Holotype. – Gambier Islands: Mangareva, Station 88, Aukena Islet, along trail near gap. Collected by Donald Anderson and C. M. Cooke, Jr., on May 28, 1934. BPBM 138706.

Range. – Aukena, Mangareva, Agakauitai, and Akamaru Islets, Mangareva, Gambier Islands.

Paratypes. – Same as list of material.

Material. – Mangareva: Aukena Islet (Stations 82, 88, 102, 103) in the vicinity of the gap (302 specimens, BPBM 9417, BPBM 9664-7, BPBM 138684, BPBM 138705-6, BPBM 138755, BPBM 138797); Mangareva Islet (Stations 105, 142, 277) vicinity of Ganhutu (65 specimens, BPBM 9634, BPBM 9640-1, BPBM 9643, BPBM 138941, BPBM 138943, BPBM 138968, BPBM 138970, BPBM 138973-4, BPBM 140993); Mangareva Islet (Station 197) northeast of Vaituatai Bay (6 specimens, BPBM 9645, BPBM 139014); Mangareva Islet (Stations 155, 156, 187, 189) vicinity of Rikitea (36 specimens, BPBM 9650, BPBM 9656, BPBM 9658, BPBM 9676, BPBM 9680, BPBM 9704, BPBM 139002, BPBM 139004, BPBM 141407, BPBM 141667, BPBM 141692-3); Agakauitai Islet (Station 195), northwest side (4 specimens, BPBM); Akamaru Islet (Station 97), northwest side (3 specimens, BPBM 138827).

Remarks. – On both Aukena and Mangareva Islets there is considerable variation in size, shape, and apertural barriers (table LXX). The frequency of the variants differs on the two islands. While many specimens can be sorted into apparently different forms, intergrading examples were seen and probably only extreme individual variation is involved.

On Aukena Islet the great majority (210 of 302 specimens) have the form of the holotype (fig. 88a, b) with either faint traces of accessory palatal traces above the upper palatal (as in fig. 88c) or, more commonly, without any such lamellar traces (fig. 88a). Three specimens (BPBM 9666) have strong accessory traces developed between the major palatals (as in fig. 89d). A number of individuals approached the size of the smaller form that was so common on Mangareva Islet, but most of the remainder were probably juvenile examples.

On Mangareva Islet, variation is more extensive and complex. Only a very few (eight of 107) individuals reach the size of the Aukena examples. These varied greatly in the number of major and minor parietals. Most of these larger individuals from Ganhutu (BPBM 138941, Station 142, 1 specimen), Rikitea (BPBM 139002, Station 155, 3 specimens), and Vaituatai (BPBM 139014, Station 197, 2 specimens) are only moderately elevated with looser coiling than in the remaining shells (fig. 88c). The majority of Mangareva Islet *A. obesa* were distinctly smaller in size (table LXX), usually with more closely spaced sculpture (not the figured example), more tightly coiled whorls, and with more prominent margining on the suture (fig. 89a). In material of *A. obesa* from Station 88, there were 8.2 ribs/mm.; from Stations 142 and 277, there were 8.8 ribs/mm. The closer spacing of the sculpture is not reflected in greater number of ribs (table LXX) since with 24 df, "*t*" = 0.791 in respect to rib counts from Stations 142 plus 277 and 88. Generally, accessory traces were present above the upper palatal and there were one or two low, broad ridges between the lower palatal barriers. In eight specimens, however, the lower ridges had been replaced by accessory traces between the parietals. Individuals with these characters could easily be confused with *Anceyodonta difficilis*, but can be separated by the characters of the columellar barrier detailed above under the "Diagnosis." The size and shape differences between the Aukena and Mangareva shells are highly significant. With 62 df "*t*" = 5.8735 in respect to diameters and "*t*" = 3.7280 when comparing H/D ratios. No nomenclatural recognition seems necessary.

Three specimens from the Rikitea area (Stations 187, 189) had very widely spaced radial ribbing and the apertural barriers were somewhat modified (fig. 89d-f). Accessory parietal traces were present, the 1st and 3rd parietals both were bifid posteriorly and the accessory traces were greatly enlarged in size and prominence. The differences of the three specimens are all a matter of degree since intermediates between this form and typical *obesa* of Mangareva Islet were seen.

The few specimens from Akamaru and Agakauitai are in the same size range as the Aukena examples. The larger and smaller forms of Mangareva were found at the same stations with the latter predominating. A similar situation is found in respect to *A. hamyana,* which also has a smaller form associated with a larger at both Ganhutu and Rikitea. These variations may represent temporally separated populations, with the smaller coming from unfavorable years and the larger from more favorable periods. The Mangareva shells were mostly found on open ground, thus probably coming from a series of populations, while those from single caves on Aukena probably were from much more homogeneous samples.

Anceyodonta labiosa, new species. Figure 87c-f.

Diagnosis. — Shell quite large, diameter 3.06-4.05 mm. (mean 3.55 mm.), with 6 - 6⅞ tightly coiled whorls. Apex and spire strongly and almost evenly elevated, slightly rounded, H/D ratio 0.658-0.735 (mean 0.700). Umbilicus open, narrow, almost regularly decoiling, contained 5.48-9.80 times (mean 7.24) in the diameter. Postnuclear sculpture of prominent, crowded, almost vertical radial ribs, 78-100 (mean 91.0) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of very fine radial riblets, six to ten between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of low, rather closely set spiral cords. Sutures shallow, whorls strongly rounded above and on basal margin, almost evenly rounded on outer margin, no trace of a subsutural sulcus. Aperture ovate, slightly compressed laterally, inclined about 5° from shell axis. Parietal barriers 3 (36.4 per cent) or 4 (63.6 per cent), extending slightly less than three-sixteenths of a whorl, rarely with one or two accessory parietal traces: upper parietal a high slender blade, weakly expanded and serrated posteriorly, with gradual descension over anterior third; 2nd parietal with anterior half low and threadlike, broadly expanded in mid-section, with posterior crescentic lamellar blade arising from expanded basal portion, occupying posterior third of tooth; 3rd parietal identical in structure to 2nd, except posterior elevated portion shorter and lower; 4th parietal, when present, a low threadlike trace. Accessory parietal traces rarely present between 2nd and 3rd, 3rd and 4th parietals. Columellar barrier a high crescentic blade, displaced onto basal margin, descending abruptly to lip edge. Palatal barriers 4, extending one-eighth whorl, rarely one or two accessory traces: lower palatal greatly reduced in height, a raised lamellar ridge; 2nd and 3rd palatals very high, slightly flattened above, with gradual anterior descension; 4th palatal reduced in height, a V-shaped ridge, lying opposite 1st parietal. Palatal traces, when present, either both above 4th palatal, or one above 4th palatal and the other between 2nd and 3rd palatals.

The general appearance of *Anceyodonta labiosa* is very similar to that of *A. hamyana,* but the descension of the columellar barrier to the basal lip in *A. labiosa* at once separates them. The general lack of any accessory palatal traces, much larger size and fewer parietal barriers separate *A. labiosa* from *A. soror* and *A. difficilis*, the other species with similar columellar barrier displacement.

Description. — Shell much larger than average, with 6¼ tightly coiled whorls. Spire very strongly elevated, sides slightly rounded, H/D ratio 0.735. Embryonic whorls 1⅝, sculpture eroded. Remaining whorls with relatively prominent, close set, nearly vertical radial ribs, 84 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of extremely fine radial riblets, six to ten between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of well-defined spiral cords. Sutures shallow, whorls relatively flattened above, rounded on periphery and base, no subsutural sulcus present. Umbilicus very narrow, last whorl decoiling a little more rapidly, contained 9.80 times in the diameter. Color nearly gone from shell, with traces of reddish flammulations remaining. Aperture ovate, with evenly rounded outer margin, inclined about 5° from shell axis. Parietal barriers 4, extending less than three-sixteenths of a whorl, with low accessory threads between parietals 2 and 3, 3 and 4: 1st parietal elevated, slender, weakly expanded on top, with gradual anterior descension; 2nd and 3rd parietals broadly flattened anteriorly with lamellate posterior position arising medially on the flattened lamellar plate, expanded and serrated on elevated posterior third; 4th parietal with same structure, but posterior part only slightly elevated. Columellar barrier short, very high, crescentic, displaced onto basal lip, reaching apertural margin. Palatal barriers 4, very high, extending about one-eighth whorl: lower a short threadlike ridge; 2nd and 3rd very high, almost crescentic; 4th a much lower V-shaped ridge lying opposite upper parietal. Height of holotype, 2.37 mm., diameter 3.23 mm.

Holotype. — Gambier Islands: Mangareva, Station 88, Aukena Islet, along trail near gap. Collected by Donald Anderson and C. M. Cooke, Jr., on May 28, 1934. BPBM 9414.

Range. — Aukena and Akamaru Islets, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Aukena Islet (Station 88), along trail near gap (25 specimens, BPBM 9413-4); Akamaru Islet (Station 97), on northwest side (2 specimens, BPBM 138829).

Remarks. — The holotype is a relatively small, quite high example with two accessory parietal traces, but it is in the best condition of all specimens. Of the 27 shells, nine had 3 parietals and 18 had 4. In most examples, the spiral sculpture is very weak. The two palatal traces are usually above the 4th palatal, but a few examples lacked all traces and some had one above the 4th palatal and one between the 2nd and 3rd.

The large size, short barriers, and relatively elevated shape are quite distinctive. The displacement of the columellar barrier onto the basal lip at once separates *A. labiosa* from the other large species.

Anceyodonta hamyana (Ancey, 1889). Figure 90a-f.

Pitys hamyana Ancey, 1889, Le Naturaliste, **3**, p. 84 — Gambier Islands; Pilsbry, 1892; Man. Conchol., (2), **8**, p. 95.

Endodonta (Thaumatodon) hamyana (Ancey), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Diagnosis. — Shell very large, diameter 3.09-4.93 mm. (mean 3.98 mm.), with 5¼ - 7 normally coiled whorls. Apex and spire moderately to strongly elevated, usually rounded above, last whorl not descending more rapidly, H/D ratio 0.557-0.773 (mean 0.667). Umbilicus generally barely perforate, rarely moderately open or completely closed, contained 7.31-64 times (mean 22.2) in the diameter. Postnuclear sculpture of narrow, prominent, rather closely set radial ribs, 60-120 (mean 79.3) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of very fine radial riblets, five to nine between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Usually no secondary spiral cording. Sutures well impressed, whorls strongly rounded above and on umbilical margin, slightly compressed laterally and

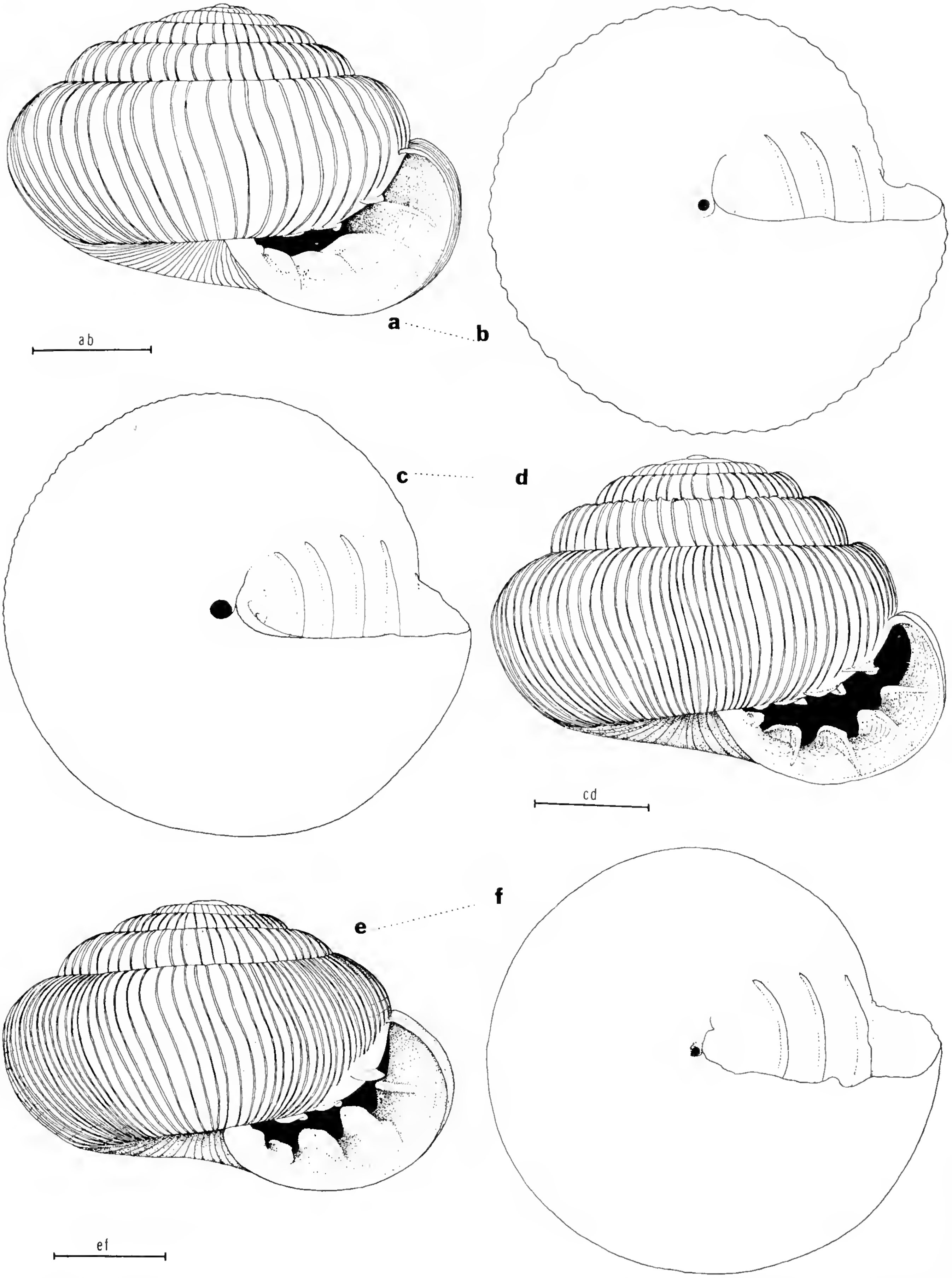

FIG. 90. *Anceyodonta hamyana* (Ancey): **a-b**, Station 142, Ganhutu, Mangareva Islet, Mangareva, Gambier Islands. BPBM 138938; **c-d**, Station 82, Aukena Islet, Mangareva, Gambier Islands, BPBM 138699; **e-f**, Station 142, Ganhutu, Mangareva Islet, Mangareva, Gambier Islands. BPBM 138939. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

basally, no subsutural sulcus present. Aperture ovate, slightly compressed laterally and basally, inclined less than 10° from shell axis. Parietal barriers 3 or 4, extending posteriorly almost one-quarter whorl, without accessory traces: upper parietal a high lamellar blade, weakly expanded and serrated posteriorly, with gradual descension over anterior half; 2nd and 3rd parietals with anterior third threadlike, posterior portion elevated to height of 1st, strongly expanded and serrated above on posterior third; 4th parietal similar in structure to 3rd, with posterior elevated portion slightly reduced in length and height. Columellar barrier a raised threadlike ridge, twisting slightly downward partway across columellar callus. Palatal barriers 4, extending three-sixteenths of a whorl, without accessory traces present: lower palatal equal in height to 2nd and 3rd, weakly flattened above, with rather gradual descension over anterior third; 2nd and 3rd parietals less recessed within aperture, more elongated and flattened above, with more gradual anterior descension; 4th palatal reduced in height, a V-shaped ridge, lying opposite 1st parietal. No palatal traces present.

The very large size, only moderately elevated spire, presence of 3 or 4 parietals, small columellar callus and barrier, and lack of accessory palatal traces combine to separate *Anceyodonta hamyana* from all other Mangarevan endodontids. *A. labiosa* differs most obviously in having the columellar barrier displaced onto the basal lip. *A. obesa* is smaller and higher with generally more crowded sculpture and has (usually) 5 parietals. The 2 columellar barriers, very thick columellar callus, supraperipheral sulcus, usually very high spire and numerous accessory palatal traces separate *A. sexlamellata* from *A. hamyana*.

Description. — Shell quite large, with 5¾ moderately tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.634. Apical whorls 1⅜, sculpture of moderately prominent, slightly protractive radial ribs with traces of finer radial and spiral ribbing barely visible between. Postnuclear whorls with broad, rounded, prominent, slightly protractively sinuated radial ribs, 78 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of relatively prominent radial riblets crossed by barely visible, much smaller spiral riblets with a secondary sculpture of a few narrow, widely spaced spiral cords visible on part of body whorl and base of shell. Sutures moderately deep, whorls strongly rounded above with almost evenly rounded outer margins. Umbilicus barely perforate, strongly constricted by growth of whorls and reflection of basal lip, contained 20 times in the diameter. Aperture compressedly ovate with slightly flattened basal margin, inclined less than 5° from shell axis. Parietal barriers 4, extending slightly more than one-quarter whorl: upper high, lamellate posteriorly with very gradual anterior descension; 2nd and 3rd with lamellate portion extending less far anteriorly; lower parietal greatly reduced in height with long, threadlike anterior portion. Columellar wall with thick, heavy callus surmounted by single, ridgelike, moderately recessed columellar barrier that slants slightly downwards across midportion of callus. Palatal barriers 4, extending slightly more than one-eighth whorl, lower 3 high, ridgelike, more gradually descending anteriorly from bottom to top: upper a much lower, threadlike ridge situated opposite upper parietal. All major barriers slightly rounded and minutely barbed above. Height of holotype 2.50 mm., diameter 3.45 mm.

Holotype. — Gambier Islands. Collected during the voyage of the "Astrolabe." Musée Royal d'Histoire Naturelle de Belgique, ex Dautzenberg, Geret, Ancey, and Dupuy collections.

Range. — Aukena, Mangareva, Agakauitai, Taravai, Akamaru Islets, Mangareva, Gambier Islands.

Material. — Gambier Islands: Mangareva; Aukena Islet (Stations 82, 88, 102, 103) on open ground (164 specimens, BPBM 9412, BPBM 9415, BPBM 9667, BPBM 138683, BPBM 138699-700, BPBM 138703, BPBM 138752-3, BPBM 138795); Agakauitai Islet (Station 195) on sandy soil (8 specimens, BPBM 9670, BPBM 138897-8); Taravai Islet (Stations 123, 126) on cliffs (4 specimens, BPBM 9674, BPBM 138880); Akamaru Islet (Station 107) on sandy soil (2 specimens, BPBM 138851); Mangareva Islet, Ganhutu (Station 142, 277) (44 specimens, BPBM 9639, BPBM 138938-40, BPBM 138966-7, BPBM 138969), Mangareva Islet (Station 197), Vaituatai Bay (6 specimens, BPBM 139010-1); Mangareva Islet, vicinity (Station 155, 187, 189) of Rikitea (16 specimens, BPBM 9648, BPBM 9678, BPBM 139000, BPBM 141664-5, BPBM 141689-90).

Remarks. — Ancey based the species *Pitys hamyana* upon a single shell from the Gambier Islands that was in a lot of *Anceyodonta sexlamellata*. The original description of this previously unfigured species indicated the presence of 4 parietal and 5 palatal barriers, "four below the periphery" and "a smaller one above." Ancey's type is a specimen with 4 parietal barriers. It is obvious that he considered the columellar as one of his lower 4 palatals.

Although reported from all five major islets of Mangareva, there are considerable differences in the abundance of this species on the various islands (table LXXI), and of the proportionate representation of those with 3 and 4 parietal barriers (table LXXIII).

Specimens were most common on Aukena Islet (table LXXIII) with three individuals of the 4-barrier form (fig. 90d) for every one of the 3-barrier variety (fig. 90a, e). Distribution was not random, since at Station 82 only the 4-barrier form was found, while at Station 88, there were nine of the 3-barrier variety for every one of the 4-barrier. On Mangareva Islet only four out of 66 specimens had 4 parietals, the remaining 62 having 3. During the original study of this material, I had the impression that shells with 4 parietals tended to be slightly higher and with a smaller umbilical perforation than those with 3 parietals, but I am uncertain whether this correlation is not based on size variation later discovered in *A. obesa* rather than barrier count. Possibly there is a stratigraphic difference between the forms, but present information does not permit any conclusions.

In the Ganhutu area of Mangareva Islet (Stations 142, 227) and near Rikitea (Station 187) some individuals had a heavier apertural callus and stronger spiral sculpture with a slight tendency toward flattening of the upper whorls (fig. 90e). No division of the entire population from these areas into two forms could be made and again I consider this to be an extreme of individual variation. Similar variants were seen in *A. obesa*.

TABLE LXXIII. - BARRIER VARIATION IN ANCEYODONTA HAMYANA

Islet	Station Number	Number of Parietal Barriers Three	Four
Aukena	82		98
"	88	36	4
"	102	5	15
"	103		3
Agakauitai	195	6	2
Taravai	126	2	
"	123		2
Akamaru	107		2
Mangareva (Ganhutu)	142	13	
" "	277	31	
" (Vaituatai)	197	6	
" (Rikitea)	155	2	
" "	189	6	2
" "	187	4	1
" "	---		1
Aukena	---		1
TOTALS		111	131

Genus **Cookeconcha,** new genus

Endodontidae with typical apical sculpture in those species with prominent palatal barriers (except *ringens*), absent on first half to whole apical whorl in species with reduced or no palatals. Postnuclear whorls with narrow-to-wide, generally prominent, protractive radial ribs, reduced only in *paucicostata*. Microsculpture typical, secondary cording only in *decussatulus* and *lanaiensis* (faintly). Some species (*hystrix*) with long periostracal hairs. Apex and spire flat or depressed (seven species), weakly elevated (seven species), moderately elevated only in *contortus* and *thwingi*. H/D ratio near 0.500 only in *henshawi*, *contortus*, *subpacificus*, *thwingi*, and *nudus*. Body whorl evenly rounded in most species, laterally compressed only in *subpacificus* and an undescribed species, compressed above and below periphery in *thaanumi*, *decussatulus*, and *lanaiensis*, greatly modified in *stellulus*. A weak supraperipheral sulcus present in *hystricellus*, extensive sulci in *stellulus*, none in other species. Whorls 4-5½, number closely correlated with size. Umbilicus widely open, generally V-shaped, moderately decoiling, margins rounded, last whorl sometimes decoiling more rapidly, contained 2.50-3.50 times in the diameter (narrower only in *paucicostatus*, *nudus*, and some *hystricellus*). Size minute to very large. Parietal barriers 2, varying from quite large with upper bifid to having the lower lost with upper a threadlike ridge. Columellar barrier normally present only in *henshawi*, *cookei*, and some *hystricellus*. Palatal barriers 4 or 5 in smaller species (*henshawi*, *cookei*, *nudus*, *contortus*, *ringens*), reduced in size and variable in number in *elisae*, *luctiferus*, *hystricellus*, and *stellulus*, absent in other species. Pallial region typically Endodontidae. Hermaphroditic duct straight or convoluted, talon with globular head and short, thick shaft. Penial retractor arising from diaphragm, inserting directly on head of penis. Vas deferens entering penis subapically, between pilaster U. Penis of varying length, without apical extension, internally either with narrow, elongated pilasters (*jugosus*) as in *Endodonta* or *Nesophila*, or shortened and enlarged (*hystrix*, *hystricellus*) as in *Australdonta*. Jaw consisting of numerous, partly to almost completely fused, narrow plates. Radula atypical in its extremely elongated teeth and equal cusping of the marginals, which have square, rather than rectangular plates.

Type species. — *Helix hystrix* Pfeiffer, 1846.

The diverse species grouped here show trends quite different from those in the related genus *Endodonta*. The latter species retain prominent apertural barriers, have the umbilicus U-shaped and used as a "brood chamber," show a strong tendency toward loss of all sculpture, have developed a keeled periphery, and are strictly terrestrial, living under twigs and dead leaves (Pilsbry and Vanatta, 1906, p. 783) or in talus slopes (Cooke, 1928, p. 14). *Cookeconcha* shows a marked tendency towards loss of the apertural barriers, has the umbilicus V-shaped and regularly

TABLE LXXIV. - LOCAL VARIATION IN COOKECONCHA

Name	Number of Specimens	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
subpacificus USNM 562090	1	77	0.97	1.86	0.522	4	3.53	2	?	?
henshawi FMNH 46563	3	48.3±1.45 (46-51)	0.96±0.883 (0.92-1.01)	1.79±0.053 (1.71-1.89)	0.538±0.0001 (0.537-0.539)	3 5/8 (3 1/2-3 3/4)	3.27±0.012 (3.25-3.29)	2	1	4+1
cookei ANSP 158823	1	60	1.24	2.29	0.538	4 5/8	3.08	2	1	4
thwingi FMNH 46466	3	66.7±0.11 (65-70)	1.15±0.078 (1.04-1.30)	2.30±0.110 (2.12-2.50)	0.499±0.0151 (0.488-0.520)	4 1/4- (4-4 1/2)	2.66±0.040 (2.62-2.74)	2	0	5+2
nudus FMNH 46422, FMNH 73197, FMNH 90319	15	83.3±1.51 (75-92)	1.67±0.024 (1.45-1.81)	3.35±0.022 (3.22-3.49)	0.497±0.0051 (0.449-0.524)	4 3/8- (4 1/2-5)	3.68±0.040 (3.38-3.92)	2	0-1	5
contortus FMNH 46603, Cardiff	4	80.8±0.14 (77-87)	2.01±0.136 (1.74-2.30)	3.88±0.098 (3.72-4.14)	0.516±0.0235 (0.465-0.556)	5 1/2 (5 1/4-5 3/4)	3.29±0.086 (3.14-3.50)	2	0	4-5
ringens BMNH 1900.12.18.1374	5	51.2±5.14 (41-70)	1.82±0.039 (1.68-1.88)	4.14±0.126 (3.91-4.61)	0.439±0.0095 (0.407-0.456)	5 1/4 (5 1/8-5 1/2)	3.39±0.093 (3.05-3.60)	2+0-1	0	4-5
luctiferus FMNH 46255, FMNH 73194, FMNH 90618	9	51.0±2.13 (42-60)	2.07±0.063 (1.81-2.47)	4.51±0.138 (3.91-5.23)	0.460±0.0064 (0.427-0.496)	5 3/8- (4 7/8-5 3/4)	3.49±0.108 (3.33-4.19)	2	0-1	1-2-3-4
hystricellus FMNH 116893	6	48.0±1.93 (43-55)	2.03±0.060 (1.81-2.24)	4.98±0.088 (4.64-5.20)	0.408±0.0091 (0.377-0.439)	5 3/8- (5 1/4-5 1/2)	2.76±0.060 (2.64-3.04)	2	0-1	3
FMNH 116894	4	REDUCED	2.74±0.140 (2.57-3.16)	6.09±0.149 (5.86-6.48)	0.449±0.0144 (0.417-0.487)	5 1/8- (5-5 1/4)	4.06±0.034 (3.74-4.38)	2	0	4

TABLE LXXIV, CONTINUED

stellulus FMNH 155099	1	19	1.58	4.28	0.369	4 1/4	3.10	2	0	3
paucicostatus FMNH 46435	1	24	1.45	3.06	0.473	4 1/8-	3.88	2	0	0
thaanumi FMNH 46237, FMNH 73193	6	51.7±1.87 (46-57)	2.35±0.154 (1.97-2.89)	4.96±0.210 (4.44-5.53)	0.471±0.0142 (0.435-0.524)	5 1/4 (4 7/8-5 1/2)	3.39±0.120 (3.07-3.73)	2	0	0
hystrix FMNH 91890	9	41.3±3.86 (31-70)	2.38±0.078 (2.04-2.70)	5.01±0.128 (4.61-5.46)	0.475±0.0147 (0.431-0.577)	5+ (4 5/8-5 1/2)	2.94±0.139 (2.63-3.94)	1-2	0	0
decussatulus FMNH 46605, FMNH 90636	3	64.7±2.34 (60-67)	1.37±0.011 (1.35-1.38)	3.52±0.019 (3.49-3.55)	0.389±0.0037 (0.383-0.396)	4 1/4- (4 1/8-4 1/4)	3.31±0.056 (3.24-3.42)	1	0	0
Australia C37190	3	71.0±2.08 (67-74)	1.53±0.029 (1.48-1.58)	4.00±0.140 (3.82-4.28)	0.384±0.0108 (0.364-0.405)	4 1/2+ (4 1/2-4 3/4)	3.19±0.116 (3.02-3.41)	1	0	0
lanaiensis BMNH 1900.12.18.1521 BMNH 1900.12.18.1376-80	6	64.3±2.63 (50-72)	1.77±0.059 (1.55-1.97)	4.72±0.115 (4.24-5.10)	0.374±0.0089 (0.354-0.414)	4 1/2+ (4 1/2-4 3/4)	3.23±0.084 (2.98-3.45)	1-2	0	0
jugosus FMNH 116899	7	62.6±3.30 (56-80)	2.45±0.060 (2.30-2.70)	5.90±0.223 (5.26-6.91)	0.417±0.0087 (0.390-0.463)	5 1/8+ (4 3/4-5 5/8)	2.48±0.029 (2.39-2.58)	1	0	0
FMNH 117043	6	- - - -	2.83±0.099 (2.63-3.29)	6.03±0.077 (5.86-6.32)	0.469±0.0111 (0.446-0.521)	5 1/4- (5-5 3/8)	2.84±0.076 (2.70-3.20)	1	0	0

decoiling without developing a U-shaped brood chamber, retains major radial ribbing, but shows a tendency towards loss of apical sculpture, never has a keeled periphery, and will live under bark on dead stumps and logs (Pilsbry and Vanatta, 1906, p. 783), in heavy moss on stones and trees (*pers. observation*), as well as in the dead leaf habitat. *Nesophila* probably is derived from a form very similar to *Cookeconcha jugosus,* and is specialized in the splitting of the parietals into threadlike traces plus shouldering of the umbilical margin.

Cookeconcha and *Endodonta* share the bifid upper parietal, otherwise seen only in the Raivavae Island *Minidonta gravacosta* and *M. micraconica,* plus the Mangarevan *Anceyodonta alternata* and *A. andersoni.* In these species the bifidity is distinctly on the lower side of the main blade (fig. 65d, e), while in the Hawaiian taxa it is much closer to the expanded upper edge and shows a distinct tendency to fuse with the main blade in the larger species of *Cookeconcha* and *Endodonta.*

Cookeconcha is unique among the Pacific Island Endodontidae in its tendency toward loss of the early apical sculpture while retaining the postnuclear sculpture. Its tendency toward reduction of the apertural barriers is more persistant and extends further than in *Libera* and thus parallels *Nesodiscus.*

Anatomically, the species show differences that in other areas are taken, together with conchological data, to indicate generic level separation. The four populations from Oahu, *hystricellus, hystrix,* and two unnamed species, one (BPBM 23902) most similar to *hystrix* and the other (BPBM 35835) most similar to *hystricellus,* have the penis altered internally much as *Australdonta raivavaeana* (fig. 125b). The pilasters are shortened, greatly broadened and enlarged, then tapering anteriorly. The totally different talon structure, lack of a fleshy head to the penis, and greatly different pattern of shell structure in *Australdonta* and *Cookeconcha* show that the similarity of pilaster pattern in the penis is convergent. *C. jugosus* has the elongated pilaster pattern found in *Endodonta* and *Nesophila* and agrees with them in all anatomical features except coiling of the hermaphroditic duct. None of the small *Cookeconcha* have been dissected. Quite probably *jugosus* and the *hystrix-hystricellus* group eventually will be placed in separate genera. The fusion of jaw plates is a correlative of large size, but the great elongation of the radular teeth and equal-sized cusps of the marginal teeth are quite different from the normal Endodontidae. Unfortunately, I could not dissect any of the *henshawi* complex.

The present review of trends is based on such limited material that I refuse to try to subdivide this group. The collection at the Bernice P. Bishop Museum contains about 2,600 sets with at least 25,000 specimens, probably representing about 160 species-level units. Despite the wide differences in size and apertural barriers (table LXXIV), even the limited material used in this study shows a clearly monophyletic assemblage. Only when the abundant Bishop Museum material is reviewed can the possibility of generic or subgeneric separation be considered. Until then, *Cookeconcha* should be viewed as more broadly defined than the other genera used in this study.

Four levels of specialization can be recognized. First, the minute-to-small species (mean diameter 1.79-3.35 mm.) in which the palatal barriers are fully developed, the upper parietal clearly bifid, sculpture is retained on the entire apex, and the last whorl of the umbilicus may decoil slightly more rapidly. The described species are:

Cookeconcha henshawi (Ancey, 1904)
C. cookei (Cockerell, 1933)
C. thwingi (Ancey, 1904)
C. nudus (Ancey, 1899)
C. subpacificus (Ladd, 1958).

Inclusion of the latter is based upon a preponderance of similarities in remaining portions of the single partial specimen, despite total absence of most apertural barriers (p. 212).

Second, there are distinctly larger, but still relatively small (mean diameter 3.88-4.14 mm.) species, which retain a full apertural barrier complement (although lacking a bifid upper parietal), either typical apical sculpture (*contortus*) or with apical sculpture absent on first whorl (*ringens*), and the umbilicus is V-shaped. The two described species are:

Cookeconcha contortus (Ferussac, 1824)
C. ringens (Sykes, 1896)

Both species have the barriers simpler and proportionately smaller than do members of the *C. henshawi* complex.

Third, there are the species in which partial-to-great reduction of the palatal barriers has taken place, the parietals are reduced in height, apical sculpture is reduced to lost, the size is fairly large (mean diameter 4.28-6.09 mm.), and the umbilicus regularly V-shaped. Included here are:

Cookeconcha luctiferus (Pilsbry & Vanatta, 1906)
C. elisae (Ancey, 1889)
C. hystricellus (Pfeiffer, 1859)
C. stellulus (Gould, 1844).

C. hystricellus is specialized in developing a supraperipheral sulcus, while *C. stellulus* has the shell appearance drastically altered through the presence of two deep sulci, enlargement of the ribs, increase in rib spacing, and recession of the palatal lamellar traces.

Fourth, there are the species in which all palatal and columellar barriers have been lost, the size increased (mean diameter 3.06-6.18 mm.), most of the apical sculpture lost, and sometimes secondary spiral sculpture (*decussatulus, lanaiensis*) developed, or the primary sculpture reduced (*paucicostatus*). The described species are:

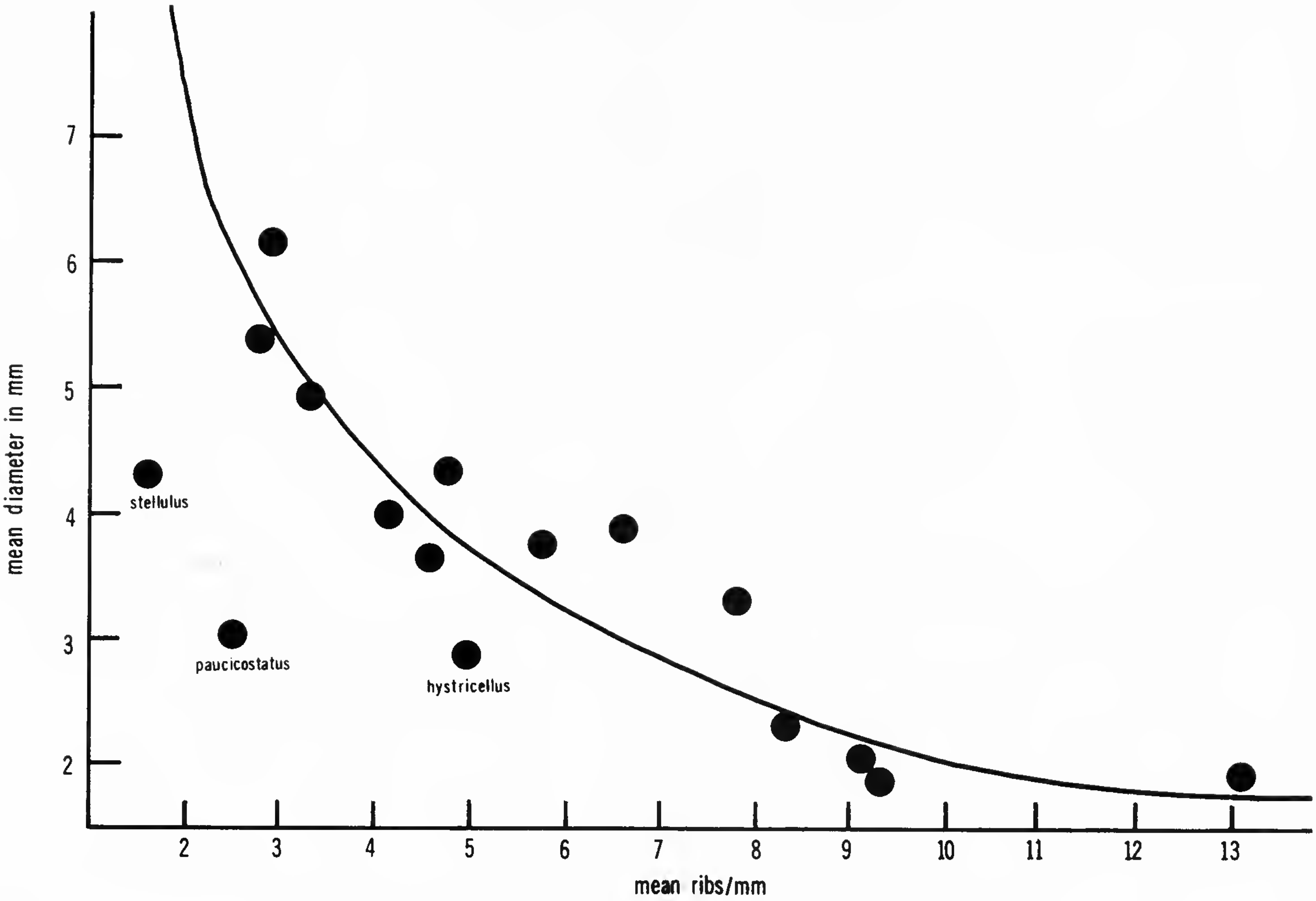

FIG. 91. Relationship between mean diameter and mean ribs per mm. in *Cookeconcha*.

Cookeconcha hystrix (Pfeiffer, 1846)
C. paucicostatus (Pease, 1870)
C. paucilamellatus (Ancey, 1904)
C. thaanumi (Pilsbry & Vanatta, 1906)
C. decussatulus (Pease, 1866)
C. lanaiensis (Sykes, 1896)
C. jugosus (Mighels, 1845).

The simplicity of apertural barrier configuration has led to recording of species in the above series from several islands. Probably most of these can be shown to be in error when the specimens are restudied.

Even casual inspection of the species show that, in general, size increase is accompanied first by simplification of the apertural barriers, then, successively, partial loss of the palatals, complete loss of the palatals with partial reduction and/or loss of the lower parietal. Plotting of the relationship between mean diameter and mean ribs/mm. (fig. 91) shows a characteristic simple, direct relationship, except for *C. paucicostatus* (rib reduction), *C. stellulus* (rib enlargement), and *C. jugosus* (gerontic rib crowding near end of body whorl).

Nothing significant can be said about distribution, since patterns suggested by the above groupings are caused by limited sampling. The *C. henshawi* complex is known mainly from Hawaii (by accident of study), but I have collected undescribed species from both Oahu (Waianae Mountains) and Kauai. Similarly, a new species of the *C. contortus* group from the Waianae Mountains has the secondary sculpture of *C. decussatulus* and the body whorl is laterally compressed. I fully expect that almost every conceivable combination of characters that are seen individually in *Cookeconcha* reviewed here, will be found in the unstudied Hawaiian material.

Cookeconcha subpacificus (Ladd, 1958). Figure 92.

Ptychodon subpacificus Ladd, 1958, Journ. Paleontol., **32**, (1) pp. 189-190, pl. 30, figs. 7-8—Drill hole 2B at 1,807-1,818 ft. depth, Bikini Atoll, Marshall Islands (Miocene *e*).

Description. — Shell very small, probably with 4 normally coiled whorls when complete (only 3½ remaining). Apex and spire barely emergent, almost flat, last whorl descending much more rapidly, H/D ratio of remaining shell 0.522. Apical whorls 1⅜, sculpture of prominent retractive radial ribs and faint indications of microsculpture near end of apex. Lower whorls with strong, retractively sinuated radial ribs, 77 on last remaining whorl, whose interstices are 1-2 times their width. Microsculpture clearly visible and consisting of very fine radial riblets and slightly finer, more crowded spiral riblets. Whorls strongly rounded above and on umbilical shoulder, compressed laterally with evenly rounded lower palatal and basal margins. Only very faint traces of irregular radial color markings left on shell above periphery, not detectable on base. Umbilicus widely open, V-shaped, rather rapidly decoiling, contained 3.53 times in diameter of remaining shell. Last one-half whorl missing, hence status of columellar and palatal barriers unknown. Aperture flattened laterally, probably inclined about 15° from shell axis. Parietal wall with partial remains of two barriers, both extending posteriorly one-quarter whorl and broken off in mid-section. Lower parietal broader, slightly lower, with longer, more gradual anterior descension than upper, but still descending rather rapidly. Both parietals with very gradual posterior descension. Height of holotype 0.97 mm., diameter 1.86 mm.

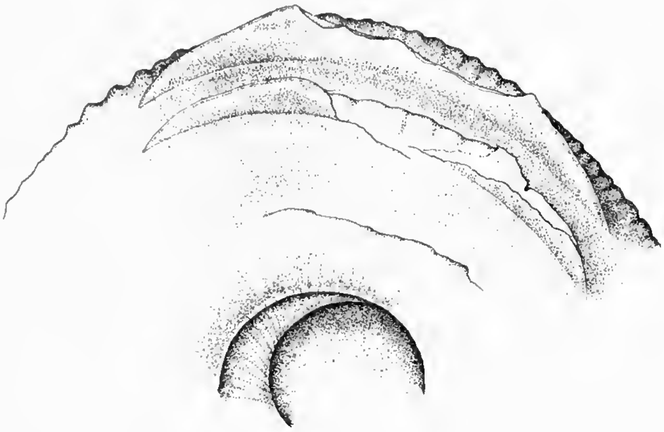

FIG. 92. *Cookeconcha subpacificus* (Ladd). Detail of parietal lamellae remnants. Greatly enlarged. (MM).

Holotype. – Marshall Islands: Bikini Atoll, drill hole 2B at 1,807-1,818 ft. depth (Miocene *e*). USNM 562090.

Range. – Fossil at Bikini Atoll, Marshall Islands.

Material. – Only the holotype is known.

Remarks. – Despite being only a fragmentary specimen, I have no hesitation in classifying this species with the *henshawi* group of *Cookeconcha*. There are a number of shell characters that agree with members of the *henshawi* complex and contrast with the character states seen in *Minidonta*, the other logical possibility. These are the only two genera in the Endodontidae which have species reaching the size range of *subpacificus*. Although *Minidonta* has seven species with a mean diameter 2.00 mm. or less, while only *Cookeconcha henshawi* is known to be that size, it cannot be overemphasized that the Hawaiian *Cookeconcha* probably number eight or ten times the species discussed here. Particularly when allowance is made for the missing half whorl of *subpacificus*, an actual diameter of slightly over 2 mm. is probable. Whorl count in the 1.68-1.83 *Minidonta* is 41/16 to 4½; 3½ in *subpacificus* and *C. henshawi*. The umbilicus is U-shaped and rather narrow (mean D/U ratios 3.67-7.10) with the last whorl decoiling more rapidly in the small *Minidonta*; V-shaped, regularly or with a slightly more rapidly decoiling last whorl and wider [mean D/U ratios 2.66-3.68 in *Cookeconcha*; V-shaped, widely open, and rather rapidly decoiling (D/U 3.53) in *subpacificus*]. The missing half whorl increases the D/U ratio and also raises the H/D ratio. Probably the true D/U ratio of *subpacificus* would be about 3.2-3.3, well within the range of *Cookeconcha*, but below the range of *Minidonta*. In the latter genus, the spire is moderately to strongly elevated in all small species except *M. gravacosta*, with mean H/D ratios of 0.573-0.625; in the small *Cookeconcha*, the spire is barely emergent and the mean H/D ratio 0.497-0.538. Considering that the missing half whorl of *subpacificus* means a slightly (8-10 per cent) higher H/D ratio, its barely emergent spire and H/D ratio of 0.522 follow the *Cookeconcha* pattern. The small *Cookeconcha* and *subpacificus* have the aperture inclined 10-15° from the shell axis, while in *Minidonta* it is usually inclined 5°, only in *M. micra* and *M. hendersoni* reaching 10°. Thus the 15° inclination of *subpacificus* agrees with *Cookeconcha*. Lateral compression of the body whorl is common in *Minidonta*, but rarely seen in *Cookeconcha*. In this respect, *subpacificus* resembles *Minidonta*, but the shift from evenly rounded to laterally compressed, or *visa versa*, is a common change. *Minidonta* normally has 3 parietals: when reduced to 2 in number, the lower parietal is very gradually descending. The 2nd parietal in *Minidonta* always extends significantly beyond the anterior end of the upper parietal. In *Cookeconcha* there are only 2 parietals, the 2nd of which only extends slightly beyond the upper and is either threadlike or sharply descending anteriorly. The 2 parietals of *subpacificus*, with the 2nd sharply descending and extending only slightly beyond the upper clearly indicate relationship to *Cookeconcha* rather than *Minidonta*. Rib frequency in *subpacificus* (13.18 ribs/mm.) is more similar to *Minidonta* (ribs/mm. 10.7-25.2) than to the small *Cookeconcha* (ribs/mm. 7.79-13.5), but is within the range of observed variation. Finally, the appearance and spacing of the microsculpture in *subpacificus* more closely resemble that of *Cookeconcha* than *Minidonta*.

Only in lateral compression of the body whorl and rib spacing does *subpacificus* more closely resemble *Minidonta*. The great majority of features – whorl count, umbilical shape, umbilical width, spire elevation, H/D ratio, apertural inclination, number of parietal barriers, position of the 2nd parietal, and microsculpture – *subpacificus* agrees with *Cookeconcha*.

Unfortunately, the tops of the parietal barriers in *subpacificus* are broken off and the entire columellar and palatal whorls are missing for one-half whorl. Only the extremely unlikely prospect of new coring work on Bikini and collection of additional specimens will allow a more detailed analysis of *subpacificus*. Study of the complete parietal and palatal barriers would be needed to be certain whether *subpacificus* belongs to the *Cookeconcha henshawi* complex; is a *Cookeconcha* belonging to a group more generalized than any now living in Hawaii; or is generically separable from *Cookeconcha*. I consider that either of the first two statements has a much greater probability of being correct than the third. In the absence of data differentiating *subpacificus* from the *henshawi* group, I prefer to consider it only specifically separable.

Cookeconcha henshawi (Ancey, 1904)

Endodonta (Thaumatodon) henshawi Ancey, 1904, Jour. Malacol., **11**, p. 67, pl. 5, figs. 15, 16 - Palihoukapapa, Hamukua slope of Mauna Kea, Hawaii, Hawaiian Islands.

Diagnosis. — Shell minute; diameter 1.71-1.89 mm. (mean 1.79 mm.), with 3½-3¾ rather tightly coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.537-0.539 (mean 0.538). Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 3.25-3.29 times (mean 3.27) in the diameter. Apical sculpture of larger radials with very fine microradials and microspirals. Postnuclear sculpture of high, prominent, protractive radial ribs, 46-51 (mean 48.3) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of very fine radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on basal margin, evenly rounded on outer margin. Aperture subcircular, with evenly rounded outer margins, inclined about 10° from shell axis. Parietal barriers 2, extending posteriorly less than three-sixteenths of a whorl: upper very high on posterior half, indistinctly bifid, with gradual anterior descension from front edge of expanded portion; 2nd slightly lower, broadly expanded above on posterior half, with sharp, then gradual, anterior descension to point in front of upper parietal termination. Columellar barrier high and bladelike, broadly expanded posteriorly, lying parallel to plane of coiling, with moderate to sharp anterior descension almost to lip edge. Palatal barriers 4, extending posteriorly less than one-eighth whorl, slightly recessed within aperture, with one prominent accessory trace between 3rd and 4th palatals: lower greatly reduced in height, a raised crescentic ridge, broadly expanded above; 2nd twice as high as 1st, flattened and broadly expanded above on posterior half, with gradual anterior descension, upper edge lying close to top of 2nd parietal; 3rd slightly reduced in height, pointing between parietals, with equal posterior expansion and more gradual anterior descension; 4th supraperipheral, equal in height to 1st palatal, but much less expanded above, moderately recessed within aperture.

Range. — Hamakua slope of Mauna Kea, Hawaii, Hawaiian Islands.

Material. — Hawaiian Islands: Hawaii, "Mana" (5 specimens, FMNH 46563, ex Webb, Gude, Hartley).

Remarks. — The indistinctly bifid upper parietal is a character shared with *C. nudus, C. thwingi,* and *C. cookei.* The much smaller size, heavier ribbing, lower whorl count, and more elevated spire separate *C. henshawi* from the other species.

Ancey's types were larger (diameter 2 mm. with 4 to 4¼ whorls) than the specimens seen during this study. The latter are subadult and future use of the diagnosis presented above should allow for this fact in comparing size and shape factors.

Cookeconcha cookei (Cockerell, 1933)

Endodonta (Thaumatodon) cookei Cockerell, 1933, Nautilus, **47**, (2), p. 58 — dead tree fern on Mt. Tantalus, Koolau Mountains, Oahu, Hawaiian Islands.

Description. — Shell very small, with 4⅝ normally coiled whorls. Apex and spire almost evenly elevated, slightly rounded above, body whorl descending moderately more rapidly, H/D ratio 0.538. Embryonic whorls 1⅜, sculpture eroded except for faint traces of radial ribbing in unclogged portion of sutures, visible in umbilicus as major radials with one or two microradials between, plus weak microspirals, present to top of apex. Postnuclear sculpture worn off spire, on lower whorls consisting of very high, prominent, strongly protractively sinuated radial ribs, 60 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of extremely fine radial riblets, six to ten between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. No secondary microsculpture. Sutures deep, whorls strongly rounded above and on basal margin, with evenly rounded, slightly laterally compressed outer margin. Color mostly leached from shell, traces of widely spaced, narrow to broad, reddish flammulations visible above periphery, fading out on body whorl. Umbilicus broadly U-shaped, regularly decoiling until last third of body whorl, which decoils a little more rapidly, contained 3.08 times in the diameter. Aperture ovate, strongly rounded above and on basal margin, slightly compressed laterally, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly three-sixteenths of a whorl: upper a high lamellar blade, bulbously expanded and serrated above on posterior third, bulbous section descending to three-eighths point, then the blade continuing anteriorly without descension until just before termination, when it descends sharply; 2nd slightly less elevated than 1st, more broadly and bulbously expanded above over posterior five-eighths, swollen section then tapering to about one-eighth from end, then descends more gradually than upper to point anterior to upper termination. Columellar barrier high and crescentic, thick, but only slightly expanded above, slanted downwards from plane of coiling at 45° angle, with abrupt descension to top of columellar callus. Palatal barriers 4, extending posteriorly about one-eighth whorl, deeply recessed: lower basal in position, short, crescentic, slightly higher than wide, much lower than columellar; 2nd and 3rd equal in height to columellar, crescentic, broadly expanded and serrated above, subperipheral, with progressively more gradual anterior descension; 4th supraperipheral, more deeply recessed, slightly higher than 1st, much lower than 3rd, crescentic, with abrupt anterior descension. Height of holotype 1.24 mm., diameter 2.29 mm.

Holotype. — Hawaiian Islands: Oahu, slopes of Mt. Tantalus, Koolau Mountains. Collected in a dead tree fern by T. D. A. Cockerell on July 16, 1924. ANSP 158823.

Range. — Mt. Tantalus, Koolau Mts., Oahu, Hawaiian Islands.

Material. — Only the holotype was seen.

Remarks. — The wider umbilicus, more prominent and crowded ribbing, deeper recession, and larger size of the apertural barriers separate *C. cookei* from *C. henshawi.* In the latter the parietal and palatal barriers are much less expanded above and have a distinct gap, while in *C. cookei* the upper parietal and 3rd palatal almost overlap. *C. thwingi* is more depressed, has a wider umbilicus (table LXXIV), lacks a columellar barrier, and has two accessory palatal traces. The great expansion of the apertural barriers in *C. cookei* is not equalled by any other described member of the genus, but is equivalent to the situation seen in some *Minidonta, Anceyodonta,* and *Thaumatodon.*

Cookeconcha thwingi (Ancey, 1904)

Endodonta thwingi Ancey, 1904, Jour. Malacol., 11, (3), p. 66 — extinct crater on Kona coast, Hawaii, Hawaiian Islands.

Diagnosis. — Shell very small, diameter 2.12-2.50 mm. (mean 2.30 mm.), with 4-4½ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending distinctly more rapidly, H/D ratio 0.488-0.520 (mean 0.499). Umbilicus widely open, V-shaped, regularly decoiling, contained 2.62-2.74 times (mean 2.66) in the diameter. Post nuclear whorls with high, prominent, protractively sinuated radial ribs, 65-70 (mean 66.7) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above, with evenly rounded outer margins. Aperture circular, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly less than three-sixteenths of a whorl: upper rather high, bluntly bifid on posterior expanded quarter, with gradual anterior descension; 2nd reduced in height, moderately expanded posteriorly, with sharper descension to an elevated ridgelike portion that descends gradually. Columellar wall without barriers. Palatal barriers 5, extending posteriorly about one-eighth whorl, reaching lip edge, with two accessory traces located one between 1st and 2nd, one between 2nd and 3rd palatals: lower at baso-columellar margin, very high, moderately strongly expanded posteriorly, with rather sharp anterior descension; 2nd and 3rd equal in height and expansion, with progressively more gradual anterior descension; 4th and 5th greatly reduced in height and length, broadly expanded above, more deeply recessed within aperture, scarcely larger than traces but recognizable as majors by being less deeply recessed than the traces.

Range. – Extinct crater on Kona coast of Hawaii, Hawaiian Islands.

Material. – Hawaiian Islands: Hawaii (4 specimens, FMNH 46466 ex Webb, Gude).

Remarks. – Ancey did not publish a formal description of this species, but in comparative remarks about *C. henshawi* stated: "A similar species, also probably extinct, but with a larger umbilicus, was detected by the Rev. E. W. Thwing, in an extinct crater of the Kona coast; it is undoubtedly another new species which I propose to name *E. thwingi,* after its discoverer." In 1904, such comparative remarks were considered perfectly adequate for species differentiation. While under current rules it could be argued (probably successfully) that the lack of a formal description invalidates this name, I choose to consider that the citation of a formal name and comparative remarks are sufficient to allow acceptance of this name from Ancey's paper.

The larger size (table LXXIV), wider umbilicus, absence of a columellar barrier, 5 palatals with two accessory traces and greater number of major ribs separated *Cookeconcha thwingi* from the otherwise very similar *C. henshawi.* The much larger *C. nudus* lacks accessory traces, has a narrower umbilicus, and sometimes has a columellar barrier.

Cookeconcha nudus (Ancey, 1899)

Endodonta (*Thaumatodon*) *nuda* Ancey, 1899, Proc. Malacol. Soc. London, **3**, (5), p. 268, pl. 12, fig. 1 – Olaa, Central Hawaii; Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 288; Ancey, 1904, Jour. Malacol., **11**, p. 66–Palihoukapapa, Hamakua slope of Mauna Kea, Hawaii, Hawaiian Islands.

Diagnosis. – Shell small, diameter 3.22-3.49 mm. (mean 3.35 mm.), with 4½ - 5 normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.449-0.524 (mean 0.497). Umbilicus open, V-shaped, last whorl often decoiling more rapidly, contained 3.38-3.92 times (mean 3.68) in the diameter. Apical sculpture typical. Postnuclear whorls with narrow, prominent, protractively sinuated radial ribs, 75-92 (mean 83.3) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, three to five between each pair of ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on basal margin, with evenly rounded outer margin. Aperture subcircular, with evenly rounded outer margin, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly one-quarter whorl: upper very high, weakly to prominently bifid on posterior five-eighths, with gradual anterior descension; 2nd much lower, strongly expanded on posterior half, with rather sharp descension to threadlike or raised lamellar anterior third that terminates beyond edge of upper parietal. Columellar barrier usually absent, sometimes (12.1 per cent) present as a low, moderately recessed lamellar ridge lying parallel to plane of coiling. Palatal barriers 5, extending posteriorly more than one-eighth whorl: lower at baso-columellar margin, lower than 2nd, strongly expanded above posteriorly, with sharp descension to lip edge; 2nd and 3rd higher, less expanded above, with progressively more gradual anterior descension; 4th very slightly reduced in height, with more gradual anterior descension; 5th supraperipheral, more flattened above on posterior expanded portion, reduced in height, moderately recessed, with sharper anterior descension.

Description. – Shell rather small, with slightly less than 4½ normally coiled whorls. Apex flat, lower whorls descending slightly, last whorl more rapidly, H/D ratio 0.465. Apical whorls 1⅜, sculpture of fine radial riblets, with two or three microradials and barely visible spirals. Postnuclear whorls with narrow, high, protractively sinuated radial ribs, 67 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, three to six between each pair of major ribs, with barely visible, very crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on basal margin, with evenly rounded outer margin. Color light yellow-white, with narrow, irregularly spaced, reddish flammulations that are strongly zigzagged just above periphery and fade out on shell base. Umbilicus V-shaped, last whorl decoiling more rapidly, contained 3.59 times in the diameter. Aperture subcircular, with evenly rounded outer margin, inclined about 15° from shell axis. Parietal barriers 2, structure as in diagnosis except bifidity of upper well developed. Columellar barrier a small deeply recessed, threadlike ridge, parallel to plane of coiling. Palatal barriers 5, shape as in diagnosis: 1st slightly lower than 2nd; 3rd a little larger than 2nd; 4th slightly lower than 1st; 5th further reduced in height. Height of holotype 1.18 mm., diameter 3.19 mm.

Holotype. – Olaa, Central Hawaii, Hawaiian Islands. FMNH 46358 ex Webb, Gude, Ancey collections.

Range. – Hawaii, Hawaiian Islands.

Material. – Hawaiian Islands: Hawaii, Olaa (1 specimen, FMNH 46358); Kaiwiki, drift of Hilo, at 2,500 ft. elevation (15 specimens, FMNH 46422, FMNH 73197, FMNH 90319).

Remarks. – The most obvious difference of *C. nudus* lies in the presence of 5 major palatals and its size, which is much larger than the other species with bifid upper parietal – *thwingi, cookei,* and *henshawi.* The other species with well-developed palatals, *contortus* and *ringens,* lack any trace of bifidity in the upper parietal barrier.

Cookeconcha contortus (Ferussac, 1824)

Helix contorta Ferussac, 1824, Voy. "Uranie"...Freycinet, Zool., p. 469 – Sandwich Islands; Ferussac, 1832, Histoire nat. moll. terr. fluv., pl. 51a, fig. 2 – Sandwich Islands; Pfeiffer, 1848, Mon. helic. viv., **1**, pp. 185-186; Deshayes, 1851, Hist. nat. moll. terr. fluv., **1**, pp. 10-11; Pfeiffer, 1852, Syst. Conchyl. Cab., (1), **12**, (2), p. 197, pl. 100, figs. 1-5 (plate issued in 1850); Pfeiffer, 1853, Mon. helic. viv., **3**, p. 144; Reeve, 1854, Conchol. Icon., *Helix*, pl. 133, fig. 647; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 155; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 220; Pease, 1871, Jour. de Conchyl., **19**, p. 96 – Oahu; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 256; Tryon, 1887, Man. Conchol., (2), **3**, p. 63, pl. 12, figs. 8-10.

Helix intercarinata Mighels, 1845, Proc. Boston Soc. Nat. Hist., **2**, pp. 18-19 – Oahu.

Endodonta contorta (Ferussac), Albers, 1850, Die Heliceen, p. 89; von Martens, 1860, Die Heliceen, ed. 2, p. 90; Pilsbry, 1893, Man. Conchol., (2), **9**, p. 26.

Pitys contorta (Ferussac), H. & A. Adams, 1858, Genera Recent Moll., **2**, p. 113; Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474; Ancey, 1889, Bull. Soc. Malacol. France, **6**, pp. 181-182.

Patula (*Endodonta*) *contorta* (Ferussac), Clessin, 1881, Nomen. helic. viv., p. 96.

Helix (*Pitys*) *contorta* (Ferussac), Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 – Oahu.

Endodonta (*Thaumatodon*) *contorta* Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 288–Oahu.

Diagnosis. – Shell slightly smaller than average, diameter 3.72-4.14 mm. (mean 3.88 mm.), with 5½-5¾ rather tightly coiled whorls. Apex and spire slightly and usually evenly elevated, body whorl descending more rapidly, H/D ratio 0.465-0.556 (mean 0.516). Umbilicus broadly V-shaped, regularly decoiling, contained 3.14-3.50 times (mean 3.29) in the diameter. Apical sculpture typical. Postnuclear sculpture of narrow, prominent, strongly protractively sinuated radial ribs, 77-87 (mean 80.8) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, four to six between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls with evenly rounded outer margin, strongly rounded basal margin. Aperture circular, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly slightly more than three-sixteenths of a whorl: upper high and thin, weakly expanded above on posterior third, with very gradual anterior descension; 2nd distinctly lower, more broadly expanded on posterior elevated portion, anterior half a raised threadlike ridge extending beyond end of upper parietal. Columellar wall without barriers. Palatal barriers 4 or 5, usually 4, extending posteriorly slightly more than one-eighth whorl: lower at baso-columellar margin, lower than 2nd, slightly recessed, crescentic, moderately expanded above, with rather sharp anterior descension; 2nd and 3rd higher, thinner, with more gradual descension both anteriorly and posteriorly; 4th supraperipheral, half the height of 3rd, weakly expanded, more deeply recessed; 5th, when present, located between 2nd and 3rd, equal in height.

Range. – Probably Waianae Mountains, Oahu, Hawaiian Islands.

Material. – Hawaiian Islands: Oahu (4 specimens, FMNH 46603, ex Webb, Gude, Geret, Ancey; Cardiff ex Tomlin collection).

Remarks. – I suspect that several Waianae species of the *contortus-hystricellus* syndrome have been confused under this name. Ferussac (*loc. cit.*) figured a flat (or depressed) shell with no visible major radial sculpture, prominent setae, parietal barriers of equal length and palatal barriers equally spaced. Pfeiffer, in the *Conchylien Cabinet,* showed a shell with distinctly elevated spire, narrower umbilicus, rather crowded radial sculpture and mentioned that there are 3 - 5 palatal barriers. Reeve (*loc. cit.*) has a typically vague figure that cannot be used for identification purposes, but probably is based on a specimen from the same set used by Pfeiffer.

The single specimen in Field Museum agrees well with Pfeiffer's illustration and originated from the Ancey collection, coming to Chicago through the collections of Geret, Gude, and Webb. It is unusual in having a 5th palatal barrier located midway between the normal 2nd and 3rd. The National Museum of Wales' examples are very similar.

In the available specimens, positioning of the barriers is the same as in the smaller *nudus, thwingi,* and *henshawi,* but, of course, there is no trace of bifidity in the upper parietal, the palatals are much less expanded and crescentic, rather than being flattened above. The increase in size is accompanied by a major increase in whorl count. In all specimens the microradial ribbing is rather large, with four to six between each pair of major ribs. The major ribs themselves are rather crowded (mean ribs/mm. 6.64).

The type of *Helix intercarinata* Mighels, 1845 is no longer extant (see Johnson, 1949, p. 226). Following the historical precedent of considering this a synonym of *Helix contorta* rather than trying to interpret Mighel's abbreviated description will save time and avoid confusion. When an analysis of the Waianae *Cookeconcha* is accomplished, then selection of a lectotype for *Helix contorta* from one of the several British Museum, Brussels, or Bishop Museum sets would be justified. At present it would be a waste of time and paper.

Cookeconcha ringens Sykes, 1896

Endodonta ringens Sykes, 1896, Proc. Malacol. Soc., London, **2**, (3), pp. 126-127 – behind Koele, mountains of Lanai, Hawaiian Islands.

Endodonta (*Thaumatodon*) *ringens* Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 288-289, pl. 11, figs. 39, 40 – in wet forest above Pelekunu, Molokai, Hawaiian Islands.

Diagnosis. – Shell of average size, diameter 3.91-4.61 mm. (mean 4.14 mm.), with 5⅛-5½ whorls. Apex and early spire flat, body whorl descending much more rapidly, H/D ratio 0.407-0.456 (mean 0.439). Umbilicus U-shaped, regularly decoiling, contained 3.05-3.60 times (mean 3.39) in the diameter. Apical sculpture absent on first whorl, reduced in prominence on rest. Postnuclear whorls with high, prominent, strongly protractive radial ribs, 41-70 (mean 51.2) on the body whorl, whose interstices are 4-6 times their width. Microsculpture of very fine radial riblets, eight to twelve between each pair of major ribs, crossed by exceedingly fine microspirals visible only under 96× magnification. Sutures impressed, whorls strongly rounded above and on basal margin, with evenly rounded outer margin. Aperture subcircular, with evenly rounded outer margin, inclined about 15° from the shell axis. Parietal barriers 2, extending posteriorly three-sixteenths of a whorl, rarely with a short accessory trace: upper very high and slender, weakly expanded on posterior third, with gradual anterior descension; 2nd much lower posteriorly, weakly expanded, with anterior half a raised threadlike ridge extending beyond end of upper parietal. Columellar wall without barriers. Palatal barriers 4, rarely 5, extending posteriorly about one-eighth whorl, slightly recessed; lower at baso-columellar margin, a thin, low crescentic blade; 2nd and 3rd high and bladelike, with rather sharp anterior descension, weakly expanded above; 4th supraperipheral, reduced in size, very thin, with more gradual anterior descension; 5th, when present, located between 2nd and 3rd palatal.

Description. – Shell of average size, with 5¼ moderately tightly coiled whorls. Apex and early spire flat, last whorls descending moderately, H/D ratio 0.452. Apical whorls 1⅜, first whorl smooth, sculpture of fine, somewhat irregularly prominent radial ribs, very crowded, with a secondary sculpture of extremely fine spiral riblets on remaining part. Postnuclear whorls with high, lamellate, prominent, protractively sinuated radial ribs, 46 on the body whorl, whose interstices are 4-6 times their width. Microsculpture of fine, crowded radial riblets, moderately prominent, with a barely visible sculpture of exceedingly fine and crowded spiral riblets. Color light yellow-white with broad, prominent, zigzag, reddish flammulation, fading out on shell base. Sutures deep, whorls strongly rounded above, slightly flattened basally with evenly rounded periphery. Umbilicus broadly U-shaped, slightly and regularly decoiling, contained 3.50 times in the diameter. Aperture subcircular, somewhat flattened basally, inclined about 15° from shell axis. Parietal barriers 2, extending three-sixteenths of a whorl: upper parietal with anterior half gradually descending, becoming high, weakly expanded above posteriorly, remaining thin for entire length; lower parietal with anterior three-eighths low and threadlike, becoming moderately elevated posteriorly, but much broader than upper parietal. Palatal barriers 4, short, crescentic: lower a lamellate ridge located at baso-columellar margin, nearly reaching lip; 2nd and 3rd much higher, very slightly expanded above; upper palatal supraperipheral, slightly recessed within aperture with more gradual anterior descension, reduced in size, evenly rounded above. Height of lectotype 1.88 mm., diameter 4.15 mm.

Lectotype. — Hawaiian Islands: Lanai, behind Koele. 1900.12.18.1374.

Range. — Lanai and possibly Molokai, Hawaiian Islands.

Paratype. — BMNH 1900.12.18.1375.

Material. — Hawaiian Islands: Lanai (4 specimens, BPBM 14329, BMNH 1900.12.18.1381-3); behind Koele (2 specimens, BMNH 1900.12.18.1374-5). Molokai, above Pelekunu (3 specimens, BMNH 1900.12.18.1366-8).

Remarks. — The Molokai specimens that Sykes (*loc. cit.*) reported as this species are much larger (diameter 4.77-4.84 mm.), with a narrower umbilicus (D/U ratio 3.67 - 4.14), and have the lower palatal barrier almost shifted onto the columellar wall. Whether they are taxonomically distinct from the Lanai populations is unknown.

In form of shell and barriers, *ringens* shows many similarities to *contortus*. It differs in its flat spire, much more widely spaced radial ribs (mean ribs/mm. 3.92), and more slender barriers.

Cookeconcha elisae (Ancey, 1889)

Pitys elisae Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 180 — Sandwich Islands; Pilsbry, 1892, Man. Conchol., (2), **8**, p. 95.

Endodonta elisae (Ancey), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27; Caum, 1928, Bull. B. P. Bishop Museum., **56**, p. 65.

Helix (Pitys) elisae Ancey, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16.

Endodonta (Nesophila) elisae (Ancey), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 290 — ? Hawaiian Islands.

Range. — Unknown, probably a Hawaiian species.

Material. — None.

Remarks. — Although Sykes (1900, p. 290) and Caum (1928, p. 65) questioned that this was a Hawaiian species, its status will remain uncertain until the Hawaiian fauna is revised. The wide umbilicus, rounded aperture, single parietal barrier, and the presence of one or two columellar and/or palatal barriers provide a character complex typically Hawaiian, but not usually duplicated on other islands of the Pacific.

Cookeconcha luctiferus (Pilsbry & Vanatta, 1905). Figure 94d-f.

Endodonta (Thaumatodon) luctifera Pilsbry and Vanatta, 1905, Proc. Acad. Nat. Sci., Philadelphia, **57**, p. 575, p. 39, figs. 4, 5, 6 — Sandwich Islands.

Diagnosis. — Shell a little larger than average, diameter 3.91-5.23 mm. (mean 4.51 mm.), with 4⅞ - 5¾ normally coiled whorls. Apex and spire flat or depressed, last whorl descending much more rapidly, H/D ratio 0.427-0.496 (mean 0.460). Umbilicus broadly V-shaped, last whorl decoiling regularly or slightly more rapidly, contained 2.96-4.19 times (mean 3.49) in the diameter. Apical sculpture absent on first three-quarters whorl, typical on rest. Postnuclear sculpture of narrow, prominent, strongly protractively sinuated radial ribs, 42-60 (mean 51.0) on the body whorl, whose interstices are 4-6 times their width. Microsculpture of fine radial riblets, ten to fourteen between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Suture impressed, whorls strongly rounded above and on umbilical margin, evenly rounded on outer margin, sometimes slightly flattened above periphery. Aperture subcircular, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly slightly less than one-quarter to more than one-quarter whorl: upper a low lamellar ridge, barely to moderately elevated on posterior third, not expanded above, with gradual anterior descension; 2nd a low ridge, at most weakly elevated posteriorly, anterior five-eighths threadlike, extending even with or slightly in front of upper parietal termination. Columellar wall frequently (22.2 per cent) with a moderately recessed, very short, threadlike trace lying parallel to plane of coiling. Palatal wall with 1-4, usually 2 or 3, short, low, crescentic to threadlike barriers: lower usually on basal margin, sometimes large, sometimes smaller than 2nd and 3rd, which may be crescentic. If 2nd and 3rd threadlike, then lower lost. Occasionally a fourth supraperipheral trace can be detected.

Holotype. — ANSP 58137.

Range. — Molokai, Hawaiian Islands.

Material. — Hawaiian Islands: Molokai (4 specimens, FMNH 46255); Waikolu (1 specimen, FMNH 90618); Kamalo (4 specimens, FMNH 73194).

Remarks. — This species represents an intermediate stage in barrier reduction. The types, from an unknown locality, have only one or two palatal traces, while the material available for this study has a larger number of traces. Adequate population samples undoubtedly will show considerable variation in this character.

Cookeconcha hystricellus (Pfeiffer, 1859). Figure 165j-k.

Helix hystricella Pfeiffer, 1859, Proc. Zool. Soc. London, **1859**, p. 25 — Sandwich Islands; Pfeiffer, 1859, Malakol. Blatt., **6**, p. 11; Pfeiffer, 1868, Mon. helic. viv., **5**, p. 221 — Kauai; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 258.

Pitys hystricella (Pfeiffer), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474; Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 183.

Patula (Endodonta) hystricella (Pfeiffer), Clessin, 1881, Nomen. helic. viv., p. 96.

?*Helix (Pitys) hystricella* Pfeiffer, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 — Kauai.

Endodonta (Thaumatodon) hystricella (Pfeiffer), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 288 — Kaala, Oahu, Hawaiian Islands.

?*Endodonta hystricella* (Pfeiffer), Ancey, 1904, Jour. Malacol., **11**, (4), p. 67 – Makawao, Maui, Hawaiian Islands.

Range. – Waianae Mountains, Oahu, Hawaiian Islands.

Material. – Hawaiian Islands (1 specimen, FMNH 7642 ex Philip Carpenter): Oahu, Waianae Mts., Palehua (6 specimens, FMNH 116893); Popowela, Waianae Mts. (4 specimens, FMNH 116894).

Remarks. – The identity of this unfigured species is uncertain. Table LXXIV indicates the extent of variation between populations that could be referred to this name. Since no original material was available, no diagnosis has been prepared. Probably neither population will be referable to the eventually delineated nominate race, but this is the most likely named entity to use for these populations. I doubt that the Maui shells referred to this species by Ancey (*loc. cit.*) are correctly identified.

Both populations used in this survey have 2 parietals, a weak to moderate supraperipheral sulcus, 3 or 4 rather deeply recessed, small palatals, a depressed spire, and prominent color pattern. They differ widely in size, umbilical width, and sculpture (table LXXIV). Dissection of material from Popowela (BPBM 35421) and Palehua (BPBM 35835) demonstrated marked differences in penial pilaster patterns. At the present time, I prefer not to assess the systematic significance of these variations.

Description of soft parts. – Foot and tail long, tapering posteriorly, truncated anteriorly. Sole undivided. Pedal grooves rather low in foot, equally prominent, no caudal horn or middorsal groove present. Slime network of very fine ovoid reticulations. Head projecting in front of foot. Ommatophores typical. Gonopore above front margin of foot, directly behind right rhinophore.

Body color yellow-white, no darker markings.

Mantle collar rather wide, no glandular extension onto pallial roof. Pneumostome typical.

Pallial region about 5.6 mm. long. Lung roof clear, without granulations. Kidney about 2 mm. long, broad basally, with short (0.5 mm.) rectal arm. Ureter opening at anterior margin of kidney rectal arm, typical in form. Heart about half length of kidney, lying slightly off the hindgut axis. Principal pulmonary vein and hindgut typical.

Ovotestis (fig. 165j, G) of palmately clavate alveoli in overlapping clusters along a single collecting tubule, rather short, early clumps perpendicular to sides of whorls, later slanted upward. Hermaphroditic duct (GD) very narrow at first, only slightly expanded medially, narrowing and reflexing before entering carrefour. Albumen gland (GG) small, irregular in shape. Talon (GT) with bulbous head, tapering slowly to junction with carrefour (X), which is buried in albumen gland and much smaller than head of talon. Prostate (DG) with two to three rows of acini opening into a narrow tube. Uterus (UT) bipartite, extending only slightly below end of prostate.

Vas deferens (VD) typical, weakly bound to peniovidural angle, entering penis between pilasters (fig. 165k, EP), about 0.7 mm. below apex, bound to side of penis for last 0.5 mm. of length. Penial retractor (PR) arising from diaphragm at apex of penial cavity, inserting directly onto head of penis. Penis (P) about 2.7-3.7 mm. long, bulbous apically and in upper portion, tapering abruptly to moderately below, internally (fig. 165k) with two large pilasters (PP), united apically, one tapering shortly after the apex, the other grossly expanded, bifolded and with bulbous termination. Atrium (Y) rather short.

Free oviduct (UV) short, weakly demarcated from end of uterus. Spermatheca (S) typical, shaft inserting slightly above junction of penis and free oviduct, forming a very short vagina (V).

Free muscle system and digestive system not showing any significant differences from *Endodonta.*

Jaw composed of narrow, overlapping, partly fused plates that are not clearly enough separated to count, about 0.31 mm. long.

Radula with 9 or 10 laterals and 10 or 11 marginals, central about 8μ wide and 13-14μ long. All basal plates very elongated, marginals with square plates and only four or five equal cusps.

(Based on BPBM 35421, four whole and several fragmentary examples.)

Cookeconcha stellulus (Gould, 1844). Figure 93 a-c.

Helix stellulus Gould, 1844, Proc. Bost. Soc. Nat. Hist., **1**, p. 174 – Sandwich Islands; Gould, 1846, Exped. Shells Reprint, p. 194; Gould, 1852, U. S. Explor. Exped. "Wilkes," **12**, pp. 56-57–Maui; Pfeiffer, 1853, Mon. helic. viv., **3**, p. 145; Pfeiffer, 1859, Mon. helic. viv., **4**, p. 156; Gould, 1860, U. S. Explor. Exped. "Wilkes," Atlas, pl. 4, fig. 52†, 52a†, 52b†, 52c†; Pfeiffer, 1868, Mon. helic. viv., **5**, p. 222 Pfeiffer, 1876, Mon. helic. viv., **7**, p. 260; Tryon, 1887, Man. Conchol., (2), **3**, p. 61, pl. 11, figs. 84-86.

Pitys stellula (Gould), H. and A. Adams, 1858, Genera Recent Moll., **2**, p. 113; Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474 – Maui; Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 182.

Endodonta stellulus (Gould), von Martens, 1860, Die Heliceen, ed. 2, p. 90; Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Patula (Endodonta) stellula (Gould), Clessin, 1881, Nomen. helic. viv., p. 95.

Helix (Pitys) stellula (Gould), Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16; Johnson, 1964, Bull. U. S. Nat. Mus., **239**, p. 152, pl. 38, fig. 3.

Endodonta (Nesophila) stellula (Gould), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 291 – Maui.

Diagnosis. – Shell of average-to-large size, diameter 4.28-5.38 mm., with 4¼-5⅜ normally coiled whorls. Apex and spire sunken beneath level of body whorl, last whorl not descending, H/D ratio 0.369-0.394. Umbilicus cup-shaped, regularly decoiling, contained 3.10-3.15 times in the diameter, with angled basal margin. Apical sculpture absent on first half whorl, reduced on remainder. Postnuclear whorls with extremely high and prominent, protractively sinuated radial ribs, 19 on the body whorl, whose interstices are 3-4 times their width, and which are curiously twisted on crossing the protruded keels. Microsculpture of extremely fine radial riblets, more than 12 between each pair of major ribs, crossed by barely visible spiral riblets. Sutures deep on early spire, shallow on body whorl, latter flat or slightly concave up to strongly rounded supraperipheral keel, then flat down to deep supraperipheral sulcus, rising flatly to protruded keel, followed by a deep and narrow subperipheral sulcus, then flatly rounded down to strongly rounded basal margin. Aperture subquadrangular, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly one-quarter whorl: upper a high, thin blade, slightly more elevated and weakly expanded on posterior quarter, with gradual anterior descension; 2nd a very inconspicuous, threadlike trace partly obscured by protrusion of the very large radial ribs. Columellar wall without barriers. Palatal barriers 3, deeply recessed, very small and inconspicuous: lower just above sharp curve of basal margin, a short crescentic ridge extending less than one-eighth whorl; 2nd a much shorter, threadlike trace located midway between 1st palatal and outermost part of protruded keel; 3rd equal in size to 2nd, located inside outermost part of supraperipheral keel.

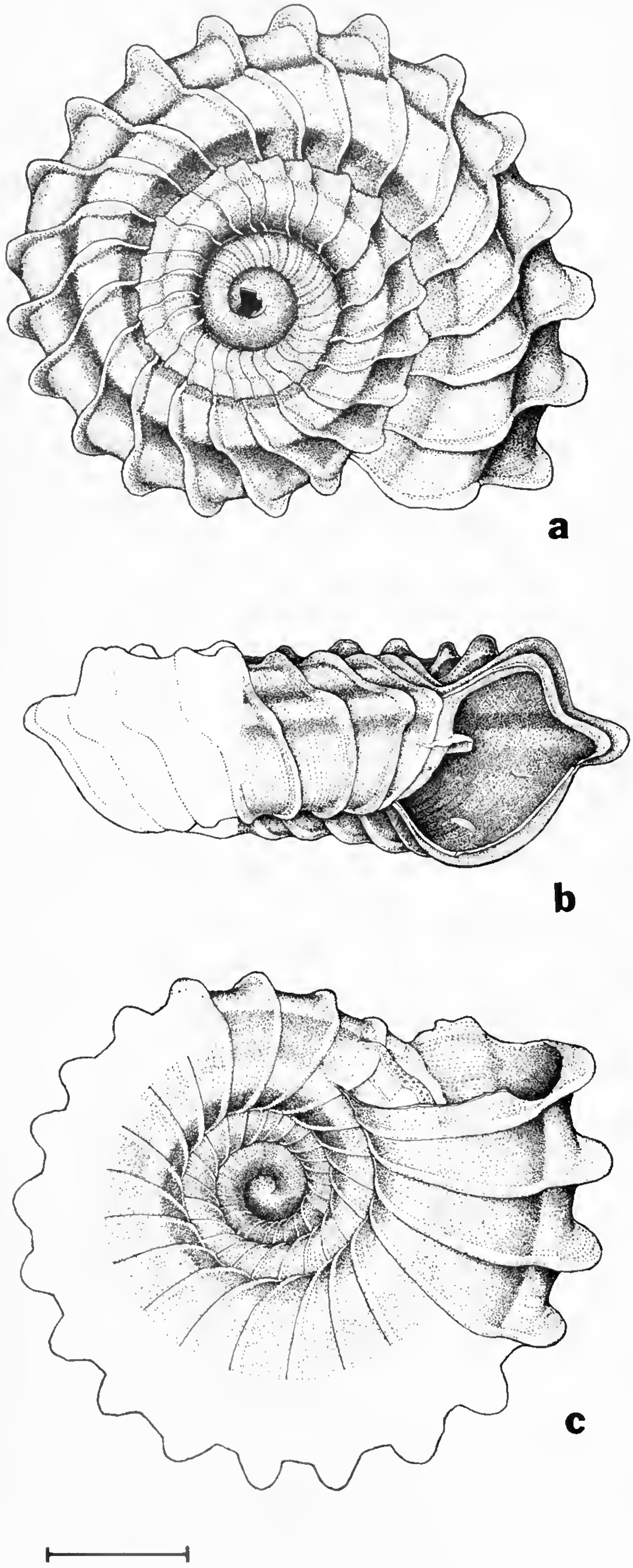

Fig. 93. *Cookeconcha stellulus* (Gould). Maui, Hawaiian Islands. FMNH 155099. (MM).

Holotype. – Maui, Hawaiian Islands. MCZ 169383 ex New York State Museum 242.

Range. – Maui, Hawaiian Islands.

Paratype. – FMNH 155099.

Material. – Hawaiian Islands, Maui (2 specimens, FMNH 155099, BMNH 42.2.21.63).

Remarks. – Casual inspection even with good optical equipment could result in missing the lower parietal and all the palatal barriers. Hence their omission from Gould's original description is not surprising. While *Cookeconcha stellulus* appears strikingly different from the remaining Hawaiian species, the alterations in whorl contour that give it this unusual appearance are the same alterations seen in the Mangarevan *Gambiodonta mirabilis* (fig. 188c-d), except for lacking a basal keel (the result of brood pouch formation in the *Gambiodonta*?), and in the Fijian *Thaumatodon spirrhymatum* Solem (1973d). In sculpture, barriers, general appearance and basic shape, *Cookeconcha stellulus* clearly is related to *C. hystricellus.* Unless anatomical peculiarities are demonstrated, I doubt that even subgeneric separation from *C. hystricellus* would be warranted. Since populations of the latter show a weak-to-moderate supraperipheral sulcus, the extensive development of keels and sulci in *C. stellulus* should be viewed as an elaboration of a trend, rather than set apart as a unique occurrence. After completion of this section, another specimen was located in the British Museum (Natural History). Its dimensions have been added to the diagnosis, but no average computed.

Cookeconcha paucicostatus (Pease, 1870)

Pitys paucicostata Pease, 1870, Jour. de Conchyl., **18,** p. 395 – Kauai; Ancey, 1889, Bull. Soc. Malacol. France, **6,** p. 184.
Pitys filicostata Pease, 1871, Proc. Zool. Soc. London, **1871,** p. 454.
Helix paucicostata (Pease), Pfeiffer, 1876, Mon. helic. viv., **7,** p. 261; Tryon, 1887, Man. Conchol., (2), **3,** p. 60.
Patula (*Endodonta*) *paucicostata* (Pease), Clessin, 1881, Nomen. helic. viv., p. 95.
Helix filicostata (Pease), Tryon, 1887, Man. Conchol., (2), **3,** p. 60.
Helix (*Pitys*) *paucicostata* (Pease), Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 – Kealia to Haena, Kauai.
Endodonta filicostata (Pease), Pilsbry, 1893, Man. Conchol., (2), **9,** p. 26.
Endodonta paucicostata (Pease), Pilsbry, 1893, Man. Conchol., (2), **9,** p. 26.
Endodonta (*Nesophila*) *paucicostata* (Pease), Sykes, 1900, Fauna Hawaiiensis, Moll., **2,** (4), p. 291.

Range. – Kauai, Hawaiian Islands.

Material. – "Marquesas" (1 specimen, FMNH 46435, ex Webb, Gude, Ancey).

Remarks. – The single specimen, 3.06 mm. in diameter with 4⅛– whorls, although mislabelled as to locality, is this unfigured species. The 2 weak parietal

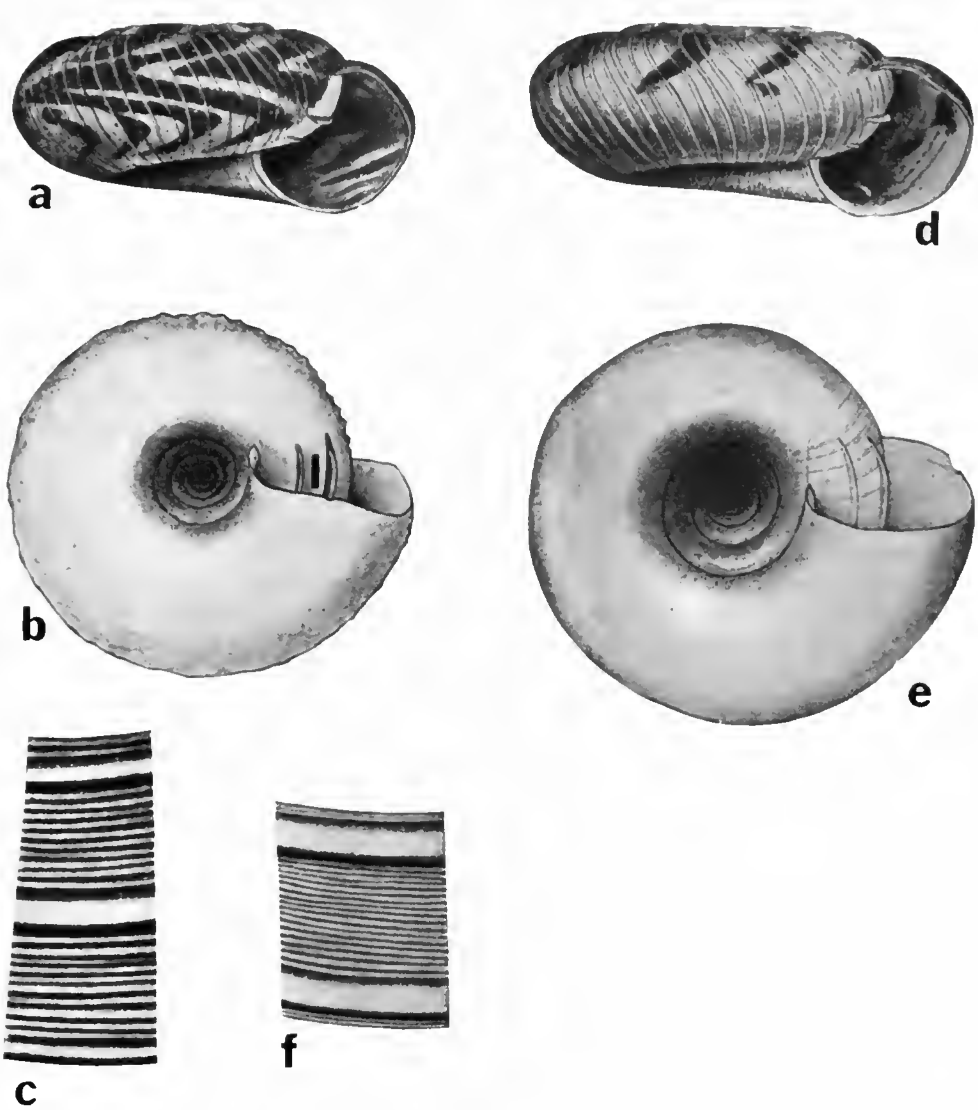

FIG. 94. **a-c**, *Cookeconcha thaanumi* (Pilsbry & Vanatta). Kaiwiki, Hilo, Hawaii, Hawaiian Islands. Holotype ANSP 89245; **d-f**, *Cookeconcha luctiferus* (Pilsbry & Vanatta). "Sandwich Islands." Holotype. ANSP 58137. Copied from Pilsbry & Vanatta (1905, pl. 39) with permission of the Academy of Natural Sciences, Philadelphia. Relabled for this use. Figures *c* and *f* incorrect in showing microradial ribs absent from surface of major ribs and no indication of microspiral ribs.

barriers, very widely spaced radial ribs, 24 on the body whorl with 2.50 ribs/mm., loss of sculpture on the first part of the apex, umbilical shape and size (D/U ratio 3.88), plus the very low spire (H/D ratio 0.473), suggest that this is derived from a type very close to *Cookeconcha luctiferus*.

Cookeconcha paucilamellatus (Ancey, 1904)

Endodonta hystricella var. *paucilamellata* Ancey, 1904, Jour. Malacol., **11**, p. 67, pl. 5, fig. 17 – Palihoukapapa, Hamakua slope of Mauna Kea, Hawaii, Hawaiian Islands.

Range. – Hawaii, Hawaiian Islands.

Material. – None.

Remarks. – The complete absence of palatal barriers, wider and more regular radial ribs, and apparently much narrower umbilicus serve to distinguish this form from the Oahu *Cookeconcha hystricellus*.

Cookeconcha thaanumi (Pilsbry & Vanatta, 1905). Figure 94a-c.

Endodonta thaanumi Pilsbry & Vanatta, 1905, Proc. Acad. Nat. Sci., Philadelphia, **57**, pp. 574-575, pl. 39, figs. 1, 2, 3, – Kaiwiki, near Hilo, Hawaii; Olaa, Hawaii; and Honokowai Gulch, West Maui, Hawaiian Islands.

Diagnosis. – Shell large, diameter 4.44-5.53 mm. (mean 4.96 mm.), with 4⅞-5½ normally coiled whorls. Apex flat or slightly depressed, lower spire descending slightly, body whorl more rapidly, H/D ratio 0.435-0.524 (mean 0.471). Umbilicus U-shaped, regularly decoiling, contained 3.07-3.73 times (mean 3.39) in the diameter. Apical sculpture absent nearly to end of apex. Postnuclear sculpture of thin, prominent, strongly protractively sinuated radial ribs, 46-57 (mean 51.7) on the body whorl, whose interstices are 4-6 times their width. Microsculpture of very fine radial riblets, eight to twelve between each pair of major ribs, with barely visible, extremely crowded spiral ribbing visible under 96× magnification. Sutures impressed, whorls strongly rounded above and on basal margin, slightly compressed laterally above and below rounded periphery. Aperture subcircular, compressed laterally above and below rounded periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly less than one-quarter whorl: upper threadlike to moderately elevated, not expanded above, extending posteriorly three-sixteenths to one-quarter whorl; lower threadlike for entire length, extending slightly further anteriorly. Columellar and palatal walls without barriers.

Types. — Kaiwiki, Hilo, Hawaii, Hawaiian Islands. ANSP 89245.

Range. — Reported from Molokai, Maui and Hawaii, Hawaiian Islands.

Material. — Hawaiian Islands: Molokai (4 specimens, FMNH 46237); Kaluaaha, Molokai (2 specimens, FMNH 73193).

Remarks. — Careful analysis of shape and sculptural variation will be required before the reported range of *Cookeconcha thaanumi* can be accepted or rejected. Differences from the other described species with 2 parietals and without palatals are simple: *C. hystrix* has undulating sculpture and a markedly hirsute periostracum, while *C. paucicostatus* has much fewer and more widely spaced ribs, is much smaller, and has a narrower umbilicus (table LXXIV). The other species have only a single parietal.

Cookeconcha hystrix (Pfeiffer, 1846)

Helix hystrix "Mighels" Pfeiffer, 1846, Symb. ad. hist. Heliceorum, **3**, (5), pp. 67-68 — Hawaiian Islands; Pfeiffer, 1848, Mon. helic. viv., **1**, p. 116 — Wahoo (= Oahu), Hawaiian Islands; Pfeiffer, 1852, Syst. Conchyl. Cab., **12**, (2), p. 132, pl. 89, figs. 8-11, (plate issued 1850); Gould, 1852, U. S. Explor. Exped. "Wilkes," **12**, pp. 55-56 — East Maui (probably a different species); Pfeiffer, 1853, Mon. helic. viv., **3**, p. 145; Reeve, 1854, Conchol. Icon., *Helix,* pl. 133, fig. 655; Pfeiffer, 1859, Mon. helic. viv., **4**, p. 156; Gould, 1860, U. S. Explor. Exped. "Wilkes," Exped. Shells, Atlas, pl. 4, fig. 52*, 52b*, 52c*; Pfeiffer, 1868, Mon. helic. viv., **5**, p. 222; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 261; Tryon, 1887, Man. Conchol., Philadelphia, 3, p. 59, pl. 11, figs. 71-73; Johnson, 1949, Occ. Pap. Moll., **1**, (14), p. 225.

Helix setigera Gould, 1844 (not Sowerby, 1841), Proc. Boston Soc. Nat. Hist., **1**, p. 174.

Patula hystrix (Pfeiffer), Albers, 1850, Die Heliceen, p. 65; von Martens, 1860, Die Heliceen, ed. 2, p. 90.

Pitys hystrix (Pfeiffer), H. & A. Adams, 1858, Genera Recent Moll., **2**, p. 113; Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 471 — Oahu; Ancey, 1889, Bull. Soc. Malacol. France, **6**, pp. 182-183.

Patula (Endodonta) hystrix (Pfeiffer), Clessin, 1881, Nomen. helic. viv., p. 95 — Sandwich Islands.

Helix (Pitys) hystrix Mighels, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 — Maui, Oahu, and Kauai.

Endodonta hystrix (Pfeiffer), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Endodonta (Nesophila) hystrix (Pfeiffer), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 290 — Mt. Kaala, Oahu, Hawaiian Islands.

Diagnosis. — Shell very large, diameter 4.61-6.27 mm. (mean 5.32 mm.), with 4⅝-5⅝ normally coiled whorls. Apex and early spire sunken, later whorls descending rapidly, H/D ratio 0.431-0.577 (mean 0.475). Umbilicus broadly open, V-shaped, regularly decoiling, contained 2.63-3.94 times (mean 2.94) in the diameter. Apical sculpture absent for most of first whorl, typical near end. Postnuclear whorls with high, very prominent, strongly protractively sinuated radial ribs, 31-70 (mean 41.3) on the body whorl, whose interstices are 3-5 times their width, some populations having the tops of major ribs with long periostracal hairs arranged in spiral rows, the hair "pits" giving a wavy, undulating effect to the sculpture. Microsculpture of fine radial riblets, eight to twelve between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures deep, whorls strongly rounded above and on basal margin, either flattened laterally above and below rounded periphery or with evenly rounded outer margin. Aperture subcircular, with rounded or variously flattened outer margins, inclined about 25° from shell axis. Parietal barriers 2, lower rarely absent, extending posteriorly slightly less than one-quarter whorl: upper threadlike for entire length or weakly elevated posteriorly; lower threadlike, anterior end slightly in front of upper.

Description (of *setigera*). — Shell of average size, with slightly less than 4¾ normally coiled whorls. Apex and first two post-nuclear whorls sunken below top of body whorl, latter portion of body whorl descending slightly, H/D ratio 0.430. Apical whorls 1⅛, sculpture of very fine radial riblets on last part, partially obscured by fungus. Postnuclear whorls with high, prominent, protractively sinuated, somewhat nodose radial ribs, 32 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of relatively prominent radial riblets, crossed by barely visible, much finer and more crowded spiral riblets. Sutures deep, whorls slightly shouldered above with rounded outer margin, slightly flattened laterally below periphery and on columellar margin. Color yellowish-white with broad, zigzag, reddish flammulations, seven on the body whorl, that become very thin and attenuated below periphery. Umbilicus broadly open, U-shaped, regularly and slightly decoiling, contained 3.37 times in the diameter. Aperture subovate, slightly compressed laterally below periphery and on columellar margin, inclined about 30° from the shell axis. Parietal wall with 2 low, threadlike barriers, extending three-sixteenths of a whorl, the upper slightly more prominent, and a faint suggestion of an upper parietal trace. Columellar and palatal walls without barriers. Height of holotype 1.91 mm., diameter 4.44 mm.

Lectotype. — Sandwich Islands (= Hawaii). Collected by United States Exploring Expedition. USNM 5453.

Material. — Hawaiian Islands (19 specimens, FMNH 46444, FMNH 91151, FMNH 91890, FMNH 117045): Oahu, Konahuanui (1 specimen, FMNH 116895); Helemanu (1 specimen, FMNH 116896); Palikea, Waianae Mts. (25 specimens, FMNH 53043, FMNH 111527).

Remarks. — The lectotype of *Helix setigera* Gould, 1844 (not Sowerby, 1841) is juvenile. A specimen mislabelled as "type" of *Helix rubiginosa* Gould, 1846 is this species. The nuclear whorls of the former are larger (0.46 mm. wide compared with 0.36 mm.) and the radial ribs more widely spaced (2.29 ribs/mm. in *setigera,* 3.21 ribs/mm. in the other).

Probably several species are confused under this name, and *Cookeconcha hystrix* should be restricted to the very large, hirsute population found on Mt. Konahuanui. The shells from East Maui with small palatal barriers reported by Gould (1852, p. 56) probably are related to *C. hystricellus* and not to *C. hystrix.* Specimens from the Mt. Konahuanui population were dissected. As mentioned above, specimens from Helemanu that were conchologically referred to as *hystrix* showed differences in penial pilaster pattern that might indicate specific separation. More studies are needed, before the many Oahu forms of this type can be classified with certainty.

Description of soft parts. — Only differences from the material of *C. hystricellus* are noted. Kidney longer and more slender with the rectal arm equal to half of length. Lobes of ovotestis larger, talon much more slender and free oviduct proportionately a little longer.

Vagina absent, since spermatheca inserts on oviducal side of peniovidueal angle. Penis about 3.95 mm. long, not as expanded and contracting near atrium rather than tapering, internally with similar pilasters, except both are narrower, with greater free edges and much longer. Larger of two pilasters (which unite apically) comes to a bluntly tapered end about five-eighths of way down length of penis. In *C. hystricellus,* the larger pilaster comes to a globosely rounded, abrupt termination about three-eighths of way from penial apex. No other significant differences could be found.

(Based on BPBM 17607, three examples.)

Cookeconcha decussatulus (Pease, 1866)

Helix decussatula Pease, 1866, Amer. Jour. Conchol., 2, p. 291 — Sandwich Islands; Pfeiffer, 1876, Mon. helic. viv., **7,** p. 261; Tryon, 1887, Man. Conchol., (2), **3,** p. 60.

Pitys decussatula (Pease), Pease, 1871, Proc. Zool. Soc. London, **1871,** p. 474 — Molokai; Ancey, 1889, Bull. Soc. Malacol. France, **6,** pp. 184-185.

Patula (Endodonta) decussatula (Pease), Clessin, 1881, Nomen. Helic. viv., p. 95.

Helix (Pitys) decussatula Pease, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 — Wahiawa and Waimea, Kauai.

Endodonta decussatula (Pease), Pilsbry, 1893, Man. Conchol., (2), **9,** p. 27.

Endodonta (Nesophila) decussatula (Pease), Sykes, 1900, Fauna Hawaiiensis, Moll., **2,** (4), p. 290 — Mountains at 4,000 ft., Molokai, Hawaiian Islands.

Diagnosis. — Shell slightly smaller than average, diameter 3.49-4.28 mm. (mean 3.76 mm.), with 4⅛ - 4¾ normally coiled whorls. Apex and spire flat or barely elevated, last whorl descending slightly more rapidly, H/D ratio 0.364-0.405 (mean 0.389). Umbilicus broadly open, V-shaped, regularly decoiling, contained 3.02-3.42 times (mean 3.25) in the diameter. Apical sculpture absent on first whorl, greatly reduced on rest. Postnuclear whorls with low, V-shaped, strongly protractive radial ribs, 60-74 (mean 67.8) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of rather large radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets that are barely visible under 96X magnification, with a secondary sculpture of narrow spiral cords that are most crowded near periphery and most widely spaced on shell base. Secondary spiral cords quite narrow, almost V-shaped. Sutures impressed, whorls flatly rounded above and on basal margin, strongly and evenly rounded on outer margin. Aperture subcircular, flattened above and below evenly rounded periphery, inclined about 25° from shell axis. Parietal wall with single supramedial, low, bladelike barrier, extending posteriorly to line of vision, with gradual anterior descension.

Range. — Maui and Molokai, Hawaiian Islands.

Material. — Hawaiian Islands: Maui, western part (2 specimens, FMNH 46605); Homokowai (*sic*) Gulch (3 specimens, AMS C37190 ex Hedley, Preston); Hokokoupi Gulch (1 specimen, FMNH 90636).

Remarks. — The secondary spiral cording and much smaller size combine to separate *Cookeconcha decussatulus* from either *C. jugosus* or *C. lanaiensis,* the other named forms with only a single parietal. The latter is very similar in general appearance and may be only subspecifically separable when adequate material has been examined.

Cookeconcha lanaiensis (Sykes, 1896)

Endodonta (Nesophila) lanaiensis Sykes, 1896, Proc. Malacol. Soc. London, **2,** (3), p. 127 — behind Koele, Mountains of Lanai, Hawaiian Islands; Sykes, 1900, Fauna Hawaiiensis, Moll., 2, (4), p. 291, pl. 11, figs. 37, 38 — ?Makaweli, Kauai, Hawaiian Islands.

Endodonta lanaiensis (Sykes), Ancey, 1904, Jour. Malacol., **11,** p. 67 — Palihoukapapa, Hamakua slope of Mauna Kea, Hawaii, Hawaiian Islands.

Diagnosis. — Shell larger than average, diameter 4.24-5.10 mm. (mean 4.72 mm.), with 4½ - 4¾ normally coiled whorls. Apex and spire flat or slightly depressed, last whorl descending slightly, H/D ratio 0.354-0.414 (mean 0.374). Umbilicus broadly open, V-shaped, regularly decoiling, contained 2.98-3.45 times (mean 3.23) in the diameter. Apical sculpture absent from first whorl, very faint on rest of apex. Postnuclear sculpture of broad, low, protractively sinuated radial ribs, 50-72 (mean 64.3) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of rather large radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls flatly rounded above and below strongly rounded periphery. Aperture ovate, inclined about 30° from shell axis. Parietal wall usually with a single, supramedial, raised threadlike ridge, extending posteriorly to line of vision, sometimes with a very inconspicuous lower accessory threadlike trace. Columellar and palatal walls without barriers.

Description. — Shell larger than average, with slightly less than 4¾ normally coiled whorls. Apex and early spire flat, later whorls descending moderately, H/D ratio 0.414. Apical whorls 1⅜, smooth at first, sculpture of fine, crowded radial ribs, whose interstices are less than twice their width, with a barely visible secondary sculpture of crowded spiral riblets. Postnuclear whorls with high, broadly rounded, irregularly sinuated, strongly protractive radial ribs, about 66 on the body whorl, whose interstices are 2-4 times their width. Major ribs varying greatly in width, often with a knob-like appearance at nearly regular intervals. Microsculpture of prominent, relatively crowded, sinuated radial riblets crossed by extremely fine and crowded spiral riblets. Color light yellowish-white with zigzag, narrow, reddish flammulations. Sutures deep, whorls strongly rounded above, flattened laterally above evenly rounded periphery and on basal margin. Umbilicus V-shaped, widely open, regularly decoiling, contained 3.45 times in the diameter. Periphery of whorl slightly angulated. Aperture ovate, slightly flattened above periphery and on basal margin, inclined about 25° from shell axis. Parietal barriers 2: upper a moderately elevated, ridgelike lamella, extending more than one-quarter whorl and supramedial in position; lower parietal an inconspicuous, threadlike ridge parallel to the upper and slightly submedial in position. No columellar or palatal barriers. Height of holotype 1.97 mm., diameter 4.77 mm.

Holotype. — Hawaiian Islands: Lanai, Mountains behind Koele. BMNH 1900.12.18.1521.

Range. — Lanai, possibly Hawaii and Kauai, Hawaiian Islands.

Paratypes. — BMNH 1900.12.18.1376-80.

Material. — Hawaiian Islands: Lanai (1 specimen, BPBM 14234); mountains behind Koele (6 specimens, BMNH 1900.12.18.1521, BMNH 1900.12.18.1376-80).

Remarks. — The single adult of several specimens from Kauai (BMNH 1900.12.18.1396-1406) that Sykes (1900, p. 291) referred to this species differs in rib count (83), whorls (5¼-) and D/U ratio (3.87). I suspect it is specifically distinct. The holotype is the only example with a 2nd parietal trace.

Cookeconcha jugosus (Mighels, 1845). Figure 165h-i.

Helix jugosa Mighels, 1845, Proc. Boston Soc. Nat. Hist., **2,** p. 19 — Waioli, Kauai, Hawaiian Islands; Pfeiffer, 1848, Mon. helic. viv., **1,** p. 188; Pfeiffer, 1853, Mon. helic. viv., **3,** p. 145; Pfeiffer, 1859, Mon. helic. viv., **4,** p. 156; Pfeiffer, 1868, Mon. helic. viv., **5,**

p. 222; Pease, 1871, Jour. de Conchyl., **19**, pp. 95-96; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 266; Pfeiffer, 1877, Syst. Conchyl. Cab., (1), **12**, (4), p. 554, pl. 166, fig. 19-21; Tryon, 1887, Man. Conchol., (2), **3**, p. 59, pl. 11, fig. 65-68; Johnson, 1949, Occ. Pap. Moll., **1**, (14), p. 226.

Helix rubiginosa Gould, 1846, Proc. Bost. Soc. Nat. Hist., **2**, p. 173; Gould, 1846, Exped. Shells, Reprint, p. 21 – Kauai; Pfeiffer, 1848, Mon. helic. viv., **1**, p. 187; Gould, 1852, U. S. Explor. Exped. "Wilkes," **12**, pp. 50-51 – Kauai; Pfeiffer, 1853, Mon. helic. viv., **3**, p. 145; Pfeiffer, 1859, Mon. helic. viv., **4**, p. 156; Gould, 1860, U. S. Explor. Exped. "Wilkes," *Atlas*, pl. 4, fig. 49, 49a, 49b, 49c; Pfeiffer, 1868, Mon. helic. viv., **5**, p. 222; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 266; Johnson, 1964, Bull. U. S. Nat. Mus., **239**, p. 143.

Endodonta jugosa (Mighels), Albers, 1850, Die Heliceen, p. 89; von Martens, 1860, Die Heliceen, ed. 2, p. 90; Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Endodonta rubiginosa (Gould), Albers, 1850, Die Heliceen, p. 89; von Martens, 1860, Die Heliceen, ed. 2, p. 90.

Pitys jugosa (Mighels), H. & A. Adams, 1858, Genera Recent Moll., **2**, p. 113; Pease, 1871, Proc. Zool. Soc. London, **1871**, pp. 452, 474 – Kauai; Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 178.

Pitys rubiginosa (Gould), H. & A. Adams, 1858, Genera Recent Moll., **2**, p. 114; Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 179 – Kauai and Oahu (?).

Patula (Endodonta) jugosa (Mighels), Clessin, 1881, Nomen. Helic. viv., p. 94.

Helix (Endodonta) jugosa Mighels var. *rubiginosa* Gould, Clessin, 1881, Nomen. Helic. viv., p. 95; Tryon, 1887, Man. Conchol., (2), **3**, p. 59, pl. 11, figs. 68-70.

Helix (Pitys) jugosa Mighels, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16–Waioli and Kapaa, Kauai.

?*Helix (Pitys) rubiginosa* Gould, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 – Waianae Mts., Oahu.

Endodonta (Nesophila) jugosa (Mighels), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 290 – Waioli to Kapaa, Kauai.

Diagnosis. – Shell very large, diameter 5.26-7.37 mm. (mean 6.18 mm.), with 4¾ - 5⅝ normally coiled whorls. Apex and early spire flat to moderately elevated, last whorls descending distinctly more rapidly, H/D ratio 0.390-0.521 (mean 0.450). Umbilicus widely open, V-shaped, regularly decoiling, contained 2.38-3.20 times (mean 2.66) in the diameter. Apex with sculpture absent on first whorl, reduced on remainder. Postnuclear sculpture of low, narrow, strongly protractively sinuated radial ribs, 47-80 (mean 62.0) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of very fine radial riblets, five to eight between each pair of major ribs, with spiral riblets that are barely visible under 96× magnification. Sutures impressed, whorls with evenly rounded outer margins. Aperture circular, inclined about 25° from shell axis. Parietal wall with a single medial or slightly supramedial, raised, threadlike ridge, sometimes slightly elevated posteriorly, not expanded above, that extends almost one-quarter whorl posteriorly. Columellar and palatal walls without barriers.

Range. – Kauai, Hawaiian Islands.

Material. – Hawaiian Islands: Kauai, Milolii (1 specimen, FMNH 116900); north fork Wailua River (2 specimens, FMNH 116898 ex BPBM 81197); Kapaa (6 specimens, FMNH 117043); Haena (1 specimen, FMNH 116897); Kapiliwahine, east of Wahiawa dam (7 specimens, FMNH 116899).

Remarks. – A specimen in the United States National Museum (USNM 5449) that I had thought might be a type of *Helix rubiginosa* Gould, 1846 and that Johnson (1964, p. 143) listed as the "holotype" is a mislabeled example of *Cookeconcha hystrix* with 2 parietals and remnants of the periostracal hair pits. It is quite different from Gould's (*loc. cit.*) type figures, and is not at all similar in sculpture to the specimens known under this name. While Johnson's holoytpe "designation" switches the name *rubiginosa* to the synonymy of *hystrix*, and possibly would replace the latter, since both names were proposed in 1846, all the *references* listed above are to the original concept of the name *rubiginosa*. Nomenclatural quibbling would require a transfer of names and references, plus dredging historical records to establish the relative priority of *hystrix* and *rubiginosa*. No scientific utility would be served by such a procedure, and I strongly recommend that the historical usage of these names be continued.

Local populations show marked variation in spire height and umbilical width (table LXXIV), but whether this is indicative of subspeciation remains to be determined. Dissections are based on specimens from the north fork of the Wailua River. These shells are quite large and have a relatively elevated spire.

Other named Hawaiian species with only 1 parietal barrier differ in having secondary spiral sculpture (*decussatulus*) or in being much more depressed with a narrower umbilicus (*lanaiensis*).

Description of soft parts. – Foot and tail about equal in length to shell diameter. Sole undivided. Pedal grooves sharply defined, relatively high on foot, no caudal horn or mid-dorsal groove present. Slime network strongly demarcated, with irregularly ovate divisions, varying greatly in size. Head at least partly retracted in all available examples. Ommatophores typical. Gonopore position not determined.

Body color yellow-white, without darker markings.

Mantle collar with thickened edge, no glandular extension onto pallial roof. Pneumostome and anus in typical position.

Pallial region about 9.5-11 mm. long. Lung roof clear, without granulations. Kidney about 4.2 mm. long, rectal arm slightly less than half total length, rounded posteriorly and extending over loop of intestine. Ureter typical, slightly reflexed along weak rectal extension, opening at rectal arm of kidney termination next to hindgut. Heart about 1.6 mm. long, lying parallel to hindgut. Principal pulmonary vein typical, fading out before mantle collar. Hindgut typical, following parietal-palatal margin about one-eighth whorl above apex of pallial cavity.

Ovotestis (fig. 165h, G) of numerous clumps of palmately clavate alveoli, overlapping along a single collecting tubule, first few clumps lying perpendicular to plane of coiling, more apical clumps lying at a lesser angle than in *E. fricki*. Hermaphroditic duct (GD) slightly to moderately convoluted medially, very narrow at either end, reflexing slightly before entering carrefour (X). Albumen gland (GG) relatively larger than in *Nesophila tiara*, but still rather small. Talon (GT) large, finger-like, not tapered basally, but sharply constricted before entering carrefour. Latter oval, tapering into shaft after entrance of hermaphroditic duct prior to splitting into prostatic and uterine ducts. Prostate (DG) typical, two or three rows of large acini opening into a narrow tube. Uterus (UT) bipartite, lower expanded chamber extending below end of prostate.

Vas deferens (VD) typical, lightly bound to peniovidical angle, entering penis about 1 mm. below apex of penis, with penial pore lying outside pilaster ring, but near to edge of one pilaster. Penial retractor (PR) inserting directly on head of penis, arising from diaphragm at apex of pallial cavity. Penis (P) moderately twisted in partly retracted individuals, about 3.5-4.0 mm. long, not tapered until just before base, internally (fig. 165i) with two large, rounded, hemispherical pilasters united at apex, either united (as in figured example) or tapering off basally. Atrium (Y) short, but a distinct region.

TABLE LXXV. - RANGE OF VARIATION IN OPANARA AND KLEOKYPHUS

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
Opanara										
altiapica	24	80.0(64-91)	2.03(1.74-2.30)	2.82(2.63-3.03)	0.719(0.664-0.761)	5 1/4-(4 7/8-5 5/8)	4.69(3.91-5.53)	3	1	4
caliculata	8	120.3(117-125)	2.02(1.84-2.24)	3.27(3.09-3.39)	0.617(0.595-0.660)	5-(4 5/8-5 1/4)	4.74(4.09-5.22)	3	1	4
bitridentata	81	79.1(70-91)	1.76(1.48-1.97)	3.36(3.03-3.88)	0.524(0.483-0.580)	5 3/8+(5-5 7/8)	5.31(3.58-8.45)	2-3+0-1	1	4-5-6+3-11
perahuensis	12	61.8(55-64)	1.81(1.61-1.88)	3.15(2.83-3.49)	0.579(0.555-0.620)	5 1/2+(5 1/4-5 5/8)	28.2 (15.3-CLOSED)	3	1	4
fosbergi	5	104.3(93-112)	1.30(1.19-1.39)	3.77(3.61-4.01)	0.344(0.330-0.375)	5 1/2(5 3/8-5 5/8)	7.10(5.74-8.07)	3-4	0	5[2]
areaensis areaensis	790	60.2(49-80)	1.94(1.55-2.30)	3.53(3.03-3.98)	0.549(0.505-0.634)	5 5/8-(5 1/8-6 1/4)	3.67(2.97-4.73)	3-4+0-1	1[1]	4
areaensis densa	19	103.5(90-113)	1.90(1.69-2.19)	3.32(3.15-3.68)	0.572(0.537-0.616)	5 3/8+(5 1/8-5 3/4)	3.62(3.31-3.97)	3	1[1]	4
areaensis microtorma	5	77.0(73-83)	2.10(1.99-2.19)	3.60(3.54-3.64)	0.584(0.551-0.607)	5 3/4-(5 1/2-6)	4.11(3.86-4.27)	3	1[1]	4
depasoapicata	15	81.0(78-84)	1.54(1.49-1.59)	3.11(3.05-3.15)	0.494(0.489-0.505)	5 7/8-(5 5/8-6)	2.92(2.88-2.97)	3	1	4-5-6
megomphala megomphala	14	73.7(71-76)	1.64(1.38-1.88)	3.21(2.83-3.52)	0.511(0.486-0.564)	5 3/4-(5 1/4-6 1/8)	2.22(2.15-2.35)	4-6+0-3	MANY	
megomphala tepiahuensis	121	64.6(54-81)	1.46(1.16-1.66)	3.36(2.98-3.77)	0.434(0.353-0.481)	5 7/8(5 1/2-6 1/8)	1.95(1.72-2.08)	4-6+0-3	MANY	
duplicidentata	39	84.2(70-100)	2.37(2.01-2.76)	4.32(3.72-4.84)	0.549(0.508-0.594)	6-(5 5/8-6 1/4)	3.03(2.49-3.65)	4+0-1	1	5+6
Kleokyphus										
callimus	4	REDUCED	2.57(2.37-2.73)	4.40(4.28-4.47)	0.583(0.554-0.615)	7 1/2-(7 1/4-7 5/8)	6.87(6.50-7.30)	4	1	5
hypsus	1	WORN OFF	4.51	6.60	0.683	8	5.61	3+3	0	4

1. Deflected onto basal lip.
2. Columellar lamella displaced onto palatal wall.

Free oviduct (UV) quite short, indistinctly demarcated from terminal section of uterus. Spermatheca (S) with elongately oval head in normal position, lower part of shaft sometimes expanded, inserting just on oviducal side of peniovidueal angle. Vagina (V) not effectively present as a distinct morphologic zone.

Free muscle system and digestive system as in *Endodonta* and *Nesophila*.

Jaw of many narrow, partly fused, overlapping plates, too indistinct to count, about 0.41 mm. long.

Radula with 14 laterals and many more than 8 marginals, central about 6μ wide and 14μ long. Basal plates of marginals square, four or five almost equal cusps.

(Based on BPBM 81197, several whole and partly broken examples.)

Genus **Kleokyphus**, new genus

Large Endodontidae with a narrow, U-shaped umbilicus, more than 7 tightly coiled whorls, a dome-shaped spire, 3-4 large parietals and 4-5 large palatals. Sutures shallow to deep, body whorl obtusely angulated to laterally compressed, aperture inclined 20-25° from shell axis. Apical sculpture typical of subfamily, postnuclear major sculpture prominent (?) to greatly reduced above periphery. Anatomy unknown.

Type species. — Kleokyphus callimus, new species.

The size and form of the parietal and palatal barriers is essentially the same as in *Mautodontha boraborensis* and *M. zimmermani*. The narrow umbilicus, many whorls, and very large size of the two *Kleokyphus* immediately separate them from *Mautodontha*. Very few *Mautodontha* have 4 parietals and 5 palatals. In *M. daedalea*, also known from Makatea, the barriers are very reduced in size, the spire is depressed and the umbilicus wide and shallow (fig. 73d). The form of the umbilicus in *K. hypsus* recalls that of *Mautodontha (Garrettoconcha) consobrina*, but the differences in whorls and barriers are too great for the species to be congeneric.

Kleokyphus and *Mautodontha* probably evolved from a single stock, but the former has developed more specialized barriers, more and tighter coiled whorls (cf. tables LXV, LXVI, and LXXV), a narrower umbilicus that apically may be wider than below, and altered sculpture in the one species where this is known with certainty. The structural gap between *Kleokyphus* and any *Mautodontha* is much greater than the gaps that exist between species within *Mautodontha*. *Kleokyphus* is another experiment towards the brood chamber level of specialization.

The single specimen of *K. hypsus* has no trace of sculpture left on the upper surface. On the shell base a few obscure rugosities suggest that it has typically developed radial sculpture, but this cannot be determined with any certainty. The sculpture of *K. callimus* is remarkable. After typical endodontid apical sculpture, a pattern of major radials begins, quickly is reduced in prominence, and by the end of the first post-nuclear whorls, the "major" ribs are no wider than the microradials. The major ribs remain slightly elevated and in strong lateral lighting can be distinguished. They are very widely spaced, but it proved impossible to make an accurate count of the "major" ribs. Just below the obtusely angulated periphery, a nearly normal pattern of ribbing is seen, with the major radials being several times the size of the microradials and having an obvious secondary sculpture of spiral cording.

The specimen that Aubert de la Rüe and Soyer (1958, p. 365) identified as "*Endodonta daedalea*" may belong to a third species or may be a young example of *K. hypsus*. The specimen was 1.35 mm. high, diameter 3.78 mm., with 4¼- whorls, H/D ratio 0.547, D/U ratio 3.00, with about 110 ribs on the body whorl, 3 parietals and 4 palatals. Unfortunately, it broke during an attempt to clean the aperture. The wide umbilicus suggests *Mautodontha daedalea*, but the great shell elevation and different ribbing argue against this. The main reason against considering that it was a juvenile *K. hypsus* is the wide umbilicus. Without more material, its identity will remain uncertain.

The occurrence of two endemic genera, *Kleokyphus* and *Pseudolibera*, on Makatea is one of the most unexpected results of this study. The name *Kleokyphus*, from the Greek words for report (*kleos*) and humpbacked (*kyphos*), was chosen to emphasize the domed shape of these species and the remarkable nature of this find.

Kleokyphus callimus, new species. Figure 95a-c.

Libera heynemanni Aubert de la Rüe & Soyer, 1958 (not Pfeiffer, 1862), Bull. Mus. Nat. d'Hist. Nat., Paris, n. s., **30**, (4), pp. 365-366 — Makatea, Tuamotu Islands.

Diagnosis. — Shell relatively large, diameter 4.28-4.47 mm., (mean 4.40 mm.), with 7¼-7⅝ rather tightly coiled whorls. Apex flat, spire moderately elevated, last whorl not descending, H/D ratio 0.554-0.615 (mean 0.583). Umbilicus narrow, U-shaped, slightly wider apically than at last whorl, contained 6.50-7.30 times (mean 6.87) in the diameter. Postnuclear sculpture of very weak, quite widely spaced, protractively sinuated radial ribs, that are much more prominent below periphery of body whorl than above and are scarcely larger than the microradials. Microsculpture of fine radial riblets, nine to twelve between each pair of major ribs, crossed by much finer and very crowded spiral riblets, with a secondary sculpture of very fine spiral cords most clearly visible on shell base. Sutures not impressed, whorls flatly rounded above obtusely angulated periphery, with evenly rounded lower palatal and basal margins, sloping to sharply rounded umbilical margin. Aperture ovate, periphery obtusely angulated, inclined about 20° from shell axis. Parietal barriers 4, extending posteriorly three-sixteenths of a whorl: upper high and bladelike, weakly expanded above on posterior third, with very gradual anterior descension; 2nd and 3rd equally high and expanded on posterior quarter, anterior half to five-eighths low and threadlike; 4th parietal with posterior elevated portion distinctly reduced in height, but not in length, anterior portion threadlike. Columellar barrier a low lamellar ridge, almost parallel to plane of coiling, stopping anteriorly near apex of columellar callus, usually with one or two indistinct superior traces above. Palatal barriers 5, extending posteriorly more than one-eighth whorl, with one superior accessory trace: lower palatal slightly reduced in height, high and crescentic, with sharp anterior descension, only slightly recessed; 2nd, 3rd and 4th palatals distinctly higher, slightly more expanded above posteriorly, with progressively more gradual anterior descension and slightly deeper recession within

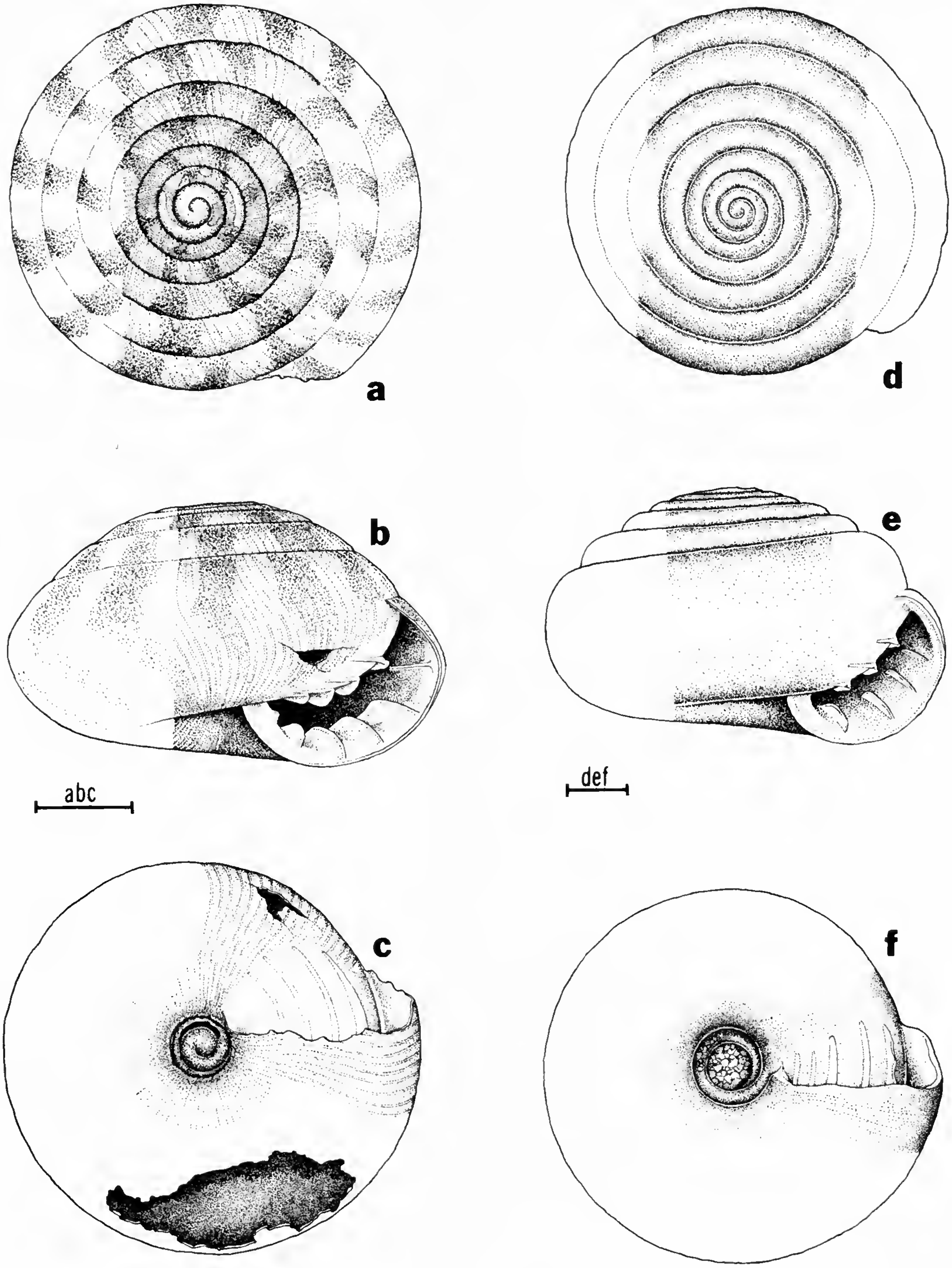

FIG. 95. **a-c**, *Kleokyphus callimus*, new species. Makatea, Tuamotu Islands. Paratype. Museum National d'Histoire Naturelle, Paris; **d-f**, *Kleokyphus hypsus*, new species. Makatea, Tuamotu Islands. Holotype. Museum National d'Histoire Naturelle, Paris. Scale lines equal 1 mm. (MM).

aperture; 5th palatal reduced in height, a prominent V-shaped ridge situated opposite 1st parietal, more deeply recessed within aperture. Accessory trace low and threadlike, deeply recessed, located just below parietal-upper palatal margin.

The presence of 4 parietals and 5 palatals at once distinguish *Kleokyphus callimus* from the much larger (diameter 6.60 mm.) *K. hypsus*, which has only 3 parietals and 4 palatals. While the supraperipheral postnuclear sculpture of *K. callimus* is very similar to that of *Libera dubiosa*, the greatly different umbilicus and apertural barriers at once separate the two species. The sculpture also serves to immediately separate all species of *Mautodontha*.

Description. – Shell rather large, with 7¼ rather tightly coiled whorls. Apex flat, spire moderately elevated, last whorl not descending more rapidly, H/D ratio 0.554. Embryonic whorls and early postnuclear whorls with sculpture mostly eroded. Remaining whorls with very low and inconspicuous, widely spaced, strongly protractively sinuated radial ribs, too indistinct to count. Microsculpture of very fine radial riblets, nine to twelve between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of weak spiral cording most clearly visible on shell base. Sutures very shallow, whorls flatly rounded above obtusely angulated periphery, evenly rounded on lower margin to sharply rounded umbilical margin. Color light yellowish-white with regularly spaced, relatively narrow, zigzag reddish flammulations that fade out on shell base. Umbilicus narrow, U-shaped, slightly wider apically than on last whorl, contained 6.50 times in the diameter. Aperture subovate, periphery obtusely angulated, inclined about 20° from shell axis. Parietal barriers 4, extending three-sixteenths of a whorl: upper parietal weakly expanded and serrated above for posterior third, with gradual anterior descension, 2nd and 3rd parietals with posterior third to quarter elevated and expanded as in 1st, anterior half low and threadlike; 4th parietal with elevated posterior portion reduced in height, with more gradual descension to anterior threadlike portion. Columellar barrier a low lamellar ridge, sharply descending anteriorly across peak of columellar callus, with two indistinct broadly rounded traces present above. Palatal barriers 5, extending over one-eighth whorl, with one superior accessory trace; lower palatal high, crescentic, bladelike, with relatively sharp anterior descension almost to apertural edge; 2nd, 3rd and 4th palatals slightly higher, progressively with more gradual anterior descension, slightly more expanded and serrated above posteriorly, a little more deeply recessed within aperture; 5th palatal slightly subperipheral in position, greatly reduced in height, a V-shaped ridge lying almost directly opposite 1st parietal. Accessory trace low and threadlike, deeply recessed, located just below parietal-palatal margin. Height of holotype 2.17 mm., diameter 4.28 mm.

Holotype. – Tuamotu Islands: Makatea. Collected by E. Aubert de la Rüe in 1955.

Range. – Makatea, Tuamotu Islands.

Paratypes. – Same as list of material.

Material. – Makatea (4 specimens, Paris, FMNH 153781).

Remarks. – Although the holotype is the smallest of the three adult specimens, its state of preservation is comparatively good. In the juvenile paratype the apical sculpture can be seen to have the typical endodontid pattern of fine radials interspersed with one or two finer radial riblets and crossed by very fine spiral riblets. All of the apical sculpture is slightly reduced in prominence. The early postnuclear whorls show relatively prominent radial ribbing, but by the third whorl this has become reduced to the point that it can scarcely be distinguished from the micro-radial ribbing. The great reduction of the supraperipheral sculpture, coupled with retention of relatively prominent radial ribs on the shell base is unique among the Polynesian Endodontidae and immediately separates this species. The effect of the supraperipheral sculpture is most similar to that found in *Libera dubiosa* from Moorea, Society Islands, but the totally different umbilical formation and apertural barriers prevent any confusion of the two species.

The form of the apertural barriers is most similar to those seen in *Mautodontha boraborensis* and *M. zimmermani* from the Society Islands, but the great number of whorls, elevated spire, very narrow umbilicus, and the reduced ribbing clearly separate *Kleokyphus callimus* from *Mautodontha*. No other genera are apt to be confused.

The specific name *callimus*, taken from the Greek, meaning most beautiful, is in recognition of the exquisite sculpture and bright color patterns of this species.

Kleokyphus hypsus, new species. Figure 95d-f.

Libera gregaria Aubert de la Rüe & Soyer, 1958 (not Garrett, 1884), Bull. Mus. Nat. d'Hist. Nat., Paris., n. s., **30**, (4), pp. 365-366 – Makatea, Tuamotu Islands.

Diagnosis and description. – Shell very large, diameter 6.60 mm., with 8 tightly coiled whorls. Apex and spire strongly elevated, slightly rounded above, last whorl descending much more rapidly, H/D ratio 0.683. Umbilicus narrowly U-shaped, last whorl decoiling very slightly more rapidly, contained 5.61 times in the diameter. Postnuclear sculpture of prominent, rather crowded, strongly protractively sinuated radial ribs. Sutures deep, whorls strongly rounded above evenly rounded outer margin. Aperture ovate, slightly compressed laterally. Parietal barriers 3, extending slightly less than three-sixteenths of a whorl, with at least three accessory traces visible: upper parietal high and bladelike, with gradual descension over anterior half; 2nd and 3rd parietals equally high for posterior third, more strongly expanded above, with anterior third low and threadlike. Accessory traces as follows: one between 2nd and 3rd parietal; two between 3rd parietal and columellar-parietal margin. No trace of a columellar barrier. Palatal barriers 4, extending about one-eighth whorl: 1st palatal an elevated bladelike lamella with rather sharp anterior descension; 2nd and 3rd slightly higher, expanded posteriorly, with much more gradual anterior descension; 4th palatal a much lower, V-shaped ridge, lying opposite upper parietal, extending slightly further anteriorly.

Kleokyphus hypsus obviously differs from the smaller *K. callimus* in its larger size, much higher spire, and presence of only 3 parietals and 4 palatals. Species of *Mautodontha* with comparable barrier numbers all are much smaller in size, much more depressed, and with much wider umbilici.

Holotype. – Tuamotu Islands: Makatea. Collected by E. Aubert de la Rüe in 1955. Museum National d'Histoire Naturelle, Paris. Height of holotype 4.51 mm., diameter 6.60 mm.

Range. – Makatea, Tuamotu Islands.

Material. – Makatea (1 specimen, Paris).

Remarks. — Despite the extremely worn condition of the single specimen, its large size, number and length of the barriers, high whorl count, compressed margin, and narrow umbilicus characterize it as a second species of *Kleokyphus.* Its general appearance is closest to some species belonging to the subgenus *Garrettoconcha,* but unquestionably it is not congeneric. The latter are much smaller, with fewer whorls, lower spires, have much greater descension of the body whorl and their umbilici tend to be much wider and differently shaped.

Genus **Opanara,** new genus

Medium-sized Endodontidae with typical apical and major radial sculpture. Microsculpture typical, only *fosbergi* with secondary sculpture. Apex and spire varying from depressed (*depasoapicata*) or flat (*fosbergi, megomphala* and *areaensis areaensis*), to very strongly elevated (*caliculata* and *altiapica*), last whorl slightly to moderately descending. Whorls laterally compressed, evenly rounded, or compressed above and below a rounded periphery. A supraperipheral sulcus present only in *duplicidentata.* Whorls 5⅝ - 6-, less only in the modified *altiapica* and *caliculata.* Umbilicus generally U-shaped, slightly to regularly decoiling, rarely extremely widely open (*megomphala*) or almost closed (*perahuensis*), sometimes with angled or margined (*caliculata* and *altiapica*) border. Parietal barriers normally 3, typical in form: either 2 or 3 in *bitridentata;* 4 in *duplicidentata;* and altered to low threads with accessory traces in *megomphala.* Columellar barrier small to large, parallel or slightly angled in most species; displaced onto basal lip in *fosbergi* by lateral compression; deflected onto basal lip in *areaensis;* and reduced to many threadlike traces in *megomphala.* Palatal barriers normally 4; increased to 5 in *duplicidentata;* broken into many fine threads in *megomphala;* accessory traces present only in *bitridentata* and *duplicidentata.* Ovotestis and hermaphroditic duct (so far as known) typical, talon relatively short with rapidly tapering shaft. Penial retractor arising from diaphragm (except columellar muscle in *duplicidentata*), inserting onto fleshy extension of penis head (no extension in *depasoapicata* and *caliculata*). Vas deferens entering penis quite near head, just below union of pilasters. Penial pilasters much higher than wide at base, simple and equal in most forms; simple and unequal in *depasoapicata, areaensis, altiapica* and *caliculata;* complexly folded in *duplicidentata;* and separated in *perahuensis.* Spermathecal shaft entering free oviduct just at peni-oviducal angle, so no vaginal region differentiated. Radula typical, tooth size reduced in *bitridentata* and *fosbergi.* Jaw of weak overlapping plates, broadly to narrowly rectangular.

Type species. — *Opanara areaensis areaensis,* new species and subspecies.

The diverse appearing species grouped here share a pattern of anatomical structure and seem to be the base group from which the other Rapan genera have been derived. The range of variation within *Opanara* approximates that seen in other stem groups such as *Mautodontha* and *Minidonta* and is much greater than in any of the derived taxa. *Opanara* shows numerous types of specialization, so that a neat, simple generic definition is impossible.

Of extralimital genera, *Opanara* shows most similarities to *Mautodontha* and the Marquesan taxa, *Taipidon* and *Planudonta. Mautodontha* has a lower mean whorl count, 4⅞ - 5⅜, except in highly specialized species; has a basic number of 4 parietal barriers (often secondarily reduced); many more ribs; differently shaped umbilici and whorl contours (except some *Garrettoconcha*); and, on the basis of fragmentary data, anatomical differences. The two partially dissected *Mautodontha* lack a fleshy extension to the penis head, have much more subapical insertion of the vas deferens, the penis tapers much more abruptly and the pilasters are low and rounded. *Opanara* has a higher mean whorl count, 5⅝-6-, except in two specialized species; has a basic number of 3 parietals (rarely reduced); fewer ribs; less rapidly decoiling umbilici with somewhat flattened sides (except *megomphala*); usually a fleshy extension to the penis head; little or no tapering to the penis; the pilasters very high; and only slightly subapical insertion of the vas deferens. The shell of *Opanara* is less specialized than many *Mautodontha,* but its anatomy is more advanced. Differences from *Taipidon* are discussed below (p. 315).

Although the range of variation within *Opanara* seems rather large, most of the changes should be viewed as drastic alterations in single character complexes that have major effects on the general appearance of the species. The very depressed shape of *O. fosbergi* (fig. 107c) is the result of compression from above and below, while the high spire and H/D ratios of *O. caliculata* and *O. altiapica* come from the greatly increased tightness of coiling (fig. 98). Undoubtedly, the high spire and relatively high H/D ratio of *O. perahuensis* derive from the umbilical contraction.

Size range is not large (table LXXV), with only *O. duplicidentata* (mean diameter 4.32 mm.) and *O. altiapica* (mean diameter 2.82 mm.) departing noticeably from a 3.11-3.77 mm. range. The variation in spire height is reflected in the greater H/D ratios of *O. caliculata, O. altiapica, O. perahuensis, O. areaensis microtorma,* and *O. a. densa,* while the extreme compression in *O. fosbergi,* depressed spire in *O. depasoapicata,* and extreme umbilical widening in *O. megomphala* have produced correspondingly low H/D ratios. Whorl count is reduced in *O. altiapica* and *O. caliculata* and disproportionately increased only in *O. megomphala* (required for umbilical widening) and *O. depasoapicata* (result of secondary size reduction?). Umbilical width and form ranges from the cup-shape of *O. megomphala* to the secondarily narrowed *O. caliculata* and *O. altiapica,* and the barely perforate *O. perahuensis.*

Rib counts are in the 60-85 range, except for *O. caliculata, O. fosbergi,* and *O. areaensis densa,* which have rib counts of over 100 and, together with the dwarfed *O. altiapica,* are the only species with really crowded ribbing. None of the species have very widely spaced ribbing (table LXXVII).

The apertural barrier pattern is conservative. Only in *O. bitridentata* is there a frequent reduction to 2 parietals; occasionally there is a 4th parietal in *O. fosbergi* and *O. areaensis;* and only in *O. duplicidentata* is there normally a 4th parietal. The

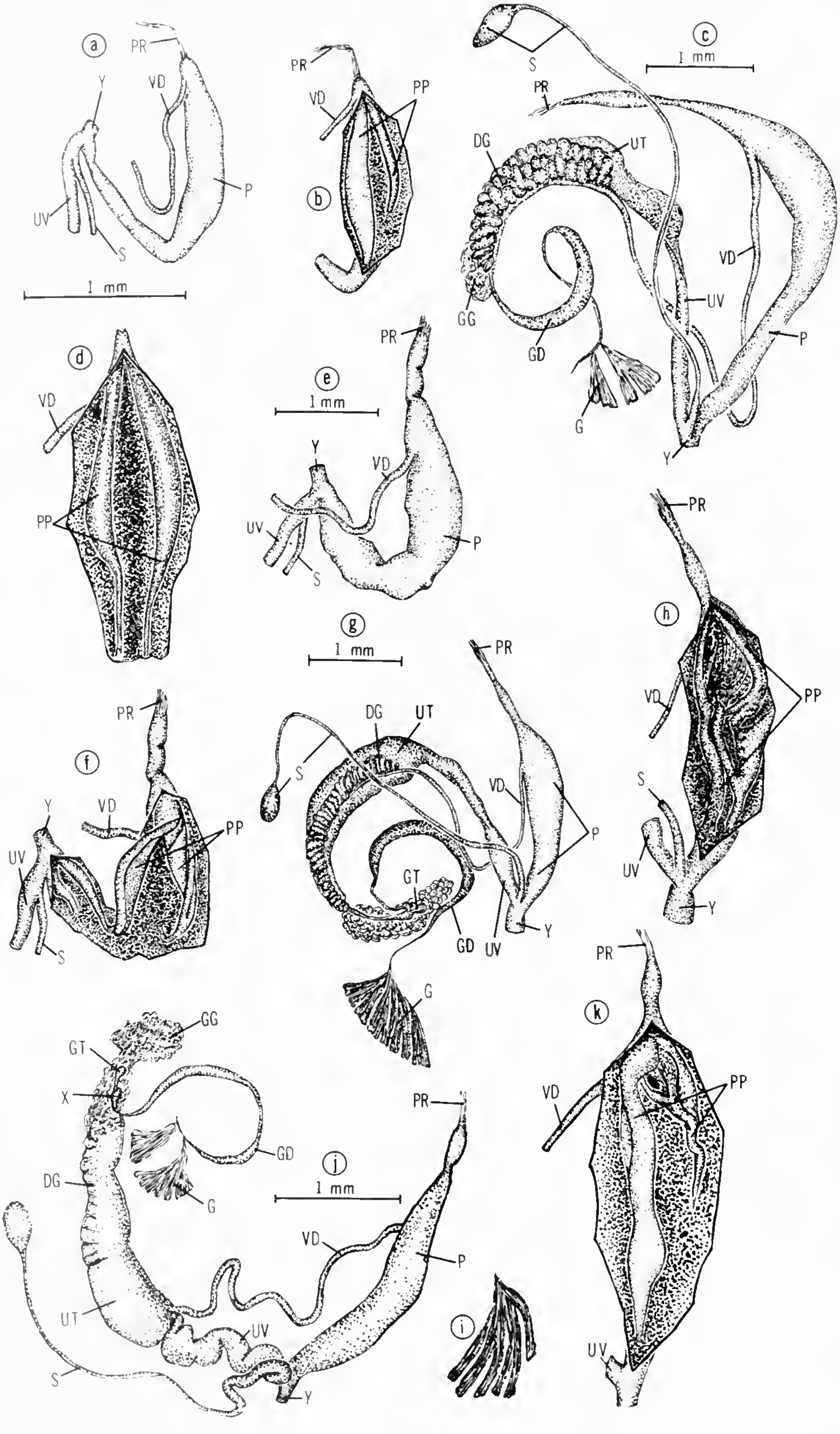

FIG. 96. Anatomy of *Opanara*: **a-b**, *O. depasoapicata*. Station 451, Mt. Perahu, Rapa. BPBM 142820. *a*, terminal genitalia, *b*, interior of penis; **c-f**, *O. bitridentata*. *c-d*, Station 512, Mt. Perahu, Rapa. BPBM 135484; *c*, genitalia, *d*, interior of penis; *e-f*, Station 451, Mt. Perahu, Rapa, BPBM 142826. *e*, terminal genitalia, *f*, interior of penis; **g-i**, *O. duplicidentata*. Station 451, Mt. Perahu, Rapa. BPBM 142817. *g*, genitalia, *h*, interior of penis, *i*, detail of ovotestis clump; **j-k**, *O. areaensis areaensis*. Station 485, Mt. Mangaoa, Rapa. BPBM 138334. *j*, genitalia, *k*, interior of penis. Scale lines refer to *a*, *c*, *e*, *g*, and *j*. (See Appendix for explanation of abbreviations.)

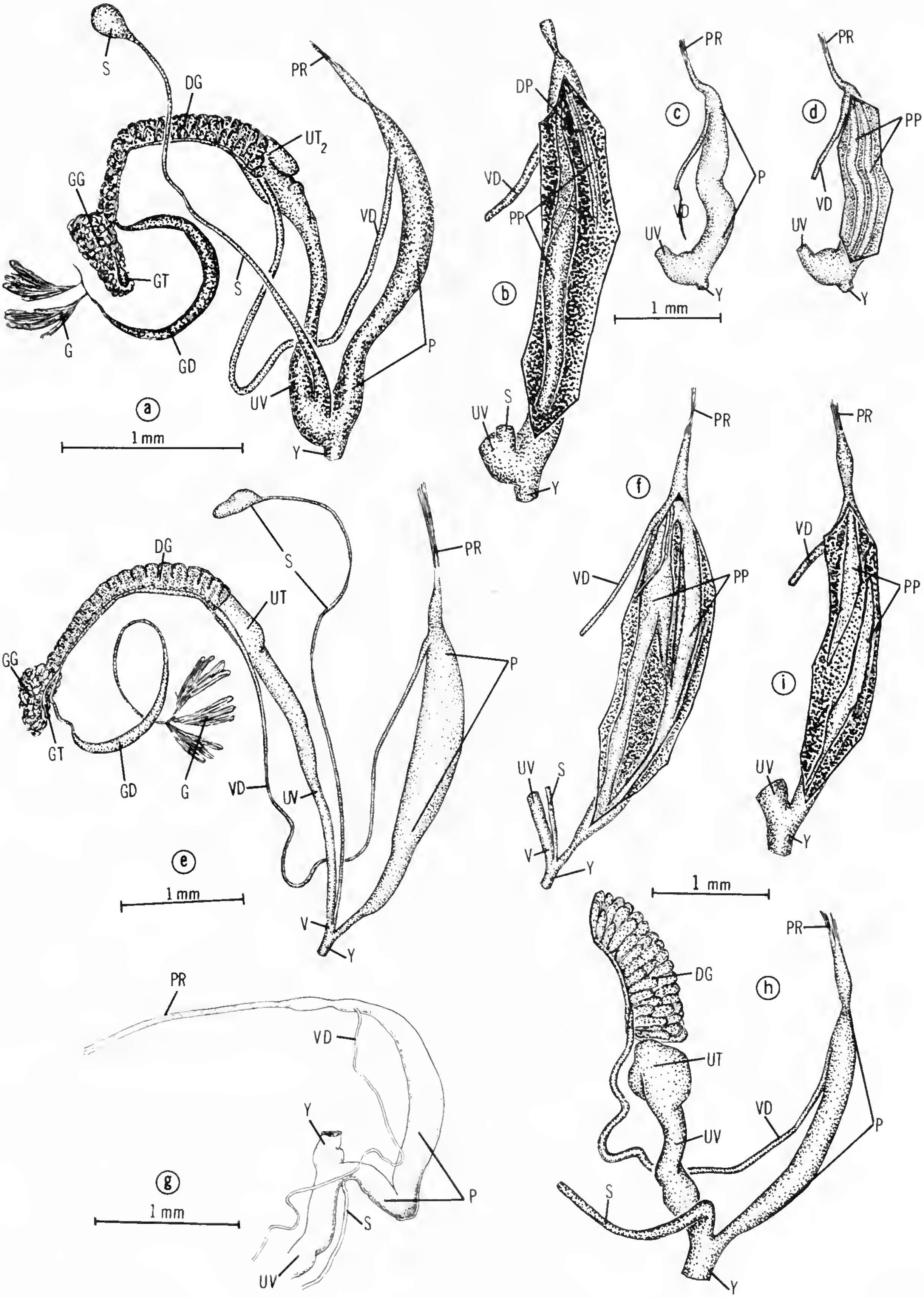

FIG. 97. Anatomy of *Opanara:* **a-b**, *O. altiapica.* Station 526, Mt. Mangaoa, Rapa. BPBM 143742. *a*, genitalia, *b*, interior of penis; **c-d**, *O. megomphala megomphala.* Station 477, Mt. Tepiahu, Rapa. BPBM 144718. *c*, exterior of penis, *d*, interior of penis; **e-f**, *O. megomphala tepiahuensis.* Station 459, Mt. Tepiahu, Rapa. BPBM 143004. *e*, genitalia, *f*, interior of penis; **g**, *O. fosbergi.* Terminal genitalia. Station 450, Mt. Perahu, Rapa. BPBM 142808; **h-i**, *O. perahuensis.* Station 453, Mt. Perahu, Rapa. BPBM 142909. *h*, terminal genitalia, *i*, interior of penis. Scale lines refer to figures *a*, *c*, *e*, *g*, and *h*. (See Appendix for explanation of abbreviations.)

columellar barrier is simple in most species, deflected onto the basal lip in *O. areaensis* and displaced in *O. fosbergi*. Its size, recession, and degree of slant is variable. *O. megomphala* has both the columellar and palatal barriers reduced to threadlike, elongated traces. Both *O. duplicidentata* and *O. bitridentata* regularly have accessory traces on the palatal wall, but only *O. duplicidentata* has 5 palatals (in *O. fosbergi* the "5th" palatal is the displaced columellar).

Anatomically, the short, relatively stubby talon contrasts greatly with the situation in *Orangia*, but is very similar to the structure found in *Ruatara*. Variability within *Opanara* in regard to penial structures is much greater than the differences from *Orangia*. *Rhysoconcha* is separated from *Opanara* by its penial insertion of the spermatheca, while *Ruatara* has a coiled hermaphroditic duct and only a single pilaster inside the penis.

Penial variation in *Opanara* concerns several features. In the very large *O. duplicidentata* the penial retractor arises from the columellar muscle; in all other species it is attached to the diaphragm. A fleshy extension to the penis head is found in all species except *O. caliculata* and *O. depasoapicata*. The pilaster pattern is quite variable, becoming complexly folded in *O. duplicidentata;* simple and grossly unequal in size in *O. depasoapicata, O. areaensis, O. altiapica*, and *O. caliculata;* the pilasters not joined above and occupying overlapping longitudinal zones in *O. perahuensis* (fig. 97i); and the pilasters of approximately equal size in the other species. All the pilasters are of the narrow, greatly elevated type found in *Orangia*, rather than the low, rounded pattern seen in more generalized Endodontidae.

The jaws show simple variation. In the very small *O. depasoapicata*, the plates are four or five times as long as wide. In *O. bitridentata* the plates are proportionately wider, but in *O. duplicidentata* size increase has been accompanied by increase in number of plates, with the length-width ratio as in *O. depasoapicata*. In *O. megomphala* and *O. perahuensis* the plates are very wide.

Form and shape of the radular teeth agree with *Orangia* and *Ruatara*. Centrals are large in *O. areaensis*, long and narrow in *O. fosbergi* (correlated with the narrowed aperture?), and reduced in size only in *O. bitridentata*. Laterals retain the same relative size and shape as the centrals.

Within *Opanara*, no species can be selected as strictly generalized, each form showing several specializations. *O. areaensis*, despite the flattened spire in the nominate race and the deflection of the columellar barrier onto the basal lip, shows comparatively few specializations and thus has been chosen as genotype.

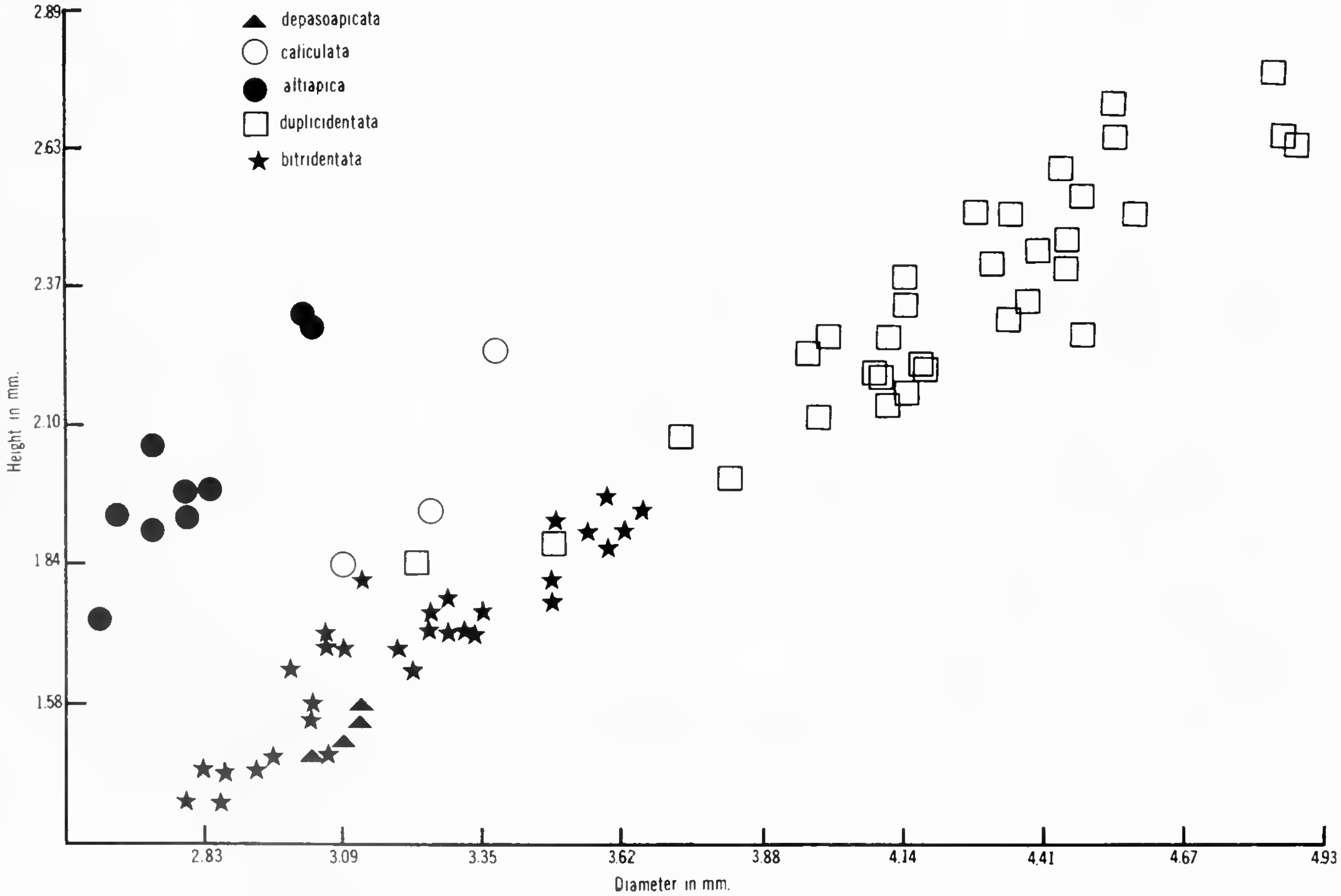

FIG. 98. Relationship of height to diameter in *Opanara altiapica, O. bitridentata, O. caliculata, O. depasoapicata*, and *O. duplicidentata*.

O. depasoapicata, O. bitridentata, and *O. duplicidentata* share a common pattern of growth (fig. 98), but show a number of differences. The smallest species, *O. depasoapicata,* has a depressed apex, with correspondingly wide umbilicus and small H/D ratio. Occasionally it has accessory palatal traces. Its penis lacks a fleshy extension to the head and the pilasters inside the penis are unequal in size. *O. bitridentata* is somewhat larger, has a distinctly elevated spire, with a correspondingly narrower umbilicus and greater H/D ratio, either 2 or 3 parietal barriers, occasionally additional palatal barriers and three to eleven accessory palatal traces. The genitalia conforms to the normal *Opanara* pattern, with large, equal-sized pilasters inside the penis. *O. duplicidentata* is by far the largest species in the genus. It has a slightly elevated spire, rather large umbilicus with angled margins, a basic number of 4 parietals and 5 palatals (the most in *Opanara*), plus six accessory palatal traces. The penial retractor originates from the columellar muscle, and the penial pilasters are very large and complexly folded, more so than in any other *Opanara.* The relative high whorl count of the small *O. depasoapicata* (5⅞-), absence of any fleshy extension to the penis head and grossly unequal pilaster size are suggestive of size reduction and may be indicative of a trend similar to that which culminated in *Rhysoconcha* (see pp. 255-256). At the other extreme, the elaboration of penial pilasters and transfer of the penial retractor muscle origin in *O. duplicidentata* often are characteristics of large size throughout the Endodontidae and may have no special significance. All three species are confined to Mt. Perahu.

As mentioned above, *O. areaensis* is specialized primarily in the deflection of the columellar barrier onto the basal lip. The pattern of this deflection is unique. Anatomically it is a generalized form. Several races are developed, the nominate form distinguished by a flat spire, widely spaced ribbing and a normal umbilicus; *densa* by its elevated spire, very crowded ribbing and slightly smaller size; *microtorma* by its elevated spire and narrower umbilicus. The nominate race is rather widely distributed (fig. 101), the others restricted to small areas. Probably *areaensis* evolved from the base stock by rapid change and is less specialized than the *depasoapicata-duplicidentata* series.

Opposite trends in variation are shown by *O. megomphala,* then by the closely related *O. caliculata* and *O. altiapica. O. megomphala* has the umbilical opening enormously enlarged, the columellar and palatal barriers reduced to threadlike traces, and the parietal barriers reduced in size with several accessory traces developed. Isolated populations on Mt. Tepiahu and Mt. Tautautu (fig. 100) differ in proportions, ribbing, and rib spacing. No anatomical differences were noted and subspecific recognition has been given to the two populations. *O. caliculata* and *O. altiapica* present an almost opposite set of specializations. Narrowing and deepening of the umbilicus has been accompanied by drastic spire elevation. The umbilical margin is distinctly angled and the umbilicus itself slightly secondarily narrowed in both species. There is no alteration in the barriers from the generalized pattern. While the conchological differences between *O. altiapica* and *O. caliculata* are no larger than those between the races of *O. megomphala,* specific level separation of the former is required because dissection demonstrated anatomical differences (see p. 17).

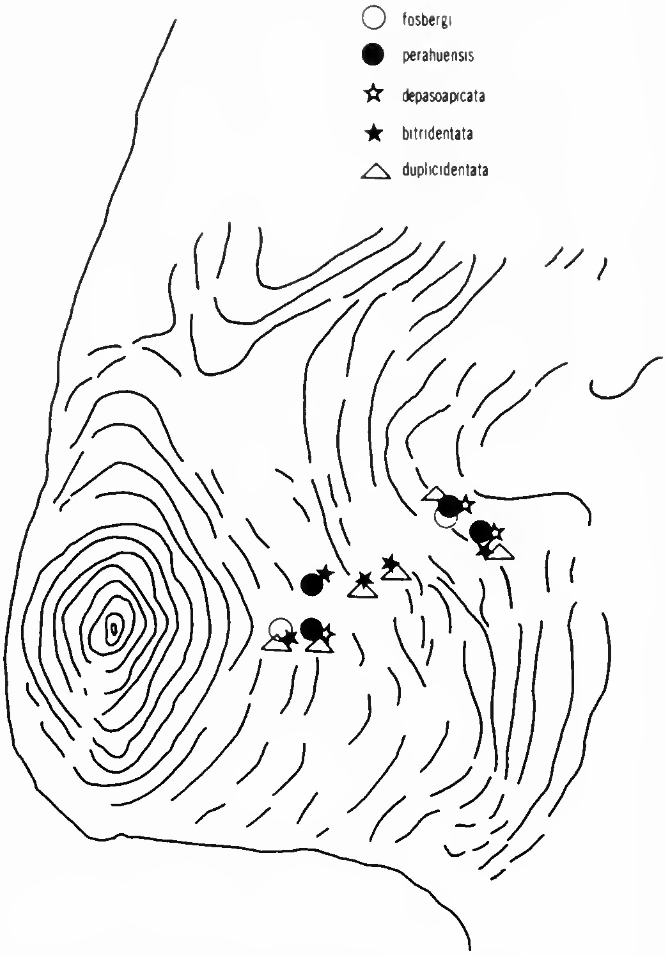

FIG. 99. Distribution of *Opanara* in the Mt. Perahu region.

The remaining two species, *O. fosbergi* and *O. perahuensis* present, respectively, simple and complex departures from the generalized pattern. *O. fosbergi* (fig. 107c-d) should be viewed as a species specialized only in being strongly compressed above and below. The evident transfer of the columellar barrier to the palatal wall, the very low H/D ratio, and narrow umbilicus all relate to this one simple fact. Otherwise it is a quite generalized species. *O. perahuensis* shows a number of unique features. The umbilicus is essentially closed by contraction, the ribbing very widely spaced with large microradials, and the penis has the two pilasters not joined above, but occupying overlapping zones in the penis. The apertural barriers are simple. *O. perahuensis* seems somewhat intermediate between *Ruatara* and *Opanara,* although anatomically belonging to the latter insofar as its anatomy is known.

Until the apical genitalia of *O. perahuensis* can be examined and *Ruatara koarana* dissected, the exact relationship of *Opanara* and *Ruatara* will remain uncertain. The latter is a derivative group and the structure of *Opanara perahuensis* indicates in umbilical contour and pilaster pattern how the structures of *Ruatara* could have developed from the *Opanara* pattern. The essential differences are: closure of the umbilicus by contraction, partial reduction, then fusion of the penial pilaster remnants, and coiling of the hermaphroditic duct. The barrier reduction in *Ruatara oparica* probably is a secondary phenomenon.

Orangia is less altered anatomically, but shows many conchological changes. The penis has unequal pilasters, which are very high apically (fig. 121k) and the fleshy penis head, lack of a vagina, and uncoiled hermaphroditic duct are typical. *Orangia* differs in its very long talon. Conchologically, the presence of only 2 parietals, closure of the umbilicus by reflection, angulated periphery, development of secondary microsculpture, and generally much larger size easily separate *Orangia* from *Opanara*. *Kondoconcha* also is derivable from *Opanara,* but differs in many features from *Orangia,* although similar in size and barriers.

The many features separating *Rhysoconcha* and *Opanara* are discussed under the former genus.

Distributional patterns of *Opanara* are simple. A majority of the species are restricted to the slopes of Mt. Perahu (figs. 99, 100): *O. caliculata, O. fosbergi, O. perahuensis, O. depasoapicata, O. duplicidentata,* and *O. bitridentata*. *O. altiapica* is a derivative of *O. caliculata* found in another part of the island (fig. 100), *O. megomphala* has two subspecies (fig. 100) on separate mountains, and only *O. areaensis* (fig. 101) has a relatively broad distribution. Compared with the patterns shown by *Orangia, Ruatara,* and *Rhysoconcha,* this is quite restricted and suggests that *Opanara* is in the process of being replaced by the derivative genera.

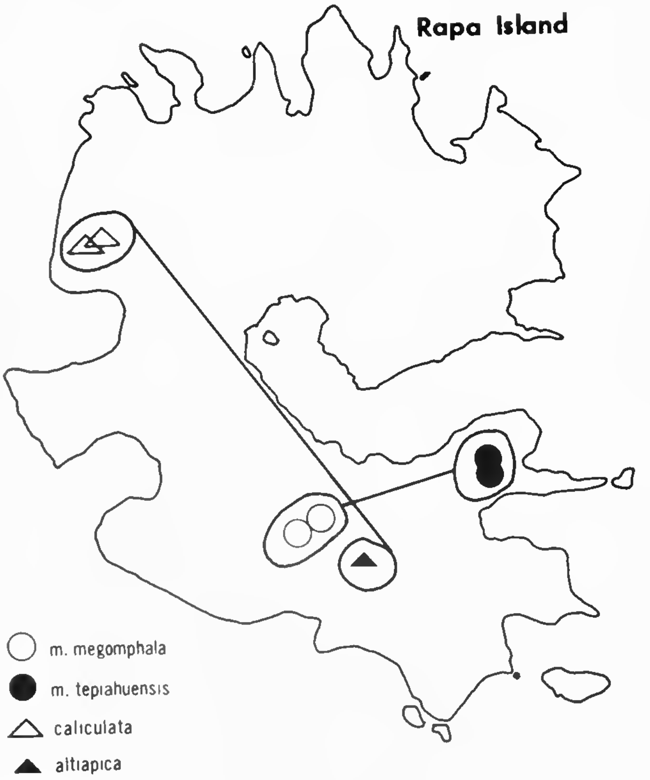

FIG. 100. Distribution of *Opanara megomphala, O. caliculata,* and *O. altiapica.*

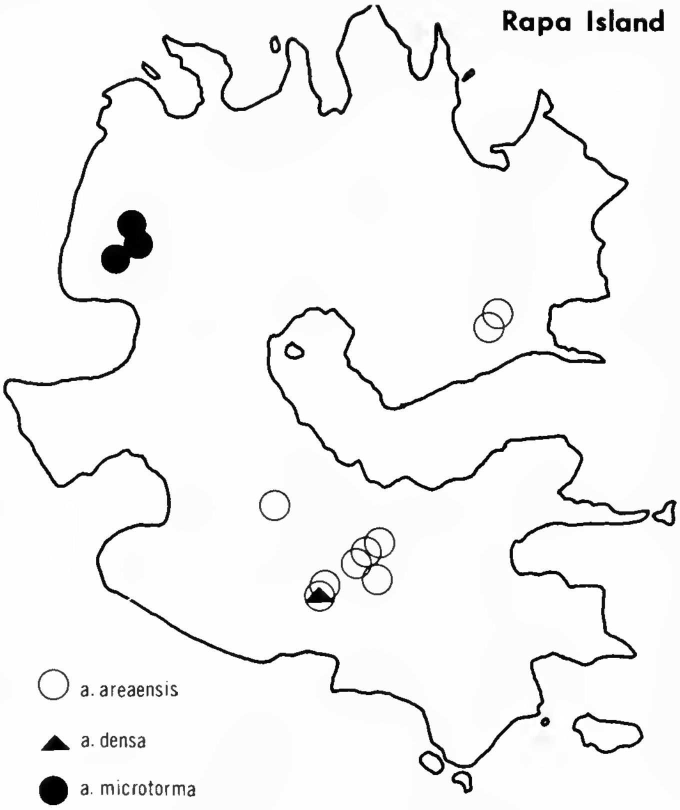

FIG. 101. Distribution of *Opanara areaensis.*

KEY TO THE GENUS *Opanara*

1. Umbilicus moderately to widely open, contained less than 9 times in the diameter 2
   Umbilicus closed or narrowly perforate, contained more than 12 times in the diameter .... *Opanara perahuensis,* new species
2. Palatal barriers reduced to many fine traces 3
   Palatal barriers 4-6, large 4
3. Mean H/D ratio less than 0.450; Mt. Tepiahu.
   Opanara megomphala tepiahuensis, new subspecies
   Mean H/D ratio more than 0.500; Mt. Tautautu.
   Opanara megomphala megomphala, new subspecies
4. Columellar barrier present, simple 5
   Columellar barrier absent or deflected onto basal lip 9
5. Accessory palatal barriers absent 6
   Accessory palatal barriers present 8
6. Apex and spire moderately to strongly elevated; D/U ratio more than 3.50 7
   Apex and spire sunken; D/U ratio less than 3.25.
   Opanara depasoapicata, new species
7. Less than 100 ribs on body whorl; mean H/D ratio more than 0.700 .... *Opanara altiapica,* new species
   More than 110 ribs on body whorl; mean H/D ratio less than 0.650 .... *Opanara caliculata,* new species

8. Parietal barriers 2 or 3; umbilicus narrower, mean D/U ratio more than 5.00 .... *Opanara bitridentata*, new species
Parietal barriers 4; umbilicus wider, mean D/U ratio about 3.00. *Opanara duplicidentata*, new species
9. Columellar barrier deflected onto basal lip (fig. 104e); H/D ratio more than 0.500 10
Columellar barrier absent, H/D ratio less than 0.400. *Opanara fosbergi*, new species
10. Apex and spire distinctly elevated 11
Apex and early spire flat. *Opanara areaensis areaensis*, new subspecies
11. Less than 90 ribs on body whorl; mean ribs/mm. about 7.00. *Opanara areaensis microtorma*, new subspecies
More than 90 ribs on body whorl; mean ribs/mm. about 9.75. *Opanara areaensis densa*, new subspecies

Opanara depasoapicata, new species. Figures 96a-b; 107e-f.

Diagnosis. – Shell rather small, diameter 3.05-3.15 mm. (mean 3.11 mm.) with 5⅝-6 tightly coiled whorls. Apex and early spire sunken below level of antipenultimate whorl, last two whorls descending slightly, H/D ratio 0.489-0.505 (mean 0.494). Umbilicus broadly open, U-shaped, last whorl slightly decoiling, contained 2.88-2.97 times (mean 2.92) in the diameter. Postnuclear sculpture of narrow, prominent, normally spaced, slightly protractively sinuated radial ribs, 78-84 (mean 81.0) on the body whorl, whose interstices are 3-4 times their width. Microsculpture of very fine radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on umbilical margin, evenly rounded on outer margin, umbilical walls very slightly flattened. Aperture ovate, evenly rounded on outer margin, inclined slightly more than 5° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl: upper high and bladelike, expanded and serrated above on posterior quarter, with very gradual anterior descension until just before end; 2nd parietal with posterior elevated portion slightly lower and shorter, middle two-thirds an elevated bladelike ridge, with gradual anterior descension, extending well beyond end of upper parietal; 3rd parietal greatly reduced in height posteriorly, scarcely elevated, a broad and threadlike ridge equal in length to 2nd parietal. Columellar wall with a single broad, very deeply recessed threadlike ridge, barely visible without tilting of aperture. Palatal barriers 4, sometimes 5 or 6, short, extending less than one-eighth whorl: 1st palatal a high crescentic lamella with abrupt anterior descension, only slightly recessed within aperture; 2nd palatal slightly reduced in height, a little more flattened above, with more gradual anterior descension and deeper recession; 3rd palatal greatly reduced in height, a low lamellar ridge, weakly expanded above, with very gradual anterior descension, located below level of upper parietal; 4th palatal supraperipheral, lying above level of upper parietal, a short deeply recessed threadlike ridge, very slightly elevated posteriorly.

The absence of any palatal traces, very small size, depressed apex, and presence of only 3 parietal barriers immediately distinguish *Opanara depasoapicata* from *O. duplicidentata*. The latter is much larger, has 4 parietals, several palatal traces, and a much larger, more prominent columellar barrier. *O. bitridentata* has a much narrower umbilicus, elevated spire, and either 2 or 3 parietals. *O. areaensis* is immediately separable in having the columellar barrier large and sharply deflected onto the basal lip.

Description. – Shell very small, with 5⅞ tightly coiled whorls. Apex and early spire sunken below level of antipenultimate whorl, last two whorls descending slightly, H/D ratio 0.505. Apical whorls 1½, sculpture of fine radial riblets interspersed with finer microradials and crossed by microspiral riblets. Postnuclear whorls with narrow, prominent, almost vertically sinuated radial ribs, 84 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, four to eight between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on umbilical margin, slightly compressed laterally with evenly rounded outer margin, inner walls of umbilicus somewhat flattened. Color light yellow-brown, with vague traces of widely scattered, reddish flammulations. Umbilicus broadly U-shaped, last whorls decoiling slightly, contained 2.97 times in the diameter. Aperture ovate, slightly compressed laterally, with angulated umbilical margin, and flattened columellar wall, inclined less than 5° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl: upper parietal high and bladelike, expanded and serrated above on posterior quarter, middle two-thirds with very gradual descension, becoming sharp near anterior end; 2nd parietal elevated above posteriorly, with more gradual anterior descension, anterior portion reduced in height, extending further anteriorly than upper parietals; 3rd parietal a raised threadlike ridge for entire length, extending equally far anteriorly as 2nd parietal. Columellar barrier a low lamellar ridge, deeply recessed in aperture, clearly visible only by tilting shell. Palatal barriers 4, short, extending about one-eighth whorl; lower palatal basal in position, a high crescentic lamella with abrupt anterior descension, almost reaching lip edge, expanded and serrated above; 2nd palatal slightly reduced in height, a little flattened above, with equally abrupt anterior descension; 3rd palatal greatly reduced in height, expanded and serrated above posteriorly, a raised lamellar ridge, with very gradual anterior descension; 4th palatal reduced to a high threadlike trace, shortened, moderately recessed within aperture, with very gradual anterior descension. Height of holotype 1.58 mm., diameter 3.12 mm.

Holotype. – Austral Islands: Rapa Island, Station 451, east ridge of Mt. Perahu at 1,200-1,500 ft. elevation. Collected by Yoshio Kondo on July 21, 1934. BPBM 142820.

Range. – East ridge of Mt. Perahu at 1,200-1,800 ft. elevation, Rapa Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Rapa: east ridge of Mt. Perahu (Stations 451, 452, 509) at 1,200-1,800 ft. elevation (15 specimens, BPBM 135441, BPBM 142819-22, ex BPBM 142823, BPBM 142824, BPBM 142876, ex BPBM 142873).

Remarks. – Two specimens had additional palatal barriers: BPBM 142824 had extra palatals between the 1st and 2nd, then 2nd and 3rd; one of three specimens in BPBM 142819 had a 5th palatal located between the 1st and 2nd. In both cases the extra barriers were equal in size and shape to the normal palatals. There was no variation noted in the parietal barrier pattern.

The depressed apex and very wide umbilicus found in *O. depasoapicata* immediately separate it from other species found on Rapa. While *O. megomphala* has an even wider umbilicus, it has the apertural barriers reduced to threadlike traces. *O. duplicidentata* is much, much larger, has 4 parietals and 5 palatals, and much more widely spaced radial ribbing.

Opanara depasoapicata was a relatively rare species, taken in lesser number than *O. duplicidentata* at Stations 451 and 452, then in almost equal, although sparse, numbers at Station 509.

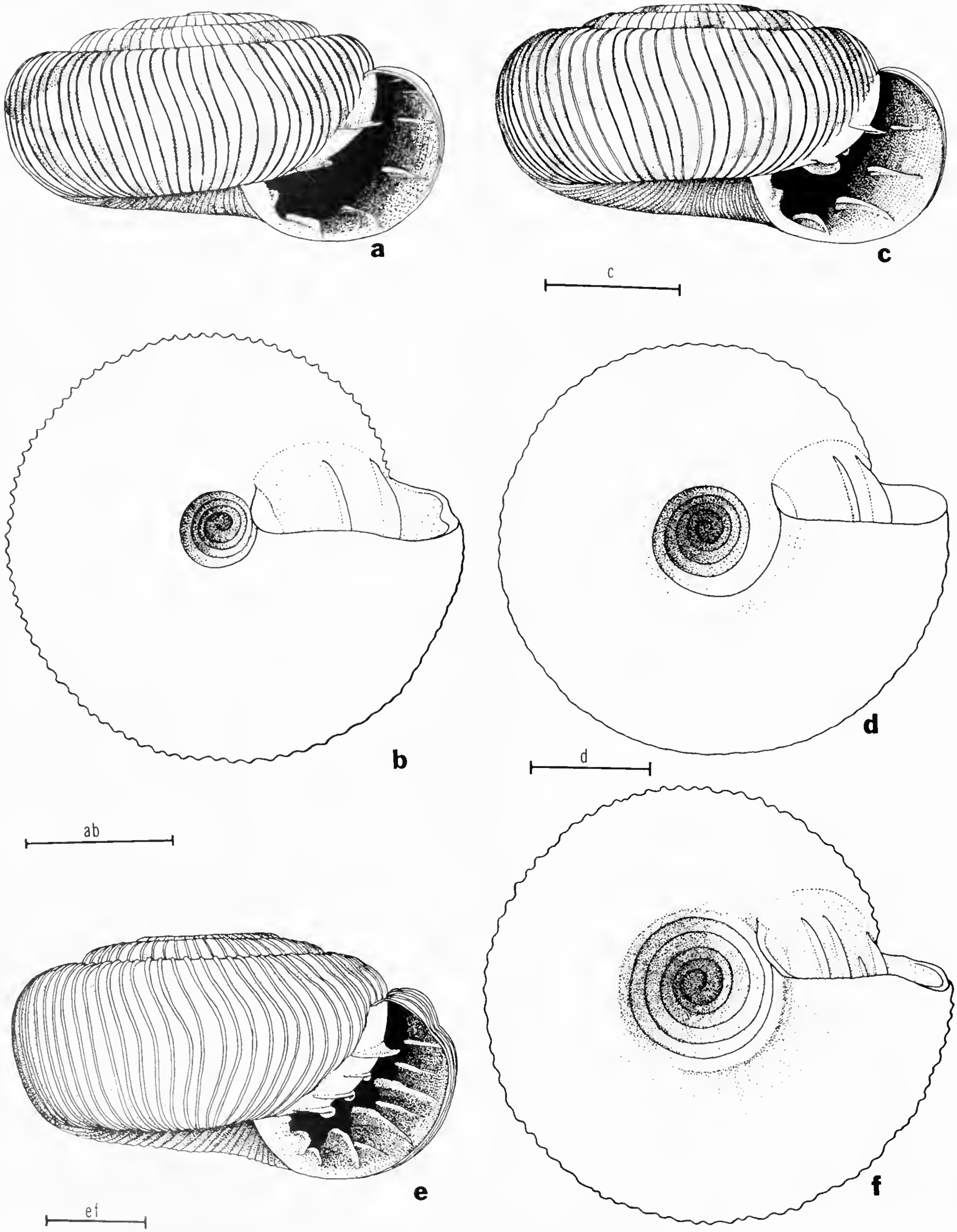

FIG. 102. **a-d**, *Opanara bitridentata*, new species. *a-b*, narrowly umbilicated form with 2 parietals. Station 512, Mt. Perahu, Rapa Island, Austral Islands. Paratype. BPBM 135483, form with 3 parietals; c, Station 512, Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 135484; *d*, widely umbilicated example. Station 451, Mt. Perahu, Rapa Island, Austral Islands. Paratype. BPBM 142826; **e-f**, *O. duplicidentata*, new species. Station 451, Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 142817. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Unfortunately, only fragmentary soft parts were available. The penis is unusual for *Opanara* in lacking a fleshy head, a character shared only with *O. caliculata*. All other dissected forms have a fleshy head to the penis. Internally, the penial pilasters are very simple and lack the rather complex folding seen in such species as *O. duplicidentata*. Other features of the soft parts could not be studied.

Description of soft parts. — Penial retractor inserting directly on head of penis, no fleshy extension. Vas deferens (fig. 96a VD) entering penis to one side of pilaster, about 0.33 mm. below penis apex. Penis (P) about 2.35 mm. long, swollen on upper half, internally (fig. 96b) with two very high pilasters (PP), one much longer and larger than the other, united above. Attached edge of pilasters narrower than medial section, pilaster much, much higher than wide. Spermathecal shaft (S) joining free oviduct (UV) just above penioviducal angle.

Jaw composed of clearly separate plates, moderately overlapping, each plate four or five times as long as wide.

Radula with about 5 laterals, central 10 μ wide and 11 long, marginals missing or folded under.

(Based on fragmentary and torn individuals from BPBM 142820.)

Opanara bitridentata, new species. Figures 96c-f; 102a-d.

Diagnosis. — Shell of slightly less than average size, diameter 2.79-3.88 mm. (mean 3.26 mm.), with 5⅞ normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a trifle more rapidly, H/D ratio 0.483-0.580 (mean 0.524). Umbilicus broadly (fig. 102d) to narrowly (fig. 102b) open, U-shaped, last whorls slightly to moderately decoiling, contained 3.58-8.45 times (mean 5.31) in the diameter. Postnuclear whorls with narrow, prominent, slightly protractively sinuated lamellar radial ribs, 70-91 (mean 79.1) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets barely visible under 96× magnification. Sutures impressed, whorls strongly and almost evenly rounded on outer margins, with more strongly rounded subsutural and umbilical margins. Aperture subcircular, with strongly rounded outer margins, inclined about 10° from shell axis. Parietal barriers 2 (61.8 per cent) or 3 (38.2 per cent), extending posteriorly slightly more than three-sixteenths of a whorl, rarely (1 of 81 specimens) with a small accessory trace near parietal-columellar margin: upper parietal high and bladelike, expanded and serrated above on posterior half, with gradual anterior descension until just before anterior end; 2nd parietal more strongly expanded and serrated above on posterior half, equally elevated, with rather sharp anterior descension to a threadlike trace or threadlike ridge occupying anterior three-eighths of barrier and terminating beyond end of upper parietal; 3rd parietal, when present, located between 1st and 2nd, deeply recessed, equally high and serrated posteriorly, but without anterior threadlike portion, terminating somewhat past mid-point of 1st parietal. Columellar wall with a single, low, moderately recessed threadlike trace to lamellar ridge, slanting slightly downward from plane of coiling. Palatal barriers normally 4, often 5 (15.1 per cent) or occasionally 6 (6.1 per cent), extending posteriorly over one-eighth whorl: 1st palatal basal in position, a low lamellar blade, flat above, expanded and serrated above on posterior three-quarters, moderately recessed, with relatively sharp anterior descension; 2nd palatal normally indistinctly higher, expanded and serrated above on posterior half, with more gradual anterior descension; 3rd palatal equal in height to 2nd or slightly reduced, similarly expanded and serrated above, a little more deeply recessed, with slightly more gradual anterior descension; 4th palatal supraperipheral in position, greatly reduced in height, more deeply recessed, a low threadlike trace lying above level of upper parietal. Additional palatals, when present, located between various pairs of lower palatals. Accessory traces three to eleven in number, most frequently present above upper palatal, when more numerous with one or two between each pair of lower palatals.

The pronounced variation in diameter, number of parietal barriers, and umbilical width found in *Opanara bitridentata* makes confusion with other species relatively easy. *Opanara depasoapicata* differs in its always much wider umbilicus and slightly depressed (not elevated) spire. *O. duplicidentata* is generally much larger, almost always has a much wider umbilicus, always has 4 parietals, 5 palatals, and six palatal traces. *O. areaensis microtorma* has a much thicker body whorl, greatly enlarged and deflected columellar barrier, and much larger parietal and palatal barriers.

Description. — Shell of average size, with 5¼ normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.525. Apical whorls 1⅜, sculpture typical. Postnuclear whorls with narrow, lamellar, rather crowded, protractively sinuated radial ribs, 76 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, four to six between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification. Sutures deep, whorls strongly rounded above and on umbilical margin, with strongly and evenly rounded outer margins. Color light yellow-horn, with prominent, strongly zigzagged, reddish flammulations that tend to coalesce and broaden near umbilicus. Umbilicus U-shaped, relatively wide, last whorls only slightly decoiling contained 4.31 times in the diameter, internal wall strongly rounded below, somewhat flattened apically. Aperture subcircular, with strongly rounded outer margins, inclined about 10° from shell axis. Parietal barriers 3, 2nd deeply recessed, extending posteriorly more than three-sixteenths of a whorl: upper high and bladelike, expanded and serrated above on posterior third, with extremely gradual anterior descension until just before its terminations; 2nd parietal equally high and expanded above posteriorly, much shorter than elevated portion of 1st parietal, descending sharply to a very slender threadlike trace that terminates before anterior quarter of upper parietal; 3rd parietal with posterior elevated portion as in 2nd, slightly longer, with a little more gradual anterior descension to raised threadlike ridge that extends anteriorly slightly beyond termination of 1st parietal. Columellar barrier a broad, low, lamellar ridge, slanting slightly downward from plane of coiling and stopping short of lip margin. Major palatal barriers 4, with numerous accessory traces both above upper palatal and between lower pairs: lower palatal high and bladelike, expanded, serrated, and slightly flattened above, with rather gradual anterior descension; 2nd palatal slightly higher, longer, with posterior elevated portion proportionately shorter and with more gradual anterior descension, a little more deeply recessed within aperture; 3rd palatal as in 2nd, with more gradual anterior descension and slightly deeper recession; 4th palatal slightly supraperipheral, greatly reduced in height, a raised threadlike ridge lying above plane of upper parietal. Palatal traces very fine and numerous. Height of holotype 1.71 mm., diameter 3.26 mm.

Holotype. — Austral Islands: Rapa Island, Station 512, east end of main ridge of Mt. Perahu at 1,500-1,850 ft. elevation. Collected under moss and between leaves of bird's nest ferns by Donald Anderson and natives on July 28, 1934. BPBM 135484.

Range. — East ridge of Mt. Perahu at 1,500-1,900 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa: east ridge of Mt. Perahu at 1,200-1,900 ft. elevation (Stations 446, 450, 451, 453,

TABLE LXXVI. - LOCAL VARIATION IN OPANARA, RUATARA KOARANA AND KONDOCONCHA OTHNIUS

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
Opanara						
altiapica						
BPBM 143741-3, -6, BPBM 143335 Sta. 481, 526	8	2.02±0.069 (1.76-2.32)	2.83±0.053 (2.65-3.05)	0.714±0.0120 (0.664-0.761)	5 1/4- (4 7/8-5 5/8)	4.59±0.134 (3.91-5.12)
caliculata						
BPBM 142908, EX. BPBM 135484 Sta. 453, 512	3	2.02±0.119 (1.85-2.25)	3.27±0.086 (3.11-3.41)	0.617±0.0214 (0.595-0.660)	5- (4 5/8-5 1/4)	4.74±0.335 (4.09-5.22)
bitridentata						
BPBM 135483-5 Sta. 512	13	1.60±0.044 (1.39-1.82)	3.08±0.055 (2.81-3.38)	0.519±0.0069 (0.483-0.580)	5 1/4- (5-5 3/4)	5.49±0.250 (4.31-6.93)
BPBM 142799, -801 Sta. 450	7	1.77±0.048 (1.59-1.92)	3.33±0.085 (3.01-3.58)	0.533±0.0049 (0.519-0.550)	5 1/2- (5 1/8-5 5/8)	4.61±0.178 (3.84-5.26)
BPBM 142826 Sta. 451	4	1.90±0.044 (1.79-1.99)	3.60±0.034 (3.51-3.68)	0.529±0.0085 (0.510-0.551)	5 5/8+ (5 5/8-5 3/4)	4.29±0.510 (3.58-5.79)
perahuensis						
BPBM 142909 Sta. 453	4	1.88±0.008 (1.85-1.89)	3.20±0.086 (3.05-3.34)	0.590±0.0175 (0.555-0.620)	5 1/2+ (5 1/2-5 5/8)	22.2±2.35 (15.3-25.3)
fosbergi						
BPBM 135444, BPBM 142808 Sta. 450, 509	5	1.30±0.032 (1.19-1.39)	3.77±0.066 (3.61 4.01)	0.344±0.0081 (0.330-0.375)	5 1/2 (5 3/8-5 5/8)	7.10±0.389 (5.74-8.07)
depasoapicata						
BPBM 142820, BPBM 142876 Sta. 451-2	4	1.54±0.022 (1.49-1.59)	3.11±0.024 (3.05-3.15)	0.494±0.0038 (0.489-0.505)	5 7/8- (5 5/8-6)	2.92±0.025 (2.88-2.97)
megomphala megomphala						
BPBM 144717-8 Sta. 477	5	1.63±0.087 (1.39-1.89)	3.15±0.093 (2.85-3.34)	0.516±0.0134 (0.488-0.564)	5 3/4- (5 1/4-6 1/8)	2.22±0.036 (2.15-2.35)
megomphala tepiahuensis						
BPBM 143003-5, -7 Sta. 459	24	1.46±0.025 (1.16-1.66)	3.36±0.035 (2.98-3.77)	0.434±0.0061 (0.353-0.481)	5 7/8 (5 1/2-6 1/8)	1.95±0.016 (1.72-2.08)
duplicidentata						
BPBM 142745 Sta. 446	4	2.20±0.010 (2.19-2.22)	4.20±0.028 (4.14-4.27)	0.525±0.0020 (0.520-0.528)	5 7/8	2.59±0.070 (2.49-2.80)
BPBM 142872 Sta. 452	6	2.38±0.093 (2.15-2.78)	4.32±0.119 (4.14-4.87)	0.552±0.0102 (0.520-0.575)	6- (5 5/8-6 1/4)	3.04±0.090 (2.78-3.32)
BPBM 142817-8 Sta. 541	15	2.40±0.059 (2.02-2.72)	4.34±0.090 (3.74-4.87)	0.553±0.0065 (0.508-0.594)	6 (5 3/8-6 7/8)	3.17±0.075 (2.63-3.65)
Ruatara						
koarana						
BPBM 142521 Sta. 357	3	1.69±0.077 (1.56-1.82)	2.95±0.119 (2.81-3.05)	0.612±0.0306 (0.567-0.670)	5 1/8- (4 3/4-5 1/2)	BARELY OPEN TO CLOSED
Kondoconcha						
othnius						
BPBM 142462, -3, -7 Sta. 346	6	2.30±0.064 (2.09-2.55)	4.06±0.067 (3.81-4.24)	0.567±0.0086 (0.548-0.601)	6 3/8- (6 1/8-6 3/4)	5.55±0.225 (5.00-6.40)

TABLE LXXVII. - RIBS/MM. IN OPANARA

depasoapicata	8.38(7.93-8.82)
bitridentata	7.94(6.65-0.09)
duplicidentata	5.99(5.13-7.17)
a. areaensis	5.68(4.18-7.47)
a. microtorma	6.86(6.47-7.30)
a. densa	9.75(8.63-11.03)
altiapica	8.93(7.38-10.35)
caliculata	11.76 ----
m. megomphala	7.09(6.69-7.31)
m. tepiahuensis	6.39(5.34-7.54)
fosbergi	8.57(8.04-8.96)
perahuensis	6.18(5.78-6.72)

512, 513) under stones, moss and debris (81 specimens, BPBM 135483-7, ex BPBM 135488, BPBM 135573, BPBM 142747, BPBM 142799-807, BPBM 142826, BPBM 142906-7).

Remarks. — Considerable variation exists within this species (table LXXVI) and some of it seems to be clinally oriented. While H/D ratios and rib counts are essentially identical, other parameters vary widely. Specimens taken at 1,200-1,500 ft. elevation (Stations 446 and 451) are distinctly larger and with a wider umbilicus than specimens taken at 1,500-1,900 ft. elevation (Stations 450, 453, 512, and 513). Comparing material from Station 512 and Station 451, with 15 df, "*t*" = 5.0527 in respect to diameter and "*t*" = 2.2684 for D/U ratio. Comparing specimens from Station 450 with Station 451, there is less difference in D/U ratio, since with 9 df, "*t*" = 2.3303 for diameter and "*t*" = 0.7263 for D/U ratio. The percentage changes involved between Stations 450 and 451 in height, diameter, and D/U ratios are, respectively, 7.3 per cent, 8.1 per cent, and 7.5 per cent. Between Stations 512 and 450, the percentage changes in height and diameter are 10.6 per cent and 8.1 per cent, respectively, but there is a 19.1 per cent change in D/U ratio. This probably indicates the relatively greater decoiling of the last umbilical whorl in larger individuals. Stations 450, 512, and 451 are at progressively greater elevations and there is an obvious decrease in height and diameter with a narrowing of the umbilicus. Limited data suggests that this is accompanied by changes in rib spacing. Thirteen examples from Stations 450 and 512 averaged 78.5 ribs, with 8.12 ribs/mm. (range 7.30-9.09), while three specimens from Stations 446 and 451 averaged 82.0 ribs, with 7.17 ribs/mm. (range 6.65-7.87). Probably this is another example of the phenomenon noted in *Opanara areaensis,* where increase in mean diameter produced an increase in rib spacing (see table LXXX).

TABLE LXXVIII. - PARIETAL BARRIER VARIATION IN OPANARA BITRIDENTATA

Station	2 Pr	3 Pr
450	2	7
453	0	3
512	10	3
513	2	0
446	2	0
451	5	0
TOTAL	21	13

Barrier variation primarily concerns the number of parietals. Only part of the material was checked for total counts, 34 of the 81 specimens, and the results are tabulated in Table LXXVIII. The results are quite discordant, with stations showing reverse dominance despite the overall approach toward a two-to-one ratio. The number of accessory palatal traces was quite variable and an occasional specimen had one or two extra palatals.

The name *bitridentata* refers to the variable nature of the parietal barriers.

Dissection of specimens from Stations 451 (BPBM 142826) and 512 (BPBM 135484) showed no differences, with the penial pilasters equal and disparate in size within the same sample. The pilasters are very high and slender, tapering rapidly submedially. The insertion of the vas deferens is clearly subapical.

One preserved specimen had a single egg in the umbilicus. The umbilical diameter was 0.58 mm. and the maximum egg diameter 0.55 mm. Removal of the egg capsule showed a fully formed shell covering with clearly defined sculpture.

Description of soft parts. — Foot and tail shorter than shell diameter, narrow, not tapered, bluntly rounded behind. Sole undivided. Pedal grooves prominent, rather high on foot, no caudal horn or middorsal groove. Slime network very faint. Head extending in front of the truncated foot. Ommatophores typical. Gonopore behind right rhinophore, above front margin of foot.

Body color light yellow-white, without darker markings.

Mantle collar with thickened edges, particularly around pneumostome, no glandular extension onto pallial roof.

Pallial region extending five-eighths whorl apically. Lung roof clear, white granules clustered just above apex of kidney. Kidney almost 1.5 mm. long, rectal arm equal to half length, very slender anteriorly. Ureter typical, originating subapically, reflexing sharply for about one-quarter of length to open at anterior end of rectal kidney arm next to hindgut. Heart about 0.6 mm. long, parallel to hindgut, less than half length of kidney. Principal pulmonary vein narrow, fading out short of mantle collar. Hindgut typical.

Ovotestis (fig. 96c, G) with six to seven clumps of palmately clavate alveoli, normally oriented to shell axis, individual clumps less split than in *O. duplicidentata.* Hermaphroditic duct (GD) very slender at first, moderately to strongly expanded medially, sharply reflexed just before entering carrefour. Albumen gland (GG) slender, more elongated than in many species. Talon evenly tapering from head to carrefour, head not grossly expanded. Carrefour enlarged more laterally than in *O. duplicidentata*, clearly distinguishable from talon in all views.

Prostate (DG) with two or three rows of acini opening into slender tube. Uterus (UT) bipartite, lower chamber greatly expanded, slightly larger than prostate.

Vas deferens (VD) typical, entering penis about 0.33 mm. below penial apex and to one side of pilaster U. Penial retractor (PR) originating from diaphragm just at apex of pallial cavity, inserting on fleshy head of penis. Penis (P) about 2.65 mm. long, with very prominent fleshy head, moderately swollen below insertion of vas deferens, then narrowing and maintaining even diameter up to atrial junction. Internally (fig. 96d, f), penis with two pilasters, united above, sometimes equal in size, sometimes with one much higher and larger, not united anteriorly. Pilaster shape typical. Atrium (Y) short and rather broad.

Free oviduct (UV) larger than prostate, point of origin from uterus clearly marked by a constriction. Spermatheca (S) with elongately oval head, one specimen with a large, hooked, sperm packet with only a weak membranous covering. Shaft inserting on free oviduct just above penioviducal angle.

Free muscle system and digestive system typical.

Jaw of large overlapping plates, individual plates about three or four times as long as wide.

Radula with elongated basal plates that are longer than wide, rather short cusps, central about 6 μ wide and 8 μ long. Marginals partly missing in all mounts.

(Based on BPBM 135484, three individuals and several fragmentary ones, whole shell 2.82 mm. in diameter with 4½- whorls.)

Opanara duplicidentata, new species. Figures 96g-i; 102e-f; 103.

Diagnosis. — Shell very large, diameter 3.72-4.84 mm. (mean 4.32 mm.), with 5⅝ - 6¼ tightly coiled whorls. Apex and early spire flat or slightly depressed below level of antipenultimate whorl, last two whorls descending slightly, H/D ratio 0.508-0.594 (mean 0.549). Umbilicus broadly open, U-shaped, last whorls barely decoiling, contained 2.49-3.65 times (mean 3.03) in the diameter. Postnuclear sculpture of prominent, crowded, almost vertically sinuated radial ribs, 70-100 (mean 84.2) on the body whorl, whose interstices are distinctly less than twice their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above, very slightly compressed laterally above and below evenly rounded periphery, baso-columellar margin strongly angulated, inner walls of columellar region flattened. A weak supraperipheral sulcus usually present. Aperture ovate, very slightly flattened laterally above and below periphery, lying parallel to shell axis. Parietal barriers 4, extending posteriorly slightly more than one-quarter whorl, 2nd usually greatly reduced in prominence, often (25 per cent) with a single short, deeply recessed accessory trace below 4th parietal: upper parietal high and bladelike, expanded and serrated above on posterior half, with very gradual anterior descension; 2nd parietal normally only half height of the 1st, with much shorter elevated portion that descends sharply to a threadlike trace terminating well behind anterior end of 1st parietal, sometimes much larger or smaller than the normal condition; 3rd parietal with posterior half almost equal in height to 1st parietal, expanded and serrated above, with moderate descension to a raised lamellar ridge that occupies anterior half of barrier, terminating well before end of 1st parietal; 4th parietal with same shape as 3rd, usually slightly reduced in height. Parietal trace, when present, a short, threadlike structure recessed almost to mid-point of 4th parietal and stopping well short of posterior end. Columellar barrier a high bladelike ridge, expanded and serrated above posteriorly, with gradual anterior descension and twisting slightly downwards, recessed within aperture. Palatal barriers 5, extending posteriorly about three-sixteenths of a whorl, with six deeply recessed accessory traces: lower palatal greatly reduced in height, a weakly elevated lamellar ridge with very gradual anterior descension; 2nd palatal high, expanded, serrated and flattened above, with sinuated gradual anterior descension; 3rd and 4th palatals slightly higher than 2nd, similar in form, with more elongated anterior descension; 5th palatal located well above periphery, greatly reduced in height, a low lamellar ridge situated above level of upper parietal. One palatal trace located between each pair of major palatals, with two additional traces between upper palatal and palatal-parietal margin.

The presence of 4 parietals, many accessory palatal traces, flattened sides of the umbilicus, and very large size immediately separate *Opanara duplicidentata* from the other Rapan species. The other large species, the several *Orangia* and *Kondoconcha*, either have a closed umbilicus (*Orangia*) or an angulated periphery (*Kondoconcha*) and all have only 2 parietals.

Description. — Shell large, with 6¼ very tightly coiled whorls. Apex and spire flat, lower whorls descending slightly more rapidly, H/D ratio 0.547. Apical whorls 1⅜, sculpture of fine radial riblets interspersed with one or two finer microradials and crossed by rather widely spaced spiral microriblets. Postnuclear whorls with low, rather broad, closely spaced, almost vertically sinuated radial ribs, 85 on the body whorl, whose interstices are 1-2 times their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by very fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above down to very weak supraperipheral sulcus, the outer margin evenly rounded, slightly compressed laterally below periphery, with strongly angulated baso-columellar margin and flattened umbilical wall. Color light yellow-brown, with faint traces of irregular, reddish flammulations. Umbilicus broadly open, U-shaped, last whorls barely decoiling, contained 3.39 times in the diameter, inner walls flattened. Aperture ovate, with almost evenly rounded outer margin, baso-columellar

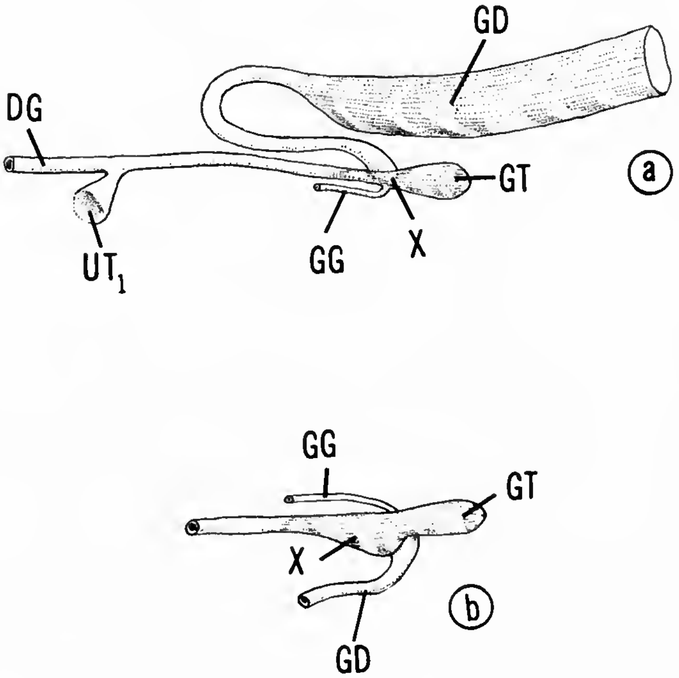

FIG. 103. Details of carrefour region in *Opanara duplicidentata:* **a**, top view with albumen gland follicles completely removed; **b**, bottom view showing enlargement of carrefour. Greatly enlarged and diagrammatic. See Appendix for explanation of abbreviations.

margin sharply angulated, lying parallel to plane of shell axis. Parietal barriers 4, extending posteriorly more than one-quarter whorl, 2nd reduced in size: upper parietal high and bladelike, expanded and serrated above on posterior five-eighths, with very gradual anterior descension; 2nd parietal greatly reduced in height, anterior threadlike and moderately recessed, with posterior elevated portion distinctly shorter and lower than 1st parietal; 3rd parietal equal in height to 1st, posterior half expanded and serrated above with rather sharp descension to anterior elevated ridgelike lamellar portion that terminates far in front of anterior end of 1st parietal; 4th parietal almost identical in size and shape to 3rd. Columellar barrier a raised lamellar ridge, expanded and serrated above posteriorly, with gradual anterior descension, slanting slightly downward across columellar wall, stopping well short of lip margin. Palatal barriers 5, extending posteriorly almost three-sixteenths of a whorl, with six short, low accessory traces: lower palatal greatly reduced in height, a weakly elevated lamellar ridge with gradual anterior descension; 2nd palatal high and bladelike, flattened and expanded above posteriorly with sinuated anterior descension; 3rd and 4th palatals distinctly higher than 2nd, with more gradually sinuated anterior descension; 5th palatal located above level of upper parietal, greatly reduced in height, scarcely larger than some of the larger accessory traces, deeply recessed within aperture. Palatal traces located as follows: one between each pair of major palatals (omitted in type figure between first and second palatals) and two above 5th palatal (omitted in type figure). Height of holotype 2.50 mm., diameter 4.57 mm.

Holotype. — Austral Islands: Rapa Island, Station 451, east ridge of Mt. Perahu at 1,200-1,500 ft. elevation. Collected by Yoshio Kondo on July 21, 1934. BPBM 142817.

Range. — East ridge of Mt. Perahu at 1,200-1,900 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: east ridge of Mt. Perahu (Stations 446, 450, 451, 452, 509, 511, 512, 513) at 1,200-1,900 ft. elevation (39 specimens, BPBM 135419, BPBM 135440, BPBM 135490, BPBM 135575, BPBM 142745, BPBM 142798, BPBM 142817, BPBM 142828, BPBM 142872-4).

Remarks. — *Opanara duplicidentata* is the only species of this genus that normally has 4 parietals. Occasionally a specimen of *O. fosbergi* will have a 4th parietal, but all other species normally have only 3 parietals. Rib variation was rather large, but not between stations.

At Stations 444, 451, and 452 *O. duplicidentata* was the most frequently collected species. Only at Station 451 were the numbers large enough (18 *Opanara duplicidentata,* 10 *O. depasoapicata,* and 16 *Orangia cookei montana*) to be meaningful. Some collecting bias may have been introduced by the distinctly larger size of *O. duplicidentata,* but since Kondo was the only collector at the station, I am inclined to accept its greater abundance.

Dissection of several individuals showed a few peculiarities of structure. The buccal retractor was not split and the penial retractor arose from the columellar muscle, not the diaphragm. Internally, the penis has the pilasters higher and much more complexly folded than in most other *Opanara.* The columellar muscle origin of the penial retractor is sometimes found in forms with increased size (see pp. 81-83) and has no particular systematic significance. The penial length of 1.5-2.0 mm. is quite short in comparison with other *Opanara.*

Description of soft parts. — Foot and tail retracted into shell in all specimens, tail not tapering, rounded behind. Sole undivided. Pedal grooves high on side of foot, prominent. Slime network very faint.

Body color yellow-white, without darker markings.

Mantle collar thin, edges expanded only around pneumostome, no glandular extension onto pallial roof. Pneumostome typical, no mantle lobes.

Pallial region extending slightly less than three-quarters whorl apically. Lung roof with scattered white granules, mainly clustered around hindgut, pulmonary vein, and edges of kidney and ureter. Kidney about 2.15 mm. long, rather broad anteriorly, rectal arm about half of length. Ureter arising subapically, reflexed and opening at anterior end of rectal kidney arm. Heart slightly less than half length of kidney, lying parallel to hindgut. Principal pulmonary vein and hindgut typical.

Ovotestis (fig. 96g, G) of six to eight clumps of palmately clavate alveoli extending for about one-half whorl above stomach, positioned as in *Endodonta fricki* (fig. 163c).

Hermaphroditic duct (GD) tapering apically, medially of uniform diameter, abruptly narrowed to a thin tube, then reflexing apicad before entering carrefour. Albumen gland (GG) longer and more slender than in most species, extending further beyond apex of talon than shown in Figure 96g. Talon (GT) with bulbous head and short tapered shaft, entering directly into carrefour, which shows asymetric lateral entrances of albumen gland duct and hermaphroditic duct (fig. 96g). Prostate (DG) with one or two rows of acini opening into a narrow tube, partly hidden by uterine area. Uterus (UT) bipartite, lower area greatly swollen, narrowing abruptly just beyond end of prostate to enter free oviduct.

Vas deferens (VD) typical, lightly bound to penioviducal angle, entering penis subapically just inside margin of apical pilaster junction, about one-quarter of length from top of penis. Penial retractor (PR) arising from columellar muscle just below point where buccal retractors join columellar muscle at apex, inserting directly onto fleshy extension of penis head. Penis (P) about 1.5 mm. long, expanded on upper third, with long fleshy extension to penis head. Internally (fig. 96h), with two complexly expanded and folded pilasters (PP) tha' are narrow, low, and fused apically, greatly modified medially, and narrowed, then fused near atrium. Central portion of pilasters very high and thicker above than on base. Atrium (Y) short, rather narrow.

Free oviduct (UV) clearly differentiated from uterus, longer than prostate. Spermatheca (S) with narrow elongated head in typical position, inserting on oviducal side of penioviducal angle.

Free muscle system typical, except buccal retractor not split in examined specimens. Digestive system without unusual features.

Jaw of large, overlapping plates, individual plates about 4-5 times as wide as long. No clear indication of fusion between plates.

Radula with cusps about equal in length to basal plate, central about 10 μ wide, 11 μ long. Generally, 5 laterals and more than 9 marginals, all specimens fragmented during mounting.

(Based on BPBM 142817, two whole and several partial specimens. One whole specimen 4.18 mm. in diameter, with 5¾+ whorls.)

Opanara areaensis, new species.

Specimens were found in greatest numbers on the lower slopes of Mt. Tanga at 250-450 ft. elevation, northwest of Mt. Tavaitahu at 600-750 ft. elevation,

TABLE LXXIX. - LOCAL VARIATION IN OPANARA AREAENSIS

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
areaensis areaensis						
BPBM 142555 Sta. 366	15	1.77±0.035 (1.56-2.02)	3.29±0.045 (3.05-3.64)	0.535±0.0054 (0.506-0.581)	5 1/4+ (5-5 5/8)	3.41±0.070 (3.07-4.04)
BPBM 140502 Sta. 383	57	1.77±0.013 (1.55-1.94)	3.28±0.016 (2.96-3.52)	0.538±0.0025 (0.500-0.584)	5 1/4- (4 3/4-5 5/8)	3.44±0.027 (2.99-4.00)
BPBM 140503 Sta. 383	8	2.01±0.027 (1.85-2.09)	3.62±0.031 (3.44-3.74)	0.555±0.0060 (0.518-0.573)	5 5/8 (5 1/2-5 7/8)	3.61±0.110 (3.27-4.23)
BPBM 144301 Sta. 382	10	1.82±0.020 (1.72-1.92)	3.40±0.026 (3.25-3.51)	0.536±0.0035 (0.520-0.550)	5 3/8- (5 1/4-5 5/8)	3.36±0.076 (3.12-3.93)
BPBM 142468 Sta. 346	8	1.77±0.041 (1.59-1.95)	3.42±0.080 (3.05-3.77)	0.519±0.0028 (0.505-0.530)	5 1/2+ (5 1/4-6)	3.46±0.088 (2.97-3.83)
BPBM 144145, -6 Sta. 340	32	2.01±0.025 (1.82-2.35)	3.64±0.027 (3.44-3.97)	0.551±0.0044 (0.510-0.634)	5 5/8+ (5 1/4-6 1/4)	3.81±0.041 (3.28-4.19)
BPBM 138334 Sta. 485	8	2.02±0.037 (1.89-2.25)	3.58±0.071 (3.25-3.91)	0.564±0.0050 (0.540-0.582)	5 5/8- (5 3/8-6)	3.78±0.085 (3.50-4.16)
BPBM 143293, -4, 8 Sta. 478	7	2.09±0.044 (1.97-2.30)	3.72±0.068 (3.45-3.98)	0.561±0.0065 (0.534-0.578)	5 7/8- (5 5/8-6)	3.83±0.081 (3.50-4.17)
BPBM 137949, BPBM 144022, BPBM 144040 Sta. 316, 317	6	1.98±0.035 (1.88-2.11)	3.55±0.070 (3.36-3.82)	0.557±0.0120 (0.534-0.615)	5 5/8- (5 3/8-5 7/8)	4.42±0.099 (4.14-4.73)
areaensis densa						
BPBM 144711, -4 Sta. 477	8	1.90±0.056 (1.69-2.19)	3.30±0.062 (3.15-3.68)	0.574±0.0092 (0.537-0.616)	5 3/8+ (5 1/8-5 3/4)	3.60±0.099 (3.31-3.97)
areaensis microtorma						
BPBM 135437, BPBM 142746, BPBM 142875, ex BPBM 142818 Sta. 446, 451-2, 509	5	2.10±0.036 (1.99-2.19)	3.60±0.017 (3.54-3.64)	0.584±0.0103 (0.551-0.607)	5 3/4- (5 1/2-6)	4.11±0.069 (3.86-4.27)

and on Mt. Mangaoa at 800 ft. elevation. Scattered examples were found in the Maitua region at 500-750 ft. elevation and on Mt. Perahu at 1,200-1,800 ft. elevation.

This was the first species complex studied. Measurements were made using material as segregated into age groups by the Bishop Museum staff in the mid-1930's. The measured material included both adult and paraneanic specimens. During study of this material, I became aware that there was a clear set of previously unrecognized criteria by which adult shells could be separated from subadult specimens (see pp. 11-13). Time did not permit restudy of the *O. areaensis* material to eliminate paraneanic specimens from the measurements. Hence the variation shown between sets (table LXXIX) is misleading. The specimens from Station 340 (BPBM 144145-6), Station 383 (BPBM 140503), and Station 485 (BPBM 138334) contain only adult and gerontic individuals selected from large samples, while measured material from Stations 366, 382, 346, and 474 contained mixtures of adults and paraneanic specimens from smaller total samples and averaged much less in size. Another set from Station 383 (BPBM 140502) contained many paraneanic specimens and no gerontic individuals, hence it averaged much smaller and slightly lower than the specimens from BPBM 140503.

Size variation, although appearing rather great, was not large once the distortion introduced by inclusion of paraneanic individuals is discounted. There were noticeable differences in shape and umbilical width. While most individuals had a flat apex and spire (fig. 104a), specimens from Stations 477 and 478 northwest of Mt. Tautautu, Station 527 on Mt. Mangaoa, and the specimens from Mt. Perahu have the spire almost evenly elevated as in Figure 104c. There was no major change in H/D ratio accompanying the spire elevation, since those forms with elevated apex and spire had the relative descension of the body whorl reduced. Umbilical width showed a normal distribution, except for the presence of narrowly umbilicated forms on Mt. Perahu and from the Maitua area (fig. 104f). The six measured Maitua shells from Stations 316 and 317 had a mean D/U ratio of 4.42, which was narrower than the Perahu populations (mean D/U ratio 4.11) and much less than the average for the nominate race (mean D/U ratio 3.62). There was no significant alteration in H/D ratio (means of 0.557 for Maitua; 0.549 for nominate race; 0.584 for Perahu shells).

Ribbing variation (table LXXX) included the presence of shells with very numerous (90-113) and crowded (8.63-11.03 ribs/mm.) major radial ribs at

TABLE LXXX. - RIB VARIATION IN OPANARA AREAENSIS

Name	Number of Specimens	Diameter	Rib Count	Ribs/mm.
areaensis areaensis				
BPBM 140502 Sta. 383	57	3.28±0.016 (2.96-3.52)	58.2±0.70 (49-70)	5.70±0.043 (4.89-6.71)
BPBM 144649-50 Sta. 474	30	3.36±0.028 (3.06-3.62)	61.7±0.98 (51-72)	5.84±0.077 (4.99-6.51)
BPBM 142468 Sta. 346	5	3.44±0.081 (3.32-3.75)	57.0±1.92 (53-64)	5.29±0.255 (4.67-6.14)
BPBM 144145-7 Sta. 340	10	3.51±0.094 (3.16-3.98)	56.0±2.27 (49-68)	5.07±0.092 (4.65-5.46)
BPBM 143293-5 Sta. 478	9	3.63±0.081 (3.32-3.98)	58.2±2.16 (51-71)	5.10±0.143 (4.18-5.68)
All Measured Specimens		3.53[1] (3.03-3.98)	60.2[1] (49-88)	5.68[2] (4.18-7.47)
areaensis densa				
BPBM 144711 Sta. 477	5	3.35±0.086 (3.13-3.65)	102.6±4.58 (90-113)	9.75±0.385 (8.63-11.03)
areaensis microtorma				
All	5	3.57±0.017 (3.52-3.62)	77.0±1.92 (73-83)	6.86±1.31 (6.47-7.30)

1. Based on 126
2. Based on 152

Stations 477 and 478 northwest of Mt. Tautautu; moderately numerous (66-88) and crowded (5.41-7.47 ribs/mm.) radial ribs on the shells from Mt. Perahu, Mt. Mangaoa (Stations 485 and 527), and Maitua (Station 316); with specimens from the other localities showing less numerous (49-71) and more widely spaced (4.18-6.71 ribs/mm.) radial ribs.

The patterns of variation outlined above are less clearly segregated and more diffuse than those in *Orangia cookei, Ruatara oparica, Opanara megomphala,* or *Rhysoconcha,* but are essentially similar.

Specimens from Mt. Perahu have a distinctly elevated apex and early spire, a narrower umbilicus than most specimens, and rather crowded and numerous radial ribs. They were taken at a much higher altitude than other *areaensis* populations and are recognized by the subspecific name *microtorma.*

Specimens from Station 477 and one of 14 specimens from Station 478 have very crowded radial ribbing, an elevated apex, and quite different appearance from the typical examples. They are recognized by the subspecific name *densa.* Other specimens from Station 478 are typical *areaensis.* A difference of only 50 ft. altitude separates the two stations. Collections from the lower station (478) were made by Kondo, from the upper (477) by Wight, Kondo, and Cooke. I suspect that the two forms actually are separated micro-geographically and the recording of one *densa* from the Station 478 *areaensis* population is a simple error in bottling field material.

The subspecies may be characterized as follows:

Opanara areaensis areaensis has a flat apex and early spire, open (mean D/U ratio 3.67) umbilicus, relatively few (mean 60.2) and widely spaced (mean ribs/mm. 5.68) radial ribs.

Opanara areaensis densa has a raised apex and early spire, open (mean D/U ratio 3.62) umbilicus, very many (mean 103.5) and crowded (mean ribs/mm. 9.75) radial ribs.

Opanara areaensis microtorma has a raised apex and early spire, narrow (mean D/U ratio 4.11) umbilicus, with an intermediate number (mean 77.0) of moderately spaced (mean ribs/mm. 6.86) radial ribs.

Opanara areaensis areaensis, new species and subspecies. Figures 96j-k; 104a-b.

Diagnosis. — Shell relatively large, diameter 3.03-3.98 mm. (mean 3.53 mm.), with 5⅛ - 6¼ rather tightly coiled whorls. Apex and early spire flat or barely elevated, later whorls descending quite rapidly in adults, H/D ratio 0.505-0.634 (mean 0.549). Umbilicus broadly open, U-shaped, last whorls barely or moderately decoiling, contained 2.97-4.01 times (mean 3.67) in the diameter, with sharply angulated margin and rather strongly flattened whorls internally. Postnuclear sculpture of narrow, prominent, rather widely spaced, slightly protractively sinuated radial ribs, 49-88 (mean 60.2) on the body whorl, whose interstices are 4-6 times their width. Microsculpture of fine radial riblets, six to ten between each pair of major ribs, crossed by barely visible and crowded spiral riblets. Sutures impressed, whorls very strongly rounded above and on umbilical margin, compressed laterally with evenly rounded outer margin. Aperture subovate, strongly rounded above on umbilical margin, inclined about 10° from shell axis. Parietal barriers 3, occasionally (6.3 per cent) with a small 4th parietal located between upper two, extending posteriorly more than three-sixteenths of a whorl: upper parietal high and bladelike, weakly expanded and serrated above on posterior eighth, with practically no anterior descension until last quarter of length; 2nd parietal slightly reduced in height posteriorly, posterior elevated portion about one-fourth length of tooth, with gradual anterior descension to a low threadlike ridge that extends anteriorly beyond termination of upper parietal; 3rd parietal, high and bladelike, expanded and serrated above on posterior third, with relatively gradual anterior descension, never becoming threadlike anteriorly; 4th parietal, when present, usually very short and greatly reduced posteriorly with anterior threadlike portion of variable length, normally situated between 1st and 2nd parietals, rarely (1.5 per cent) an accessory trace above upper or below 3rd parietal. Columellar barrier high and bladelike, weakly expanded above, posteriorly lying parallel to plane of coiling, anteriorly deflected sharply downward onto basal lip, abruptly descending to lip margin, broadly expanded at anterior end. Palatal barriers 4, rarely (3.1 per cent) with 2nd or 3rd tooth bifid, extending posteriorly for about one-eighth whorl: 1st palatal very high and bladelike, flattened, weakly expanded, and serrated above with abrupt anterior descension to lip margin, often grossly expanded at anterior end; 2nd and 3rd palatals equal in height to 1st or slightly reduced, almost reaching lip margin, with progressively more gradual anterior descension; 4th palatal greatly reduced in height, a shorter, recessed lamellar ridge, only weakly expanded above, supraperipheral, lying well above plane of upper parietal.

The abrupt and complete deflection of the columellar barrier onto the basal lip immediately separates *Opanara areaensis areaensis* from the other Rapan species. Only *Ruatara koarana* has the columellar barrier similarly deflected, and that species has the progressively more deeply recessed parietals and a barely perforate or closed umbilicus. The widely open, U-shaped umbilicus with angled margin immediately differentiate *O. areaensis* from the *Anceyodonta* that have a deflected columellar barrier, plus the deflection of the latter occurring in a different fashion. *Opanara areaensis densa* differs in its distinctly elevated spire (fig. 104c) and much more crowded radial ribs (90-113 on the body whorl). *Opanara a. microtorma* differs in its distinctly narrower umbilicus (fig. 104f).

Description. — Shell of average size, with 5⅜ normally coiled whorls. Apex and early spire flat, last two whorls descending much more rapidly, H/D ratio 0.528. Apical whorls 1⅜, sculpture of low, widely spaced radial ribs, interspersed with one or two microriblets, then crossed by very fine and rather widely spaced spiral riblets. Postnuclear whorls with narrow, prominent, lamellar, protractively sinuated radial ribs, 71 on the body whorl, whose interstices are 3-6 times their width. Sutures deep, whorls strongly rounded above and on angulated umbilical margin, slightly compressed laterally with evenly rounded outer margins. Color light yellow horn with vague traces of irregular, zigzagged, reddish flammulations. Umbilicus widely open, U-shaped, last whorl slightly decoiling, contained 3.67 times in the diameter, margin distinctly shouldered. Aperture ovate, laterally compressed, inclined about 10° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl, with a single threadlike trace situated below 3rd parietal: upper parietal high and bladelike, serrated and expanded above on posterior quarter, with very gradual anterior descension until just before end; 2nd parietal reduced in height, expanded and serrated above on posterior third, with rather sharp anterior descension to threadlike anterior half extending beyond termination of upper parietal; 3rd parietal high and bladelike, expanded and serrated above on posterior third, with very gradual anterior descension to an elevated lamellar ridge that terminates opposite end of 2nd parietal. A weak threadlike trace located below 3rd parietal. Columellar barrier a high lamellar ridge, weakly expanded above, posteriorly lying parallel to plane of coiling, deflected sharply downward onto basal lip with abrupt anterior descension, grossly expanded at anterior end. Palatal barriers 4, extending posteriorly about one-eighth whorl: lower palatal very high, bladelike, flattened, expanded and serrated above, with abrupt anterior descension almost to lip margin, weakly expanded at anterior tip; 2nd and 3rd palatals equal in height to 1st, with more gradual anterior descension, almost reaching lip margin; 4th palatal greatly reduced in height, a low lamellar ridge, weakly expanded above, shorter and more deeply recessed, lying above plane of upper parietal. Height of holotype 1.91 mm., diameter 3.62 mm.

Holotype. — Austral Islands: Rapa Island, Station 474, hillside back of Area at 400 ft. elevation. Collected under stones by Donald Anderson on July 24, 1934. BPBM 144649.

Range. — Scattered lowland to middle elevation localities on both north and south Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: hillside back of Area (Stations 366, 382, 383, 474) at 250-450 ft. elevation under stones (629 specimens, BPBM 140502-7, BPBM 142555-9, BPBM 144301-4, BPBM 144649-51); hillside and valley west of Tavaitahu (Station 346) at 750 ft. elevation under stones (11 specimens, BPBM 142468-70); area near Maitua (Stations 316, 317, 319, 353, 358) at 500-750 ft. elevation (13 specimens, BPBM 135698-9, BPBM 137949, BPBM 138535, BPBM 140017, BPBM 144022, BPBM 144040); northeast ridge and its west slope of Mt. Mangaoa (Stations 403, 485, 527) at 800 ft. elevation (41 specimens, BPBM 138334-6, BPBM 138407, BPBM 144381); northwest of Tavaitahu (Stations 340, 478) at 600-750 ft. elevation (96 specimens, BPBM 143293-8, BPBM 144145-50).

Remarks. — Tooth variation within this species was surprisingly slight. One individual had the 3rd parietal bifid, another had a 4th trace below the 3rd parietal and eight had a 4th parietal located between the 1st and 2nd. Three specimens had the 2nd palatal bifid, one had the 3rd palatal bifid, and two specimens had extra palatals.

Descension of the columellar barrier onto the basal lip near the aperture is one of the most distinctive features found in *Opanara areaensis*. While this might be taken as an "adult" character, since posteriorly the columellar barrier lies parallel to the plane of coiling, even the youngest individuals have

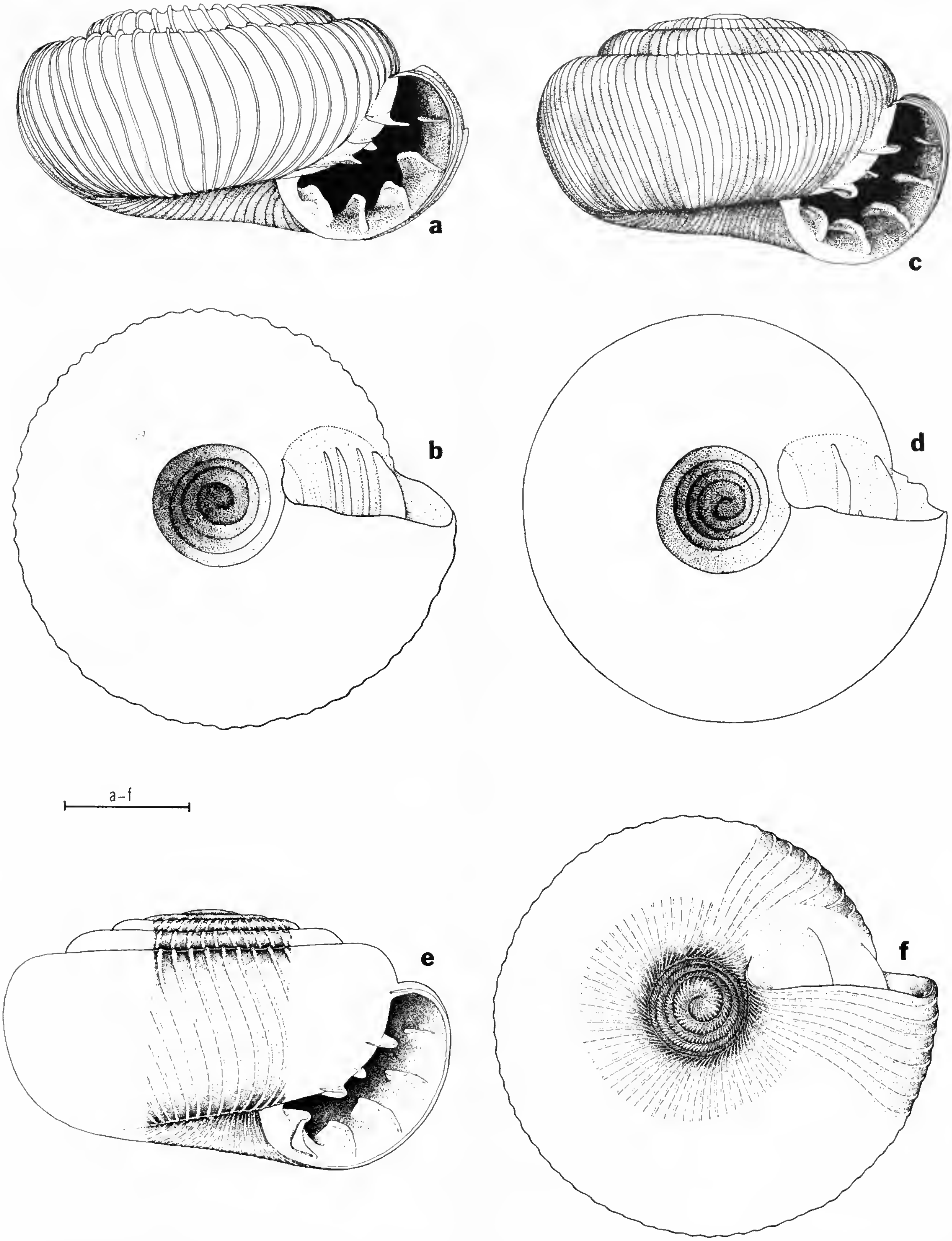

FIG. 104. **a-b**, *Opanara areaensis areaensis,* new species and subspecies. Station 474, Area, Rapa Island, Austral Islands. Holotype. BPBM 144649; **c-d**, *O. a. densa,* new subspecies. Station 477, Mt. Tautautu, Rapa Island, Austral Islands. Holotype. BPBM 144711; **e-f**, *O. a. microtorma,* new subspecies. Station 509, Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 135437. Scale lines equal 1 mm. Figures *a-d* by YK reproduced through the courtesy of Bernice P. Bishop Museum; *e-f* (MM).

the columellar displaced onto the basal lip. Continuance of this growth pattern presents some problems, since instead of the anterior addition and posterior resorption normally required during whorl increment, continuation of the basal deflection and posterior parallelism demands anterior resorption and growth plus similar changes at the posterior section of the twisted portion. A study of the growth mechanism would be very worthwhile.

Because delineation of this complex was rather difficult, several sets were borrowed for further study. Rib counts were made at a later time from both adult and paraneanic individuals (as explained above, pp. 40-44). The availability of abundant material allowed checking the effect of size increment on rib frequency. Table LXXX presents data from five sets ranked in increasing mean diameter. It is obvious that there is a general trend for an increase in mean diameter to be accompanied by a slight increase in rib spacing. There is no such trend in regard to actual rib count. This confirms data obtained from populations of *Anceyodonta obesa* (pp. 203-204) where reduction in adult shell size was not accompanied by reduction in rib count, but only by an increase in rib crowding. Comparing populations of *O. areaensis* from Stations 383 and 478 in respect to rib frequency, with 95 df, "*t*" = 4.1969. I have no doubt that this shift in rib spacing is real and important.

As noted above in the general discussion of *O. areaensis,* the Maitua populations differ in their umbilical width (see data on Stations 316-317 in table LXXIX) and tendency toward an elevated spire. In sculpture and form they are much more like *O. areaensis areaensis* then either of the other subspecies, although showing tendencies toward them.

The anatomy differs from that seen in other *Opanara* only in the variability of relative penial pilaster size and more nearly apical insertion of the vas deferens.

Description of soft parts. — Foot and tail fully retracted in all specimens examined.

Body color yellow-white, without darker markings.

Mantle collar with thickened edges, no glandular extension into pallial cavity. Pneumostome typical, no mantle lobes developed.

Pallial region extending more than five-eighths whorl apically. Lung roof clear, a few scattered specks near kidney surface. Kidney about 1.6 mm. long, tapering anteriorly, rectal arm about one-third length of pericardial. Ureter typical, originating behind kidney anterior end, reflexing basally, opening just anterior of rectal arm termination. Heart about one-half length of kidney, not parallel to hindgut. Principal pulmonary vein slender, fading out just short of mantle collar. Hindgut at parietal-palatal margin for about one-eighth whorl above pallial cavity termination.

Ovotestis (fig. 96j, G) occupying half whorl above stomach reflexion, comprising four main clumps of palmately clavate alveoli. Hermaphroditic duct (GD) slender at point of stomach reflexion, rather narrowly expanded, tapering gradually to typical reflexion before entering laterally on talon. Albumen gland (GG) very small in younger specimens, typical in appearance. Talon (GT) with enlarged head, narrow connecting shaft and enlarged lower portion buried in albumen gland. Prostate (DG) of one or two rows of large acini opening into a slender tube that continues into vas deferens, acinar section rather short. Uterus (UT) composed of a narrower upper portion (UT_1), with a wider, thicker walled lower section (UT_2).

Vas deferens (VD) very slender, entering penis head subapically, but much nearer apex than in most *Opanara.* Penial retractor (PR) originating from diaphragm just above apex of pallial cavity, inserting on fleshy head of penis. Penis (P) about 2.65 mm. long, tapering apically, internally (fig. 96k) with two pilasters, low and broad basally, becoming very slender and high apically, then tapering to a junction at constricted head of penis. Vas deferens opening (DP) located between main part and weak arm of one pilaster. Atrium (Y) very short.

Free oviduct (UV) tapering slightly from uterus to atrium, highly twisted because of animal retraction. Spermatheca (S) entering free oviduct just above atrium, shaft slightly expanded basally. Vagina (V) not morphologically differentiated.

Free muscle system typical. Right ommatophoral retractor passing through penioviducal angle.

Buccal retractors not split, uniting with pedal retractors just before columellar muscle termination. Esophagus typical. Stomach occupying almost one whorl, reflexing normally. Intestinal loops occupying first eighth whorl above pallial cavity apex.

Jaw of many very narrow overlapping plates, each plate five or six times as long as wide.

Radula with about 6 laterals and more than 7 marginals, central about 11 μ wide and 13 long with cusps as long as basal plates.

(Based on BPBM 138334, BPBM 142468, whole retracted specimens 3.16 mm. with 5⅛ whorls, 4.01 mm. with 5¾+ whorls.)

Opanara areaensis densa, new subspecies. Figure 104c-d.

Diagnosis. — Shell of average size, diameter 3.15-3.68 mm. (mean 3.32 mm.), with 5⅛ - 5¾ normally coiled whorls. Apex and early spire distinctly elevated, last whorl descending a little more rapidly, H/D ratio 0.537-0.616 (mean 0.572). Umbilicus broadly open, U-shaped, last whorl slightly decoiling, contained 3.31-3.97 times (mean 3.62) in the diameter. Postnuclear sculpture of narrow, crowded, lamellar, slightly protractively sinuated radial ribs, 90-113 (mean 103.5) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, three to six between each pair of major ribs, crossed by barely visible and extremely crowded spiral riblets. Sutures deep, whorls strongly rounded above and slightly compressed laterally, with evenly rounded outer margin, umbilical margin shouldered, columellar wall flattened. Aperture ovate, slightly compressed laterally, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly more than three-sixteenths of a whorl: upper parietal high and bladelike, strongly expanded and serrated above on posterior third, with scarcely any anterior descension until anterior eighth of barrier; 2nd parietal slightly reduced in height, posterior third expanded and elevated above, sharply descending to an anterior threadlike trace that normally terminates beyond end of upper parietal, sometimes (11.1 per cent) with threadlike portion extremely shortened; 3rd parietal high and bladelike, expanded and serrated above on posterior third, with very gradual anterior descension to an elevated threadlike lamellar ridge that terminates opposite end of 2nd parietal. Columellar barrier a high bladelike lamella, expanded and serrated above parallel to plane of coiling posteriorly, twisted sharply downward onto basal lip with abrupt anterior descension, weakly expanded at anterior tip. Palatal barriers 4, extending posteriorly more than one-eighth whorl: lower palatal high and bladelike, flattened, expanded and serrated above, with abrupt anterior descension almost to lip margin, weakly expanded at anterior tip; 2nd and 3rd palatals equal in height to 1st, with more gradual anterior descension, slightly more deeply recessed; 4th palatal supraperipheral, reduced in height and length, an elevated lamellar ridge situated above level of upper parietal.

The distinctly elevated spire and crowded, numerous radial ribs distinguish *Opanara areaensis densa* from the nominate subspecies, which has the apex and early spire flat and only 49-88 (mean 60.2) radial ribs on the body whorl. *O. areaensis microtorma* differs in its much less crowded and more widely spaced radial ribs and narrower umbilicus (D/U ratio 3.86-4.27, mean 4.11).

Description. — Shell of average size, with 5½ normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.616. Apical whorls 1⅜, sculpture typical. Postnuclear whorls with narrow, prominent, lamellar, almost vertically sinuated radial ribs, 113 on the body whorl, whose interstices are two to three times their width. Microsculpture of very fine radial riblets, three to five between each pair of major ribs, crossed by barely visible and extremely crowded spiral riblets. Sutures deep, whorls strongly rounded above, slightly compressed laterally and with evenly rounded outer margin, umbilical margin distinctly shouldered, columellar wall flattened. Color light yellow-white, with prominent, strongly zigzagged, reddish flammulations that tend to coalesce on shell base. Umbilicus broadly open, U-shaped, last whorl moderately decoiling, contained 3.54 times in the diameter. Aperture ovate, compressed laterally, inclined less than 5° from shell axis. Parietal barriers 3, extending posteriorly more than three-sixteenths of a whorl: upper parietal high and bladelike, expanded and serrated above on posterior quarter, with exceedingly gradual anterior descension until just before termination; 2nd parietal almost equally high on posterior third, expanded and serrated above, with rather sharp anterior descension to a short threadlike portion that stops well before anterior end of upper parietal; 3rd parietal very high on posterior third, expanded and serrated above, with gradual anterior descension to a raised lamellar ridge that terminates well beyond anterior end of upper parietal. Columellar barrier a high bladelike lamella, weakly expanded and serrated above, posteriorly lying parallel to plane of coiling, abruptly descending anteriorly and twisted downward onto basal margin, moderately expanded at anterior end. Palatal barriers 4, extending posteriorly more than one-eighth whorl; lower palatal very high, bladelike, expanded, flattened and serrated above, with abrupt anterior descension almost to lip margin, weakly expanded at anterior edge; 2nd and 3rd palatals equally high posteriorly, expanded and serrated above, with more gradual anterior descension; 4th palatal supraperipheral, lying above plane of upper parietal, greatly reduced in height and length, a low, lamellar blade, with very gradual anterior descension. Height of holotype 2.01 mm., diameter 3.26 mm.

Holotype. — Austral Islands: Rapa Island, Station 477, northwest of Mt. Tautautu at 800 ft. elevation, above Station 340. Collected under stones by S. Wight, Yoshio Kondo, and C. M. Cooke, Jr. on July 25, 1934. BPBM 144711.

Range. — Northwest of Mt. Tautautu at 750-800 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: northwest of Mt. Tautautu (Stations 477, 478) at 750-800 ft. elevation under stones (19 specimens, BPBM 144711-4, BPBM 143299).

Remarks. — The type of *O. areaensis densa* is slightly atypical in that the middle parietal barrier has the low anterior portion missing, although the posterior elevation is identical to that found in the nominate race. This variation was found in two of the 19 specimens. All specimens of *O. a. densa* have a strongly differentiated color pattern of alternating horn and reddish markings, while most *O. areaensis areaensis* are indistinctly flammulated or tend toward a unicolored condition.

Specimens of *O. a. densa* are immediately separable from neighboring populations by their crowded ribbing and elevated spire. Although the *O. areaensis areaensis* taken from Stations 316 and 317 have equally elevated spires, their ribbing is the type found in the nominate race.

Description of soft parts. — Foot and tail completely retracted in all available material. Sole, when dissected out, undivided, pedal grooves typical.

Body color yellowish white, no darker markings.

Mantle collar typical.

Pallial region extending apically slightly more than one-half whorl. Lung roof clear, without granulations. Kidney and ureter typical.

Genitalia as in nominate race, except penis shorter (2.15 mm. long), with roughly equal pilasters. Vas deferens entering penis almost at apex.

Jaw not successfully mounted.

Radula fragmented in mounting, teeth as in *O. areaensis areaensis.*

(Based on BPBM 144711, whole specimen 3.30 mm. in diameter, with 5½ whorls and 92 ribs on the body whorl.)

Opanara areaensis microtorma, new subspecies. Figure 104e-f.

Diagnosis. — Shell larger than average, diameter 3.54-3.64 mm. (mean 3.60 mm.), with 5½ - 6 normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.551-0.607 (mean 0.584). Umbilicus open, U-shaped, last whorl slightly decoiling, contained 3.86-4.27 times (mean 4.11) in the diameter. Postnuclear sculpture of narrow, prominent, lamellar, slightly protractively sinuated radial ribs, 73-83 (mean 77.0) on the body whorl, whose interstices are 3-4 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures deep, whorls strongly rounded above, with evenly rounded and somewhat compressed outer margin, umbilical margin strongly shouldered, columellar wall flattened. Aperture ovate, compressed laterally, inclined about 5° from shell axis. Parietal barriers as in the nominate subspecies, except that three of the five known specimens have the anterior threadlike portion of the middle parietal distinctly shortened. Columellar and palatal barriers as in the nominate subspecies.

A distinctly elevated spire, slightly more numerous ribbing, and narrower umbilicus are the characters that separate *Opanara areaensis microtorma* from the nominate subspecies. *O. a. densa* differs in its wider umbilicus, much more crowded radial ribbing, and slightly more elevated spire.

Description. — Shell larger than average, with 5¾ normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.607. Apical and early postnuclear whorls with sculpture eroded. Remaining whorls with narrow, prominent, lamellar, slightly protractively sinuated radial ribs, 75 on the body whorl, whose interstices are 3-4 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by extremely crowded, barely visible spiral riblets. Sutures deep, whorls strongly rounded above, compressed laterally on gently rounded outer margin, umbilical margin strongly shouldered, columellar wall somewhat flattened. Color light yellow horn, with irregular, narrow, somewhat zigzagged, reddish flammulations that tend to fade out on shell base. Umbilicus narrow, U-shaped, last whorls barely decoiling, contained 4.15 times in the diameter, umbilical margin strongly shouldered. Aperture ovate, slightly compressed laterally, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly more than three-sixteenths of a whorl; upper parietal high and bladelike, expanded and serrated above on posterior third, with very gradual anterior descension until just before anterior eighth of length; 2nd parietal with posterior quarter high and bladelike, somewhat expanded above and crescentic in outline, sharply descending to a narrow threadlike trace that terminates well before end of upper parietal; 3rd parietal high and bladelike, expanded and serrated above on posterior third, with very gradual descension to a low lamellar ridge that terminates beyond anterior end of upper parietal. Columellar barrier a high slender ridge, posteriorly parallel to plane of coiling, expanded and serrated above, anteriorly twisting abruptly downward onto lip margin, grossly expanded at anterior end. Palatal barriers 4, extending posteriorly slightly more than one-eighth whorl: lower palatal high and bladelike, flattened, serrated and expanded above, with abrupt anterior descension almost to lip margin, weakly expanded at anterior end; 2nd and 3rd palatals equal in height to 1st, expanded and serrated above on posterior half with progressively more gradual anterior descension; 4th palatal supraperipheral, greatly reduced in height and length, moderately recessed within aperture, lying above plane of upper parietal, a low lamellar ridge. Height of holotype 2.14 mm., diameter 3.52 mm.

Holotype. — Austral Islands: Rapa Island, Station 509, east ridge of Mt. Perahu at 1,300-1,500 ft. elevation. Collected by Yoshio Kondo, Donald Anderson and natives on July 28, 1934. BPBM 135437.

Range. — East ridge of Mt. Perahu at 1,200-1,800 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa: east ridge of Mt. Perahu (Stations 446, 451, 452, 509) at 1,200-1,800 ft. elevation (5 specimens, BPBM 135437, BPBM 142746, ex BPBM 142818, BPBM 142875).

Remarks. — So little material is available, that no real systematic importance can be attached to the 60 per cent incidence of shortening in the 2nd parietal. This was sometimes (11.1 per cent) present in *O. a. densa,* based on very limited material, and in *O. areaensis areaensis* was not observed in any specimen.

As in *O. areaensis densa,* the flammulated color pattern was strongly developed. Despite the presence of a narrowly umbilicated population (Stations 316, 317) in *O. areaensis areaensis,* the narrow umbilicus of *O. a. microtorma* combined with the raised spire and generally more crowded ribbing serve to characterize it as a recognizable taxonomic unit.

Opanara caliculata, new species. Figure 105a-b.

Diagnosis. — Shell slightly smaller than average, diameter 3.09-3.39 mm. (mean 3.27 mm.), with 4⅝ - 5¼ tightly coiled whorls. Shell sub-globose, apex and spire moderately and evenly elevated, last whorl descending only slightly more rapidly, H/D ratio 0.595-0.660 (mean 0.617). Umbilicus narrow, U-shaped, slightly narrower at last whorl than near apex, contained 4.09-5.22 times (mean 4.74) in the diameter. Postnuclear sculpture of narrow, lamellate, very crowded, slightly protractively sinuated radial ribs, 117-125 (mean 120.3) on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly and evenly rounded on outer margin, basal margin slightly flattened and extended, baso-columellar margin strongly angled, columellar wall weakly sinuated. Aperture ovate, with evenly rounded outer margin, columellar margin flattened and sinuated, inclined about 15° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl: upper parietal high and bladelike, expanded and serrated above on posterior half, with very gradual anterior descension; 2nd parietal slightly higher posteriorly, roughly crescentic on elevated portion that occupies posterior third of length, rather gradually descending to raised threadlike anterior portion that extends beyond end of upper parietal; 3rd parietal slightly reduced in height from 2nd, posterior elevated portion similar in shape but shorter, anterior threadlike portion of equal length. Columellar barrier a low, bladelike lamellar ridge, lying parallel to plane of coiling posteriorly, slanting very slightly downward at anterior end, reaching almost to lip margin. Palatal barriers 4, extending posteriorly about one-eighth whorl; 1st palatal a high, crescentic lamellar blade, weakly expanded and serrated above, sharply descending anteriorly almost to lip margin; 2nd palatal equal in height to 1st, with more gradual anterior descension; 3rd palatal slightly reduced in height with even more gradual anterior descension; 4th palatal greatly reduced in height; an elevated lamellar ridge, weakly expanded and serrated above, situated slightly above level of upper parietal, more deeply recessed within aperture.

The subglobose form, umbilicus that narrows during the last two whorls of growth, and very crowded radial ribbing at once separate *Opanara caliculata* from the other Rapan species. The very similar *Opanara altiapica* differs in its much higher spire, less crowded ribbing, and smaller size. All other *Opanara* have at most slightly elevated spires and lack the umbilical margining.

Description. — Shell of average size, subglobose, with 5¼ rather tightly coiled whorls. Apex and spire moderately and almost evenly elevated, slightly rounded above, last whorl descending more rapidly, H/D ratio 0.660. Embryonic whorls 1½, sculpture of fine radial riblets, with finer microriblets in between and rather widely spaced spiral riblets. Postnuclear whorls with narrow, lamellate, crowded, slightly protractively sinuated radial ribs, 125 on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded on outer margin, baso-columellar margin angulated, columellar wall flattened and slightly sinuated. Ground color light yellow-white, lower portion of spire with vague alternating reddish and yellow-white flammulations, body whorl a light yellow-brown with only vague remnants of flammulations. Umbilicus narrow, U-shaped, wider near apex than at last whorl, contained 4.91 times in the diameter. Slight constriction accomplished by narrowing of coiling pattern in last two whorls. Aperture ovate, with flattened and sinuated columellar margin, inclined about 15° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl: upper parietal high and bladelike, expanded and serrated above on posterior half, with very gradual anterior descension; 2nd parietal with elevated posterior portion almost crescentic, more strongly expanded above and shorter than in 1st parietal, with rather gradual descension to threadlike anterior half that extends beyond end of upper parietal; 3rd parietal slightly shorter and lower in elevated portion than 2nd, anterior threadlike portion equal in length. Columellar barrier a raised lamellar ridge, expanded and serrated above posteriorly, twisting slightly downwards during its anterior descension and almost reaching edge of columellar lip. Palatal barriers 4, extending posteriorly about one-eighth whorl, expanded and serrated above posteriorly, with gradual anterior descension until just before anterior end when descension becomes abrupt; 2nd palatal equal in height, elevated posterior portion shorter, with more gradual anterior descension; 3rd palatal reduced in height, with very short expanded posterior portion and very gradual anterior descension; 4th palatal slightly supraperipheral in position, greatly reduced in height and length, situated slightly above level of upper parietal. Height of holotype 2.24 mm., diameter 3.39 mm.

Holotype. – Austral Islands: Rapa Island, Station 453, east ridge of Mt. Perahu at 1,800-1,900 ft. elevation. Collected by Yoshio Kondo on July 21, 1934. BPBM 142908.

Range. – West ridge of Mt. Perahu at 1,500-1,900 ft. elevation, Rapa Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Rapa Island: east ridge of Mt. Perahu (Stations 453, 512) at 1,500-1,900 ft. elevation (8 specimens, BPBM 142908, ex BPBM 135484, ex BPBM 135487-8).

Remarks. – The figured holotype is one of the more elevated specimens and approaches the shape of *Opanara altiapica*. Rather than prepare duplicate drawings, this somewhat atypical example was retained as type specimen.

The few available specimens showed no significant variation in ribbing, umbilical configuration or apertural barriers. Differences from the closely related *O. altiapica*, found on Mt. Mangaoa, are both anatomical and conchological. Comparing all adults of *O. caliculata* with adults of *O. altiapica* from Station 526, with 9 df, "*t*" = 4.3201 for diameter and 4.1297 for H/D ratio. The differences in rib count and rib frequency (tables LXXV, LXXVII) are so large that no test of significance is necessary. In *O. caliculata* the penis lacks a fleshy extension to the head and the penis is much thicker and shorter than in *O. altiapica*.

Description of soft parts. – Two partly extracted animals, one subsequently squashed flat, were available. Foot and tail typical in shape, tapering slightly posteriorly, bluntly rounded behind. Sole undivided. Pedal grooves high on foot, suprapedal much weaker than pedal, distance between equal to distance between bottom of foot and lower groove, no caudal horn or middorsal groove present. Slime network weak except on sides of foot, typical. Head projecting well in front of bluntly truncated foot. Ommatophores long, eyespot small and black, with a brownish suffusion in surrounding muscle. Gonopore located slightly above and a little behind right rhinophore, well behind and below right ommatophore.

Body color light yellow-white, no darker markings.

Mantle collar with thickened edges, no glandular extension onto pallial roof.

Pallial region absent except for anterior quarter of lung roof in available specimens. Kidney, ureter, heart, and principal pulmonary vein not seen.

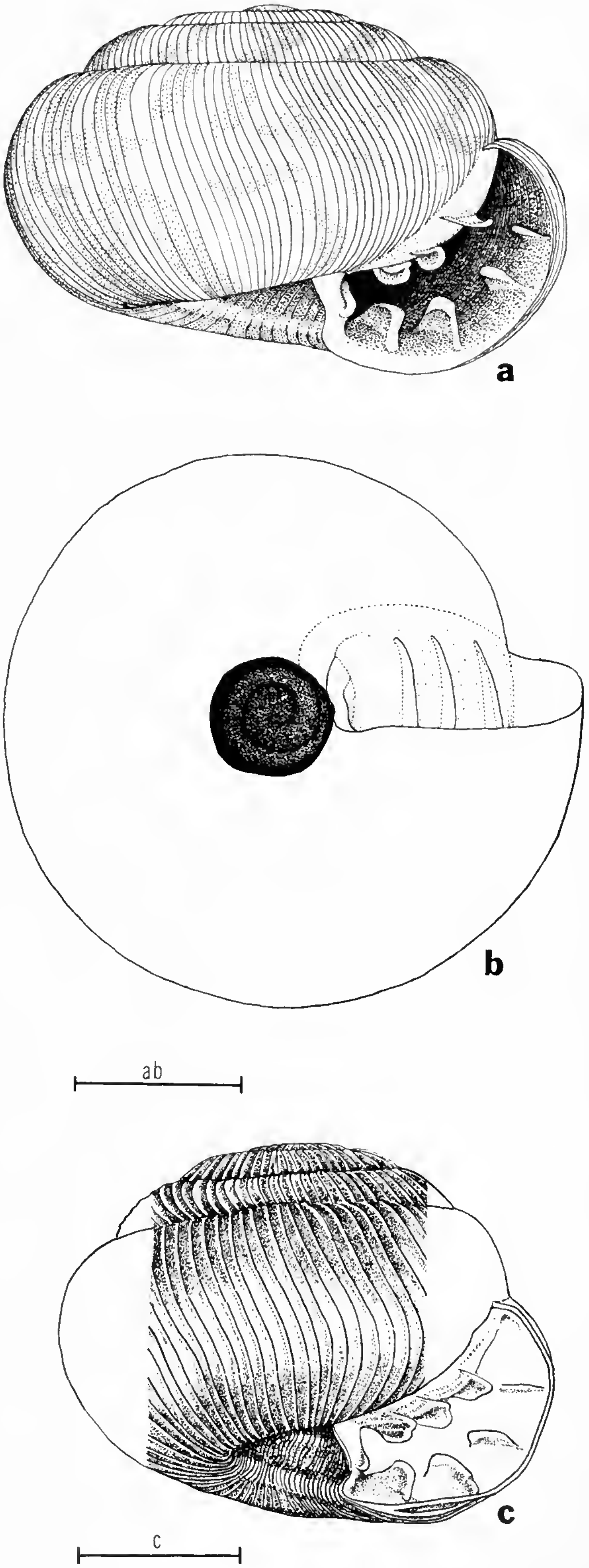

FIG. 105. **a-b,** *Opanara caliculata,* new species. Station 453, Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 142908; **c,** *O. altiapica,* Station 526, Mt. Mangaoa, Rapa Island, Austral Islands. Holotype. BPBM 143741. Scale lines equal 1 mm. Figures *a-b,* by YK reproduced through the courtesy of Bernice P. Bishop Museum; *c* (PR).

Only terminal genitalia studied. End of prostate and uterus typical. Vas deferens inserting subapically on penis, opening between two pilasters. Penial retractor apparently inserting directly on apex of penis, no sign of a fleshy penis extension. Penis about 2.0-2.7 mm. long, much fatter than in *Opanara altiapica*, sharply tapering apically, internally with same two pilasters, larger grossly expanded, very high medially, gradually descending and narrowing apically, basally broadening and slightly lowering, with apical fusion just below insertion of penial retractor.

Free oviduct tapering, internally glandularized near union with spermatheca, whose shaft widens just before union. Free muscle system with right ommatophoral retractor passing through peni-oviducal angle.

Jaw not successfully mounted.

Radula with 5 laterals, marginals broken off, centrals about 11 μ square.

(Based on BPBM 142908, two examples previously extracted from shell.)

Opanara altiapica, new species. Figures 97a-b; 105c.

Diagnosis. — Shell very small, diameter 2.63-3.03 mm. (mean 2.82 mm.), with 4⅞ - 5⅝ tightly coiled whorls. Shell globose, apex and spire moderately and evenly elevated, last whorl descending only slightly more rapidly, H/D ratio 0.664-0.761 (mean 0.719). Umbilicus narrow, U-shaped, slightly wider at apex than at last whorl, contained 3.91-5.53 times (mean 4.69) in the diameter. Postnuclear sculpture of narrow, lamellate, rather crowded, protractively sinuated radial ribs, 64-91 (mean 80.0) on the body whorl, whose interstices are 3 - 4 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures impressed, whorls strongly and evenly rounded on outer margins, baso-columellar margin sharply angulated, with a distinct columellar sulcus, inner wall of columella flattened. Aperture ovate, baso-columellar margin sharply angulated, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl: upper parietal high and bladelike, expanded and serrated above on posterior half, with gradual anterior descension; 2nd parietal almost crescentic on elevated posterior portion, equally high as 1st, with gradual anterior descension to a threadlike anterior half that extends beyond end of upper parietal; 3rd parietal equal in height and shape to 2nd, extending slightly further anteriorly. Columellar barrier a high bladelike ridge posteriorly, expanded and serrated above, twisting diagonally downward across columellar wall and almost reaching lip margin. Palatal barriers 4, extending posteriorly about one-eighth whorl: lower palatal very high, expanded, and serrated above on central portion, with very sharp anterior descension, moderately recessed within aperture; 2nd palatal slightly reduced in height, expanded portion shorter, with slightly more gradual anterior descension until just before anterior end; 3rd palatal slightly reduced in height from 2nd, expanded portion shorter, with gradual anterior descension; 4th palatal slightly supraperipheral in position, greatly reduced in height, an elevated lamellar ridge, deeply recessed within aperture.

The much smaller size, greater H/D ratio, and the more widely spaced radial ribbing immediately separate *Opanara altiapica* from the obviously related *O. caliculata*. No other Rapan species have such an elevated spire.

Description. — Shell small, with 5½ tightly coiled whorls. Apex and spire strongly elevated, rounded above, last whorl descending slightly more rapidly. H/D ratio 0.761. Apical whorls 1⅜, sculpture eroded. Postnuclear whorls with narrow, lamellate, rather crowded, protractively sinuated radial ribs, 82 on the body whorl, whose interstices are 3-4 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures impressed, whorls strongly and evenly rounded on outer margin, columellar wall flattened with a distinct columellar sulcus. Color mainly leached from shell, light yellow-brown epidermis remaining, with vague traces of irregular reddish flammulations visible above periphery on antipenultimate whorl. Umbilicus narrow, U-shaped, wider apex than on last whorl, contained 5.12 times in the diameter. Aperture ovate, with evenly rounded outer margins, baso-columellar margin angulated, inclined about 5° from shell axis. Apertural barriers as outlined above under diagnosis. Height of holotype 2.30 mm., diameter 3.02 mm.

Holotype. — Austral Islands: Rapa Island, Station 526, northeast ridge of Mt. Mangaoa at 1,000-1,100 ft. elevation. Collected by Elwood Zimmerman and Donald Anderson on July 19, 1934. BPBM 143741.

Range. — Mt. Mangaoa at 1,000-1,200 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: northeast peak and ridge of Mt. Mangaoa (Stations 481, 526) at 1,000-1,200 ft. elevation (24 specimens, BPBM 143335, BPBM 143741-6).

Remarks. — No significant variation was observed in the apertural barriers or ribbing. Anatomically, *O. altiapica* is quite generalized, the great size reduction of one pilaster being the only specialization over the typical *Opanara* pattern.

Relationship between *O. altiapica* and *O. caliculata* is of the same kind as between *O. m. megomphala* and *O. m. tepiahuensis*. Subspecific recognition in the second case was decided on in the absence of any anatomical distinctions between the morphs and distinctly smaller conchological differences than in the first pair. The conchological differences between *O. caliculata* and *O. altiapica* are caused by the tighter coiling and greater spire elevation of the latter. Shell height and D/U ratio are essentially identical.

Description of soft parts. — Foot and most of tail pulled off previous to study, presumably in routine processing.

Body color light yellow-white, no darker markings.

Mantle collar typical, no glandular extension onto pallial roof.

Pallial region extending three-quarters of a whorl apically. Lung roof clear except for clusters of white granules along pulmonary vein and kidney. Kidney about 1.45 mm. long, rectal arm about one-third length of pericardial. Ureter typical. Heart about one-third length of kidney, not lying parallel to hindgut. Principal pulmonary vein slender, bordered by white granules, stopping short of mantle collar. Hindgut slender, following parietal-palatal margin to union of esophagus and stomach.

Ovotestis (fig. 97a, G) imbedded in digestive gland above stomach reflexion, composed of many palmately clavate alveoli that are slightly iridescent with indications of developing ova (?) in some. Hermaphroditic duct (GD) relatively narrow to moderately expanded, narrowing and sharply reflexing before entering talon. Albumen gland (GG) typical, much larger than talon, rather poorly preserved in available material. Talon (GT) typical in form, buried in albumen gland. Prostate (DG) of two rows of large acini opening into a narrow duct, slightly shorter than uterus and not as long as free oviduct. Uterus (UT) typically divided into two sections.

Vas deferens (VD) inserting subapically in penis, opening (DP) between penial pilasters. Penial retractor (PR) originating on diaphragm, inserting on fleshy head of penis. Penis (P) about 1.8-2.1

mm. long, tapering apically, internally with two pilasters (PP) of highly unequal size (fig. 97b), one reduced to a low trace and terminating medially, the other very large and high, slowly descending both apically and basally from point slightly above middle. Atrium (Y) rather wide and short.

Free oviduct (UV) tapering sharply at first, widening again at basal portion just before spermathecal junction. Spermatheca (S) with typical head and early shaft, expanding basally before joining free oviduct. Vagina (V) not differentiated structurally.

Free muscle system typical, right ommatophoral retractor passing through penioviducal angle. Buccal mass, esophagus, stomach and intestinal coiling typical. Buccal retractors not split, uniting with tail fan just before end of columellar muscle.

Jaw not successfully mounted.

Radula with about 6 laterals, central about 10μ wide and 11μ long.

(Based on BPBM 143742, several fragmentary and squashed examples.)

Opanara megomphala, new species.

Populations referred to this species were seen from Mt. Tepiahu and Mt. Tautautu at 500-800 ft. elevation. They are separable into two morphs that do not overlap in respect to H/D or D/U ratios. Specimens from Mt. Tautautu (*O. megomphala megomphala*) are higher, with a greater H/D ratio, a narrower umbilicus, and a more strongly angulated umbilical margin than examples from Mt. Tepiahu (*O. megomphala tepiahuensis*). Although there are average differences in rib count (table LXXV) and rib frequency (table LXXVII), the overlap is so large that these characters cannot be utilized to separate individuals of the two forms.

The difference in mean diameter (4.7 per cent) is small, but the changes in H/D ratio (17.8 per cent) and D/U ratio (13.8 per cent) are dramatic. Both are linked to the change in shell height, a difference of 12.3 per cent. The greater shell height at a given diameter is reflected in an increase in the H/D ratio and a narrowing of the umbilicus caused by the tighter coiling. The differences are statistically significant when comparing populations (for Station 477 *megomphala megomphala* and Station 459 *m. tepiahuensis,* with 27 df: "*t*" = 2.4804 for height; "*t*" = 2.3989 for diameter; "*t*" = 5.5600 for H/D ratio; and "*t*" = 6.8650 for D/U ratio). While the changes height and diameter are below the conventional level of subspecific difference (C.D. equals 0.5347 and 0.5526, respectively), there is no question but that the H/D and D/U ratios indicate subspecific separation (C.D. equals 1.367 and 1.687, respectively).

No differences in apertural barriers were detected.

The very widely open umbilicus, and reduction of all apertural barriers to threadlike traces immediately separate *O. megomphala* from all Rapan species. Similar reduction of the parietal barriers is seen in *Australdonta radiella* and the Hawaiian *Nesophila,* but both of the latter lack all palatal and columellar barriers. The Marquesan species, *Taipidon centadentata* and *Planudonta intermedia* have partial splitting of the apertural barriers, but not nearly as much as in *Opanara megomphala.*

Opanara megomphala megomphala, new species and subspecies. Figures 97c-d; 106a-b.

Diagnosis. — Shell of slightly less than average size, diameter 2.83-3.52 mm. (mean 3.21 mm.), with 5¼-6⅛ relatively tightly coiled whorls. Apex and early spire flat or slightly depressed, last two whorls descending distinctly more rapidly, H/D ratio 0.486-0.564 (mean 0.511). Umbilicus very widely open, cup-shaped, last whorls not decoiling more rapidly, contained 2.15-2.35 times (mean 2.22) in the diameter. Postnuclear sculpture of high, prominent, rather crowded, vertically sinuated radial ribs, 71-76 (mean 73.7) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of extremely fine radial riblets, seven to twelve between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, outer margin evenly rounded and slightly compressed, umbilical margin strongly rounded, columellar margin flattened. Aperture ovate, outer margin slightly compressed, evenly rounded, inclined less than 5° from shell axis. Parietal wall with four to six threadlike traces, two or three of which may be weakly elevated, all extending posteriorly beyond line of vision, often with up to three short, lower, recessed accessory traces. Columellar and palatal wall with many fine and crowded threadlike traces that extend almost one-quarter whorl posteriorly.

The reduction of all apertural barriers to elongated, threadlike-traces at once distinguishes *Opanara megomphala* from all other Endodontidae. The Austral Islands *Australdonta radiella* (Pfeiffer) and the Hawaiian *Nesophila* differ in total lack of palatal or columellar barriers, although sharing similar parietal barriers. The extremely wide umbilicus of *Opanara megomphala* at once separates it from all other Rapan species. The nominate subspecies differs from *O. megomphala tepiahuensis* by its narrower umbilicus and much higher spire.

Description. — Shell of average size, with 6 rather tightly coiled whorls. Apex and early spire sunken beneath top of antipenultimate whorl, last two whorls descending much more rapidly, H/D ratio 0.525. Embryonic whorls 1½, sculpture of fine radial ribs interspersed with finer radial riblets, crossed by finer and slightly more crowded spiral riblets. Postnuclear whorls with prominent, rather crowded, almost vertically sinuated radial ribs, 76 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of extremely fine radial riblets, seven to twelve between each pair of major ribs, crossed by finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, compressed laterally, outer margin evenly rounded, baso-columellar margin sharply angulated, columellar wall distinctly flattened. Color light yellow-white, with irregularly zigzagged, reddish flammulations that tend to coalesce near shell periphery. Umbilicus broadly open, cup-shaped, last whorls not decoiling more rapidly, contained 2.19 times in the diameter, umbilical margin strongly angulated, inner whorls flattened. Aperture ovate, compressed laterally, inclined less than 5° from shell axis. Parietal wall with six threadlike traces that extend posteriorly beyond line of vision, one trace deeply recessed within aperture, two traces slightly more elevated than the others. Columellar and palatal walls with numerous fine, crowded, deeply recessed, threadlike traces that extend posteriorly for one-quarter whorl. Height of holotype 1.74 mm., diameter 3.33 mm.

Holotype. — Austral Islands: Rapa Island, Station 477, hillside northwest of Mt. Tautautu (above Station

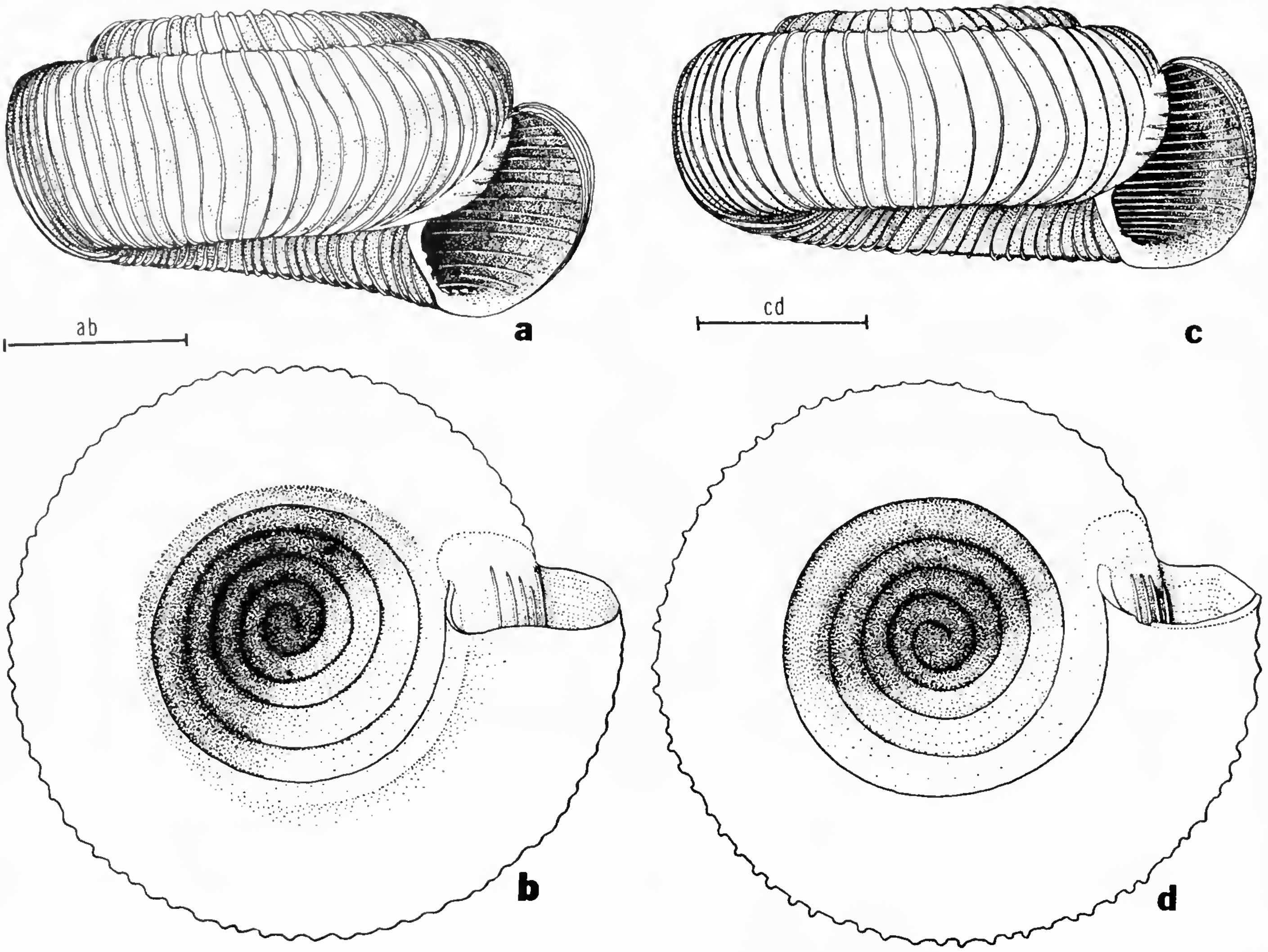

FIG. 106. **a-b**, *Opanara megomphala megomphala,* new species and subspecies. Station 477, Mt. Tautautu, Rapa Island, Austral Islands. Holotype. BPBM 144717; **c-d**, *Opanara megomphala tepiahuensis,* new subspecies. Station 459, Mt. Tepiahu, Rapa Island, Austral Islands. Holotype. BPBM 143003. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

340) at 800 ft. elevation, under stones and logs. Collected by S. Wight, Yoshio Kondo, and C. M. Cooke, Jr. on July 25, 1934. BPBM 144717.

Range. – Northwest of Tautautu at 800 ft. elevation and above Maitua at 500 ft. elevation, Rapa Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Rapa Island: northwest of Tautautu (Station 477) at 800 ft. elevation (5 specimens, BPBM 144717-8); coffee plantation above Maitua (Station 427) at 500 ft. elevation (9 specimens, BPBM 135529-31).

Remarks. – The palatal and columellar traces are too fine and crowded for accurate counts to be made. No significant variation in apertural barriers or sculpture was noted. Unfortunately, only fragmentary soft parts of paraneanic individuals were available.

Description of soft parts. – The terminal male genitalia (fig. 97c-d) shows the same pilaster and vas deferens entrance pattern observed in *O. m. tepiahuensis.* The relatively small size of the penis, length about 1.75 mm., probably is only a function of age.

(Based on BPBM 144718.)

Opanara megomphala tepiahuensis, new subspecies. Figures 97e-f; 106c-d.

Diagnosis. – Shell of average size, diameter 2.98-3.77 mm. (mean 3.36 mm.), with 5½ - 6⅛ tightly coiled whorls. Apex and early spire slightly depressed below level of antipenultimate whorl, last two whorls descending slightly, H/D ratio 0.353-0.481 (mean 0.434). Umbilicus extremely widely open, cup-shaped, regularly decoiling, contained 1.72-2.08 times (mean 1.95) in the diameter. Postnuclear sculpture of prominent, almost vertically sinuated, rather widely spaced ribs, 54-81 (mean 64.6) on the body whorl, whose interstices are 4-6 times their width. Microsculpture of extremely fine radial riblets, eight to twelve between each pair of major ribs, crossed by very much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, slightly compressed laterally, with strongly rounded to angulated baso-columellar margin, columellar wall somewhat flattened. Aperture ovate, slightly compressed laterally, with sharply rounded and angulated baso-columellar margin, inclined less than 5° from shell axis. Parietal wall with four to six threadlike traces, extending posteriorly beyond line of vision, sometimes with up to three short, deeply recessed accessory threads. Columellar and palatal walls with fine, very crowded, deeply recessed, threadlike traces, that extend posteriorly almost one-quarter whorl.

The lower spire, more widely open umbilicus with regular decoiling of the last whorl, less strongly angulated baso-columellar margin, and fewer, more widely spaced radial ribs, combine to separate *Opanara megomphala tepiahuensis* from the nominate subspecies. No other Rapan shell can be confused with it.

Description. — Shell slightly larger than average, with 6 rather tightly coiled whorls. Apex and early spire depressed below level of antipenultimate whorl, last two whorls descending slightly, H/D ratio 0.441. Apical whorls 1½, sculpture typical. Postnuclear whorls with narrow, prominent, rather widely spaced, vertically sinuated radial ribs, 71 on the body whorl, whose interstices are 4-6 times their width. Microsculpture of extremely fine radial riblets, eight to twelve between each pair of major ribs, crossed by finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, compressed laterally, basal margin strongly angulated, columellar wall somewhat flattened. Aperture ovate, slightly compressed laterally, inclined less than 5° from shell axis. Parietal wall with six low, threadlike traces that extend posteriorly beyond line of vision. Columellar and palatal walls with many crowded, deeply recessed, threadlike traces that extend posteriorly for about one-quarter whorl. Height of holotype 1.58 mm., diameter 3.59 mm.

Holotype. — Austral Islands: Rapa Island, Station 459, south side of Mt. Tepiahu at 550 ft. elevation on a hillside under stones and dead leaves. Collected by C. M. Cooke, Jr. on July 23, 1934. BPBM 143003.

Range. — South side of Mt. Tepiahu, 500-550 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: hillside on south side of Mt. Tepiahu (Stations 458, 459) at 500-550 ft. elevation (121 specimens, BPBM 142962-6, BPBM 143003-7).

Remarks. — The differences between shells of *O. m. megomphala* and *O. m. tepiahuensis* are the same order of magnitude as those between *O. altiapica* and *O. caliculata*. The latter have been given specific recognition because there are anatomical differences between the conchologically similar forms. Only subadult specimens of *O. m. megomphala* were available, so that the smaller penis size reported above has no significance.

Dissected individuals of *O. m. tepiahuensis* show rather simple pilaster patterns and almost apical insertion of the vas deferens. Otherwise the anatomy is typical of *Opanara*.

Description of soft parts. — Foot and tail partly retracted in all available material, end of tail rounded behind, not tapering. Sole undivided. Pedal grooves typical, rather high on foot, no caudal horn or middorsal groove. Slime network very faint.

Body color light yellow-white, without darker markings.

Mantle collar narrow and elongated, only slightly thickened, no glandular extension onto mantle roof. Pneumostome and anal opening typical.

Pallial region extending more than three-quarters whorl apically. Lung roof clear, without granulations. Kidney a little less than 1.50 mm. long, rectal arm half length of kidney. Heart half length of kidney, lying parallel to hindgut. Principal pulmonary vein very slender, fading out before reaching mantle collar. Hindgut typical.

Ovotestis (fig. 97e, G) with five to six clumps of very elongated, palmately clavate alveoli, upper clumps longer and more nearly parallel to plane of coiling than anterior clumps. Hermaphroditic duct (GD) greatly enlarged and nodose medially, very slender and tapering at each end, reflexing sharply before joining talon. Albumen gland (GG) small, without marked structural difference. Talon (GT) with small globular head and long tapering shaft before entering carrefour. Prostate (DG) with one to three rows of acini opening into a narrow tube buried in folds of uterus, length of prostate less than half the distance from carrefour to atrium. Uterus (UT) bipartite, rather indistinctly separated, the lower portion passing without external differentiation into free oviduct.

Vas deferens (VD) typical, not varying in diameter, moderately coiled (because of contraction) near atrium, entering penis laterally, about 0.25 mm. below apex of penis. Penial pore opening to outer side, near attached edge, on one pilaster. Penial retractor (PR) arising from diaphragm right at apex of pallial cavity, inserting directly onto fleshy extension of penis head. Penis (P) about 2.0 - 2.70 mm. long, with a long, fleshy extension to the head, somewhat swollen in upper third, tapering gradually until shortly before atrium, when it becomes a very slender tube. Internally (fig. 97f), penis with two pilasters, united above and below, very high and thin, with variously folded surface. A long, fleshy head occupies up to two-thirds of distance from penis head to end of penial retractor. Atrium (Y) short and narrow.

Free oviduct (UV) not clearly differentiated from uterus, very long and slender. Spermatheca (S) with slightly expanded, ovoid head lying at base of albumen gland, slender shaft joining free oviduct just at penioviducal angle. Vagina not a differentiated region.

Free muscle system typical. Muscle strand from edge of mantle collar to apex of columellar retractor particularly well defined. Digestive system somewhat more elongated than usual, stomach extending one full whorl apically, digestive glands extending two and one half whorls above apex of ovotestis.

Jaw of 17 large, rectangular, overlapping plates, individual plates one-quarter to one-third as wide as long.

Radula with about 6 laterals, outer marginals broken off, central about 10μ long, 8μ wide.

(Based on BPBM 143003-4, four examples, only one complete.)

Opanara fosbergi, new species. Figures 97g; 107 c-d.

Diagnosis. — Shell relatively large, diameter 3.61-4.01 mm. (mean 3.77 mm.), extremely compressed apically and basally, with 5⅜-5⅝ normally coiled whorls. Apex and spire flat, last whorl and one-half descending slightly, H/D ratio 0.330-0.375 (mean 0.344). Umbilicus narrow, U-shaped, last whorls barely decoiling, with very strongly rounded margins, contained 5.74-8.07 times (mean 7.10) in the diameter. Postnuclear whorls with narrow, prominent, lamellar, protractively sinuated, rather crowded radial ribs, 93-108 (mean 100.5) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by extremely fine and crowded spiral riblets that are barely visible under 96× magnification, with a secondary sculpture of low, crowded, spiral cords that are most clearly visible above periphery and only occasionally detectable on shell base. Sutures deep, whorls strongly rounded above, flattened laterally above evenly rounded periphery, lower palatal margin gently rounded, basal margin flattened, columellar margin evenly rounded then strongly inside umbilicus. Aperture compressedly ovate, strongly rounded above on periphery and umbilical margin, flattened laterally above periphery and strongly flattened basally, inclined about 10° from shell axis. Parietal barriers 3, somewhat irregularly placed within aperture, extending about three-sixteenths of a whorl: upper parietal high and bladelike, expanded and serrated above on posterior half, with very gradual anterior descension until last eighth of length; 2nd parietal slightly recessed, posterior half only slightly less elevated, equally expanded and serrated above posteriorly, with rather sharp descension to low threadlike trace that occupies

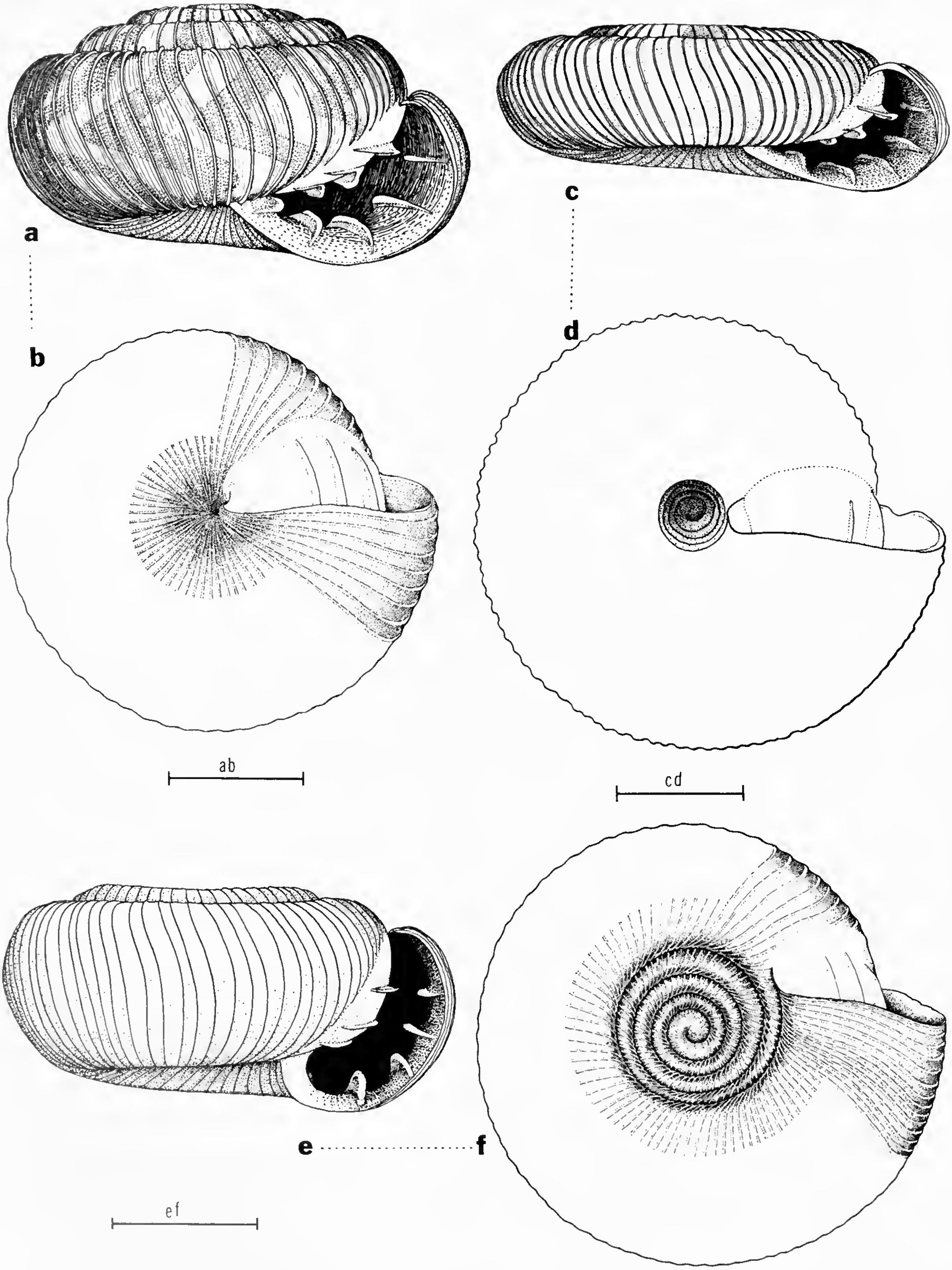

FIG. 107. **a-b**, *Opanara perahuensis*, new species. *a*, Station 453 Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 142909; *b*, Station 509, Mt. Perahu, Rapa Island, Austral Islands. Paratype. BPBM 135438; **c-d**, *O. fosbergi*, new species. Station 450, Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 142808; **e-f**, *Opanara depasoapicata*, new species. *e*, Station 451, Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 142820; *f*, paratype. BPBM 142820. Scale lines equal 1 mm. Figures *a*, *c-e* by YK reproduced through the courtesy of Bernice P. Bishop Museum; *b*, *f* (MM).

anterior third of length and terminates well behind anterior end of upper parietal; 3rd parietal deeply recessed within aperture, reduced in height, equally expanded and serrated above, with gradual anterior descension, without anterior threadlike trace, terminating anteriorly opposite mid-point of upper parietal. One (of five) specimens had a 4th parietal located between 2nd and 3rd. Columellar wall reduced to a sharply curved narrow section by basal compression of shell. Palatal wall with 5 prominent barriers, extending posteriorly more than one-eighth whorl, lower probably displaced columellar of related species: 1st palatal a broadly rounded, low, deeply recessed ridge; 2nd palatal a high lamellar blade, flattened, expanded and serrated above, moderately recessed, with gradual descension over anterior third; 3rd and 4th palatals distinctly higher than 2nd, more expanded and serrated above on posterior half, with progressively more gradual anterior descension, but only slightly deeper recession within aperture; 5th palatal supraperipheral in position, reduced in height, an elevated bladelike ridge, expanded and serrated above, with very gradual anterior descension, lying above plane of upper parietal, not more deeply recessed within aperture than 4th palatal. The 2nd through 5th palatals occupy the same positions within the aperture as normally occupied by four palatals in other species of *Opanara*.

The great two way compression of this shell has resulted in extreme narrowing of the aperture, then displacement and size change of the lower parietal and columellar barriers. The narrow umbilicus, large barriers, and very depressed spire immediately separate *Opanara fosbergi* from all other Rapan species. Only *Opanara megomphala tepiahuensis* could be confused on the basis of shape, but that species has a very widely open umbilicus and the apertural barriers reduced to fine threadlike traces.

Description. — Shell rather large, extremely compressed basally, with 5⅝ normally coiled whorls. Apex and early spire flat, last two whorls descending slightly, H/D ratio 0.375. Apical whorls 1½, sculpture eroded above, with characteristic combination of radial and microspiral sculpture showing on first whorls inside umbilicus. Postnuclear whorls with narrow, lamellar, rather crowded, protractively sinuated radial ribs, 93 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are visible only under 96× magnification, with a secondary sculpture of low, rounded, quite crowded spiral cords that are most clearly visible just above and below body whorl periphery. Sutures deep, whorls strongly rounded above, flattened laterally above evenly rounded periphery, lower palatal margin evenly rounded, basal margin flattened, with columellar wall strongly rounded into umbilicus. Color light yellow-horn, with broad, irregular reddish flammulations that tend to disappear on shell base. Umbilicus narrow, U-shaped, whorls barely decoiling from apex, contained 7.00 times in the diameter. Aperture compressedly ovate, strongly rounded above and on periphery, flattened laterally above periphery and strongly flattened on inwardly extended basal margin, inclined about 10° from shell axis. Parietal barriers 3, situated as described above under "Diagnosis." Columellar wall compressed to a narrow arc by basal shell compression, columellar barrier deflected onto basal lip. Palatal wall with five barriers, as described above under "Diagnosis." Height of holotype 1.38 mm., diameter 3.68 mm.

Holotype. — Austral Islands: Rapa Island, Station 450, upper part of east ridge, Mt. Perahu, at 1,500-1,900 ft. elevation. Collected at base of bird's nest fern by Raymond Fosberg on July 21, 1934. BPBM 142808.

Range. — East ridge of Mt. Perahu at 1,300 - 1,900 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa: east ridge of Mt. Perahu (Stations 450, 509) at 1,300 - 1,900 ft. elevation (5 specimens, BPBM 142808, BPBM 135444).

Remarks. — Although presenting a quite different appearance from the other *Opanara, O. fosbergi* is the result of one basic alteration. Extreme top and bottom compression of the whorls significantly affected the H/D ratio, height and D/U ratio, displaced the columellar barrier onto the basal lip, and probably increased the diameter significantly. If the effects of this single alteration are discounted, then *O. fosbergi* is a rather unspecialized species.

Four specimens were taken by Raymond Fosberg (Station 450), after whom this species was named, and a single example by Yoshio Kondo (Station 509). Only fragmentary anatomical material was available, with the partly crushed terminal genitalia and an isolated hermaphroditic duct confirming its classification in *Opanara*.

Description of soft parts. — In addition to the figured terminal genitalia (fig. 97g), a single hermaphroditic duct typical of *Opanara* was present.

Penis (P) about 2.83 mm. long, tapering apically, with fleshy head extension, internally with two typical pilasters. Penial retractor (PR) very long and slender. Vas deferens (VD) entering subapically on penis, well below and between union of pilasters. Spermatheca (S) joining free oviduct almost at atrial junction. Remnant of free oviduct (UV) and atrium (Y) typical. Radula and jaw not successfully mounted. Fragmentary radula showed central to be only 5 μ wide and 8 μ long.

(Based on fragmented material from BPBM 142808.)

Opanara perahuensis, new species. Figures 97h-i; 107a-b.

Diagnosis. — Shell relatively small, diameter 2.83-3.49 mm. (mean 3.15 mm.), with 5¼ - 5⅝ normally coiled whorls. Apex and spire moderately and almost evenly elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.555-0.620 (mean 0.579). Umbilicus generally narrowly perforate, contained 15.3-47.0 times (mean 28.2) in the diameter, often (18.2 per cent) closed. Postnuclear sculpture of low, prominent, narrow, protractively sinuated radial ribs, 55-64 (mean 61.8) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of rather large radial riblets, three to six between each pair of major ribs, crossed by barely visible and extremely crowded spiral riblets. Sutures impressed, whorls strongly rounded above, with evenly rounded outer margins, strongly rounded to umbilicus. Aperture subcircular, with evenly rounded outer margins, inclined less than 10° from shell axis. Parietal barriers 3, extending posteriorly slightly more than three-sixteenths of a whorl: upper parietal high and bladelike, expanded and weakly serrated above on posterior quarter, with very gradual anterior descension; 2nd parietal high and crescentic for posterior eighth, with rather sharp descension to anterior threadlike five-eighths, that extends anteriorly beyond end of upper parietal; 3rd parietal similar in shape to 2nd, slightly shorter and less elevated posteriorly, with equal anterior termination. Columellar wall with a single raised threadlike ridge, becoming broadly lamellate posteriorly, twisting slightly downward from plane of coiling, but stopping short of lip edge. Palatal barriers 4, extending posteriorly slightly more than one-eighth whorl, relatively low; 1st palatal basal in position, an elevated bladelike lamella, weakly expanded and serrated above, flattened on top, with gradual anterior descension until just before reaching lip margin; 2nd palatal slightly higher, more broadly expanded, serrated and flattened above, with gradual anterior descension, slightly more deeply recessed; 3rd palatal reduced in height, expanded and serrated above only on posterior portion with gradual and even anterior descension, moderately deeply recessed; 4th palatal peripheral in position, shortened, reduced in height, deeply recessed, a raised threadlike ridge situated almost opposite upper parietal.

Opanara perahuensis differs from *O. bitridentata* in having fewer and less crowded radial ribs, a much narrower umbilicus, higher spire, and always 3 parietals. Only the very depressed (H/D ratio 0.330-0.375) *O. fosbergi* has an umbilicus even approaching that of *O. perahuensis,* while all other *Opanara* have widely open umbilici. The 3 parietals effectively distinguish *O. perahuensis* from any species of *Orangia,* while the smaller size at a given whorl count and much more prominent barriers separate it from any *Ruatara.*

Description. — Shell relatively small, with 5½ normally coiled whorls. Apex and spire moderately and almost evenly elevated, slightly rounded above, last whorl descending more rapidly, H/D ratio 0.564. Apical whorls 1⅜, sculpture eroded. Postnuclear whorls with narrow, low, rather widely spaced, protractively sinuated radial ribs, 63 on the body whorl, whose interstices are 3-5 times their width, and often with periostracal extensions. Microsculpture of rather prominent radial riblets, three to six between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above, with almost evenly rounded outer margins and gently rounded baso-umbilical margin. Color light yellow-horn, with relatively narrow, somewhat indistinct, zigzagged, reddish flammulations that tend to coalesce on shell base. Umbilicus narrowly perforate, open to apex, contained 25 times in the diameter. Aperture subcircular, with evenly rounded outer margin, inclined about 10° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl: upper parietal a high bladelike lamella, weakly expanded and serrated above on posterior quarter, with very gradual anterior descension; 2nd parietal with posterior quarter a high crescentic blade, rather sharply descending to anterior five-eighths that is low and threadlike, extending anteriorly beyond end of upper parietal; 3rd parietal the same as 2nd, slightly reduced in height posteriorly. Columellar barrier a high lamellar ridge, broadly expanded above posteriorly with gradual anterior descension, twisted slightly downward from plane of coiling and stopping short of lip edge. Palatal barriers 4, extending about one-eighth whorl: lower palatal basal in position, a moderately elevated lamellar ridge with gradual anterior descension almost to lip edge, weakly expanded and serrated above; 2nd palatal distinctly higher, more strongly expanded and serrated above, flattened posteriorly, with more gradual anterior descension; 3rd palatal distinctly reduced in height, expanded and serrated above near posterior end, with gradual and even anterior descension; 4th palatal reduced in height and length, moderately deeply recessed, an elevated lamellar ridge, with very gradual anterior descension, lying almost opposite upper parietal. Height of holotype 1.87 mm., diameter 3.32 mm.

Holotype. — Austral Islands: Rapa Island, Station 453, east ridge of Mt. Perahu at 1,800-1,900 ft. elevation. Collected by Yoshio Kondo on July 21, 1934. BPBM 142909.

Range. — East ridge of Mt. Perahu at 1,200-1,900 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa: east ridge of Mt. Perahu (Stations 446, 452, 453, 509) at 1,200-1,900 ft. elevation (12 specimens, BPBM 135438, BPBM 142750, BPBM 142880, BPBM 142909).

Remarks. — Of the species found at the same localities, *Opanara perahuensis* is most apt to be confused with *O. bitridentata* and *Ruatara oparica.* The former has a much more widely open umbilicus (D/U ratio 3.58-8.45), several accessory palatal barriers, and a much less elevated spire, while the latter has much shorter palatal barriers, many more radial ribs (77-133), and is distinctly more elevated.

The total absence of accessory palatal traces, simple columellar barrier, and its small size suggest that it is a rather generalized species. The great constriction of the umbilicus and widely spaced radial ribbing of *perahuensis* are quite different from the average pattern seen in *Opanara,* but do not, in themselves, suggest affinity to another group. *Ruatara* has a similarly constricted umbilicus, but markedly different ribbing, while *Orangia* has the umbilicus closed by reflection, but similar ribbing. Dissection of the fragmentary individuals available did show a major change within the penis (fig. 97i). Although two pilasters are present, one occupies the upper half, the other occupies the lower two-thirds of the penis. Fusion of these two separate pilasters would result in the single pilaster structure found in *Ruatara* (fig. 64i), or could represent another case of character displacement. Unfortunately, the hermaphroditic duct was not present in any example of *O. perahuensis.* If it should prove to be partly coiled, as in *Ruatara,* then *O. perahuensis* would be intermediate between *Opanara* and *Ruatara* in both genital and shell structures.

Only limited material was obtained at scattered stations on Mt. Perahu, but no species was abundant at the particular stations.

Description of soft parts. — Foot and tail partly retracted, latter tapered on posterior visible part, rounded behind. Sole undivided. Pedal grooves high on foot, lower much more prominent, no caudal horn or middorsal groove, slime network of irregular rectangles, clearly defined.

Body color light yellow-white, no darker markings.

Mantle collar typical, no glandular extension onto pallial roof. Pneumostome and anus normal.

Pallial region represented only by anterior portion in available material. Lung roof with white granules bordering principal pulmonary vein, densely clustered in a narrow band. Kidney, ureter, and heart not present in available specimens. Principal pulmonary vein unbranched until 0.5 mm. before anterior end of pallial cavity, then splitting into five or six branches that fade out just short of mantle edge.

Apical genitalia not available. Prostate (fig. 97h, DG) with two rows of large acini opening into a narrow tube, only lower part seen. Uterus (UT) bipartite, only small part of narrower upper portion seen.

Vas deferens (VD) typical, lightly bound to penioviducal angle, entering penis below apex to side of upper penial pilaster (fig. 97i). Penial retractor inserts onto fleshy extension of penis head, origin unknown. Penis (P) 2.0-2.5 mm. long, almost uniform in diameter, with a prominent fleshy head, internally (fig. 97i) with two pilasters, one running from apex to slightly below midpoint, other from about one-third of way below apex to atrium. Both pilasters very slender and low at each end, moderately to strongly elevated medially. Atrium (Y) short and broad.

Free oviduct (UV) rather short, kinked and twisted in available material. Spermatheca (S) shaft inserting on free oviduct slightly above penioviducal angle. Vagina not a differentiated area.

Right ommatophoral retractor passing through penioviducal angle. Rest of free muscles not seen.

Jaw typical, of large rectangular plates, each plate about one-third as wide as long.

Radula with cusps distinctly shorter than basal plates, about 5 laterals, central 10μ long and 8μ wide, outer marginals broken off and could not be counted.

(Based on several fragmentary specimens from BPBM 142909.)

Genus **Rhysoconcha,** new genus

Quite small Endodontidae with very fine, but typical, apical sculpture and microsculpture, major sculpture of moderately to very crowded, quite narrow radial ribs. Apex and spire moderately to strongly elevated, last whorl usually descending distinctly more rapidly, periphery evenly rounded or slightly compressed. Whorls about 5, tightly coiled. Umbilicus widely open (*R. atanuiensis*) or secondarily constricted (*R. variumbilicata*). Parietal barriers 3 (*atanuiensis*) or 4 (*variumbilicata*) with 3rd, or 2nd and 4th, respectively, recessed. Columellar barrier deeply recessed (*variumbilicata*) or nearly reaching lip margin (*atanuiensis*). Palatal barriers normally 5, rarely 6. Ovotestis with proportionately large alveoli that lie parallel to sides of whorl and nearly fill whorl space; hermaphroditic duct with wide collecting tubule and anterior duct, proportionately very long. Spermatheca with narrow and elongated head, shaft entering on penial side of penioviducal angle. Vas deferens entering laterally on penis apex. Penis without fleshy extension, retractor inserting directly on head, internally with two rather closely set pilasters that are slightly higher than wide and unite apically above vas deferens entrance. Penial retractor originating from diaphragm. Stomach occupying one or more than one full whorl. Central teeth of radula less than 10μ long.

Type species. – *Rhysoconcha variumbilicata,* new species.

Identifying features in the anatomy are the position of the ovotestis, penial insertion of the spermatheca, apical penial insertion of the vas deferens, and absence of a fleshy head to the penis. Conchologically the very fine sculpture and peculiarly shaped parietal barriers (fig. 108a-b) offer a distinct contrast to the other Rapan taxa. The size and general shape of *Rhysoconcha* are quite similar to the more widely umbilicated species of *Minidonta.* Prior to dissection, I had associated the two small Rapan species with that genus.

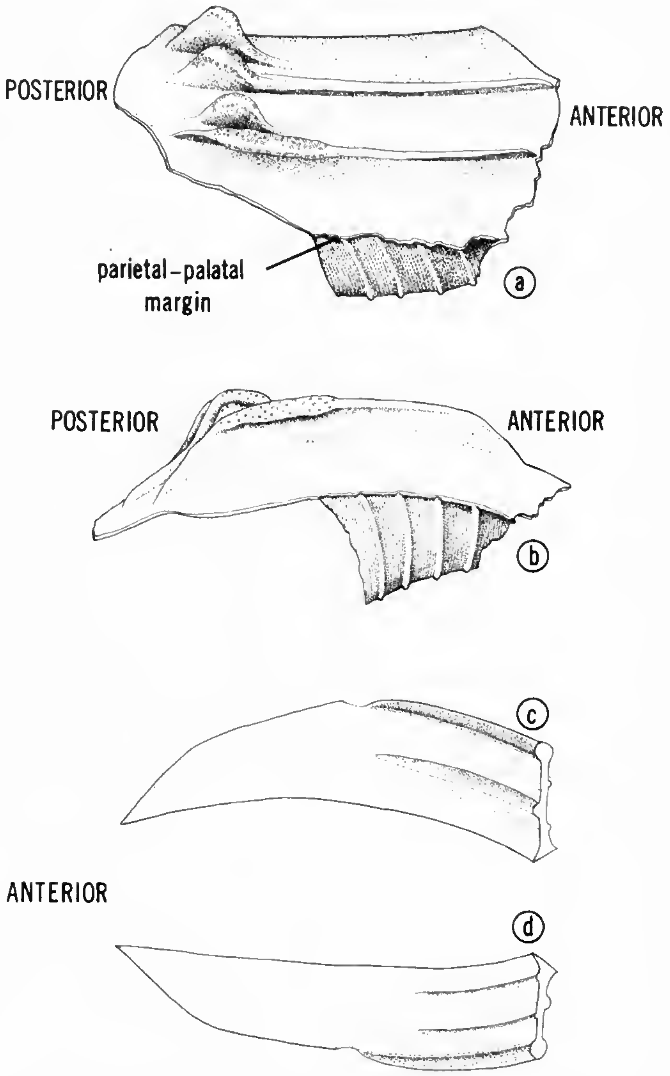

FIG. 108. Structure of parietal lamellae in *Rhysoconcha variumbilicata* (**a, b**) and *Kondoconcha othnius* (**c, d**). Greatly enlarged. (MM).

Dissection of the two *Rhysoconcha* species revealed several anatomical features that contrast quite strongly with all other dissected Endodontidae. The follicles of the ovotestis are quite large in proportion to the remaining genitalia and, after a short initial radial orientation, lie parallel to the whorl sides rather than at an angle (see *Endodonta fricki,* fig. 163c) as in all other small species dissected. The collecting tube of the hermaphroditic duct and its entrance into the talon are both proportionately wider than usual while the duct itself (fig. 64f, GD) is quite long in comparison to the ducts of *Orangia* or *Opanara.* The talon projects apicad of the albumen gland and also is quite large. The change in spermathecal insertion, from oviducal to penial side, is minor in distance, but important taxonomically, since otherwise this is seen only in the quite advanced genera *Thaumatodon, Priceconcha,* and *Aaadonta* (figs. 191, 195, 199, 200; and Solem, 1973d, figs. 20-21). Nearly all Endodontidae show clearly subapical insertion of the vas deferens into the penis. Only in the specialized *Ruatara* and *Rhysoconcha* is the insertion apical. Possibly this indicates secondary size reduction. Except for the last two genera, all Rapan endodontids show a fleshy appendage to the penis head. The pilasters in *Rhysoconcha* are higher than wide, unlike those in the generalized Endodontidae and somewhat intermediate to the very high pilasters seen in *Orangia* and *Opanara.* Both the stomach and ovotestis have proportionately narrower strips of digestive gland tissue than was seen in other Endodontidae, and apparently the stomach is longer than usual in species of the same whorl count.

Returning to a consideration of the shell, it became obvious that the size of the apical ribs (fig. 21a,b) were much smaller than in species of even less diameter, such as *Minidonta hendersoni* (figs. 25a, c-e), and that the size of both macro- and micro-radial ribs was distinctly smaller. The form of the parietal barriers (figs. 108a-b) is quite altered from the normal pattern seen in the Endodontidae (for example, fig. 37a).

In a group that was less conservative anatomically, the differences cited above would be interesting, but not especially significant. The concentration of so many alterations within one pair of species in a conservative group requires special comment. Of the Endodontidae whose anatomy is known, *Minidonta hendersoni* from Henderson Island is perhaps most similar in size and whorl count. The poor apical preservation of material in that species prevented preparation of comparative drawings and measurements. Direct visual comparisons of dissected parts were made and the following comments, although not documented by measurements, reveal significant facts. The dissected material of *Minidonta hendersoni* was subadult (diameter 1.68 mm., 4⅛ whorls) in size, although the genitalia appeared fully developed, while the specimens of *Rhysoconcha* were 2.11-2.17 mm. in diameter. Comparisons were also made with material of *Opanara areaensis*.

The ovotestis alveolar clumps in *Rhysoconcha* were the same size as those in *Opanara,* although fewer in number, but were much, much larger and less numerous than in *Minidonta*. The albumen gland acini in *Rhysoconcha* and *Opanara* are much more similar in size than are *Rhysoconcha* and *Minidonta*. Similarly, the size of the collecting tubule, narrower portion of the hermaphroditic duct and talon in *Rhysoconcha* were essentially the same as in *Opanara* and much, much wider than in *Minidonta*. Apical shell sculpture and radial microsculpture were essentially the same in *Opanara* and *Minidonta,* yet greatly reduced in *Rhysoconcha*.

Specifically, the features of *Rhysoconcha* mentioned in the preceeding paragraphs follow the pattern associated with secondary size reduction elucidated by Bernhard Rensch (1966, pp. 170-177, 209-210). The other anatomical peculiarities of *Rhysoconcha* outlined earlier can be interpreted as part of the same pattern.

If *Rhysoconcha* was evolved by size reduction from *Opanara,* without equal reduction in egg size, the actual width of the alveoli in the ovotestis, collecting tubule of the hermaphroditic duct, talon, albumen gland acini, and free oviduct could not be decreased as much as other organs. Hence the width of the tubes, proportionately, would appear much greater. Space limitations in the spire would require a reduction in the number of ovotestis alveoli and force parallel orientation with near filling of the whorl cross-section. Movement of the spermathecal insertion to the penial side would aid passage through the free oviduct. Alterations in the penis involving size reductions would first occur in the pilaster height. Loss of the fleshy extension and simplification of the vas deferens opening would save space without significant alteration in function. Looking at the shell, if *Opanara* sculpture was reduced in proportion to size change, the sculpture of *Rhysoconcha* would be the result. The cramped, crowded, peculiar parietal barriers of *Rhysoconcha* (fig. 108a-b) bear little resemblance to the typically formed barriers of *Minidonta,* but if viewed as imperfectly reduced homologues of the *Opanara* type, they make sense.

Assuming that *Rhysoconcha* is secondarily small in size and evolved from the *Opanara* complex, then all of the anatomical and sculptural peculiarities of *Rhysoconcha* could be predicted as normal consequences of size reduction. If *Rhysoconcha* is assumed to be primitively small, then numerous anatomical departures from a highly conservative pattern must be explained individually. In the many genera where size increase has been documented no similar set of changes is seen and quite different patterns of structural alteration are known.

The probability of *Rhysoconcha* representing reduced size seems quite large. Since the *Opanara* and other Rapan species are much larger than most species of *Mautodontha* or *Minidonta,* it seems likely that the ecological niche for a small endodontid on Rapa probably was vacant. The opportunity for the relatively infrequent phenomenon of evolution toward decreased size existed and *Rhysoconcha* was the result.

Collection of material suitable for sectioning and detailed histological comparisons are needed to confirm or disprove the above hypothesis. At our present level of knowledge, its acceptance raises fewer phylogenetic problems than its rejection.

The generic name is taken from the Greek *rhysos,* meaning shrunken, and refers to the hypothesized decreased size of the species.

Except for populations in the Maitua area, *Rhysoconcha variumbilicata* and *R. atanuiensis* are well-differentiated species that offer contrasting states in 10 characters of size, shape, ribbing, and apertural barriers (table LXXXII). On Mt. Mangaoa (Stations 485, 527) both species were collected at the same station (fig. 109) without evidence of any intergradation. Comparing the frequency distributions of *variumbilicata, atanuiensis,* and the Maitua area intermediate populations in respect to height, diameter, H/D ratio, D/U ratio, rib counts, and rib spacing (figs. 110, 111), the impression is given that blending occurs in the Maitua area, since these populations are essentially unimodal and almost exactly intermediate. This is an oversimplification, since individual Maitua populations show widely different degrees of similarities to one or the other species. No anatomical differences between the two species were discovered.

While breeding data obviously are lacking, the presence of extensive character mixing in the ecologically disturbed Maitua area suggested hybridization rather than a step cline between subspecies. Each

TABLE LXXXI. - RANGE OF VARIATION IN RHYSOCONCHA, RUATARA, KONDOCONCHA AND ORANGIA

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
Rhysoconcha variumbilicata	129	63.6(53-82)	1.07(0.89-1.38)	2.00(1.74-2.37)	0.535(0.474-0.587)	5-(4 1/4-5 3/8)	10.12(5.91-19.0)	4	1	5-6
atanuiensis	162	93.8(79-132)	1.04(0.82-1.22)	2.33(1.88-2.67)	0.445(0.406-0.500)	4 7/8(4 3/8-5 1/4)	2.96(2.47-3.67)	3-4	1	5-6
Ruatara koarana	4	80 (79-81)	1.66(1.55-1.81)	2.93(2.80-3.03)	0.612(0.567-0.670)	5 1/8-(4 3/4-5 1/2)	PERFORATE TO CLOSED	3	1	4
oparica oparica	42	122.9(101-154)	1.69(1.48-1.94)	2.98(2.80-3.39)	0.565(0.488-0.597)	4 3/4-(4 3/8-5 1/4)	USUALLY PERFORATE	2-3-4	1	2-3-4[3]
oparica normalis	603	98.5(77-133)	2.30(1.48-2.86)	3.81(2.70-4.87)	0.601(0.524-0.690)	5 1/2-(5-6 1/4)	PERFORATE OR CLOSED	1-2-3-4-5	1	0-3-4-5[1]
oparica reductidenta	410	78.4(66-95)	2.22(1.88-2.73)	3.74(3.29-4.34)	0.593(0.528-0.698)	5 1/2+(5-6 1/8)	CLOSED	1-2-3-4-5	1	0-1-2[2]
Kondoconcha othnius	33	REDUCED	2.30(2.09-2.55)	4.06(3.81-4.24)	0.567(0.548-0.601)	6 3/8-(6 1/8-6 3/4)	5.55(5.00-6.40)	2+3-5	1+1	5+8-10
Orangia cookei tautautuensis	9	98.3(88-114)	1.89(1.58-2.11)	3.42(3.03-3.75)	0.552(0.517-0.592)	5 5/8(5 1/8-6)	CLOSED	2	1	4-5
cookei cookei	1,285	92.6(72-135)	2.04(1.61-2.57)	4.00(3.36-4.57)	0.510(0.424-0.585)	6-(5 1/4-6 1/4)	40 - CLOSED	2	1	4-5
cookei montana	40	104.8(81-120)	2.18(1.78-2.57)	4.24(3.72-4.64)	0.513(0.474-0.564)	6-(5 1/2-6 1/4)	40 - CLOSED	2	1	4
maituatensis	22	81.1(71-89)	1.92(1.68-2.30)	4.03(3.82-4.44)	0.466(0.411-0.519)	5 3/4-(5-6 1/8)	19 - CLOSED	2	1	4
sporadica	102	50.8(38-64)	2.14(1.78-2.30)	3.99(3.65-4.28)	0.520(0.475-0.589)	6+(5 3/8-6 3/8)	30 - CLOSED	2	1	4-5-8

1. 3 P (19.2%); 4 P (73.6%); 0, 1, 2, 5 P (7.2%).
2. 0 P (84.0%); 1 P (15.5%); 2 P (0.5%).
3. 2 P (5.3%); 3 P (7.9%); 4 P (86.8%).

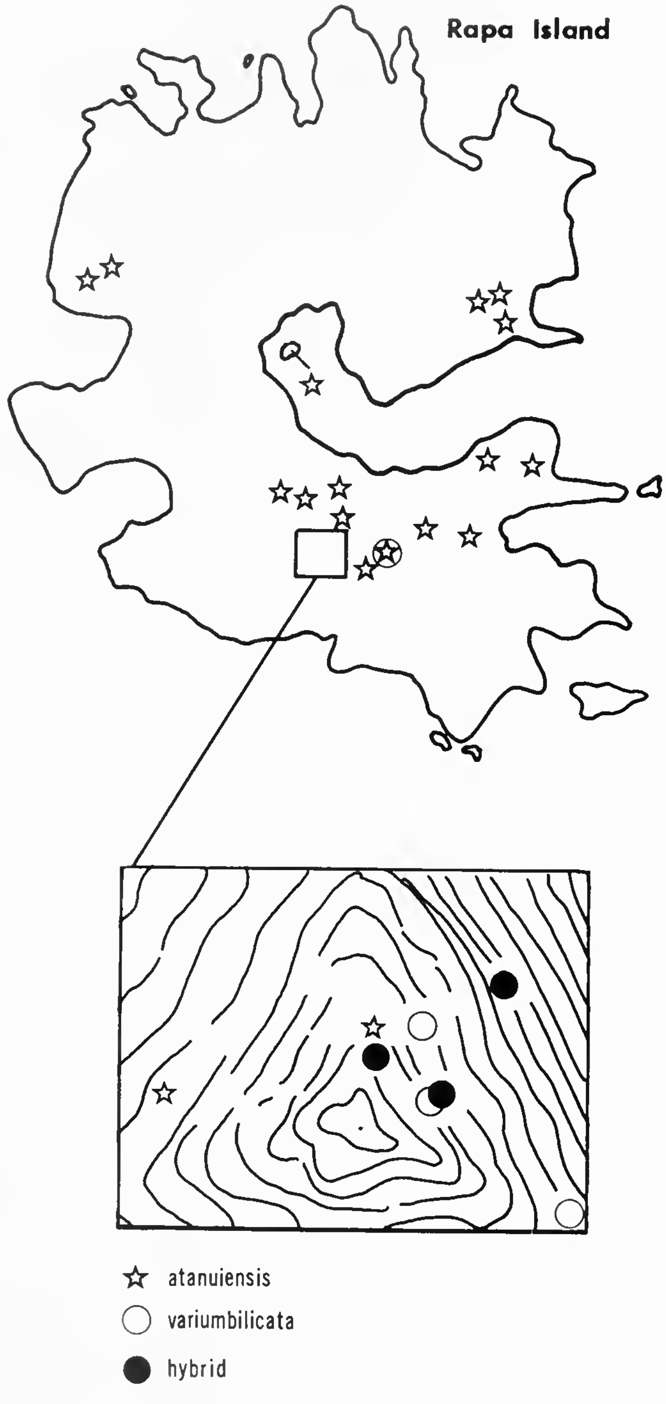

FIG. 109. Distribution of *Rhysoconcha*.

population sampled in the Maitua area has a relatively small range of variation, probably reflecting both small breeding population size and only partial genetic mixing. There is some indication of "introgressive hybridization" in a few populations of *atanuiensis* that show some *variumbilicata* characters (p. 264), but field studies are needed before any conclusions can be reached.

The two species may be characterized as follows:

Rhysoconcha variumbilicata, new species — very small (mean diameter 2.00 mm.), rather elevated (mean H/D ratio 0.535), with tiny umbilicus (mean D/U ratio 10.1), 4 parietals, a deeply recessed columellar barrier, and rather widely spaced radial ribs;

Rhysoconcha atanuiensis, new species — larger (mean diameter 2.33 mm.), lower (mean H/D ratio 0.445), with wide umbilicus (mean D/U ratio 2.96), 3 parietals, columellar barrier nearly reaching lip edge, and rather crowded radial ribs.

Variation in the two species and hybrid populations is discussed below and summarized in Tables LXXXI, LXXXII, LXXXIII, and LXXXIV. The specific differences in umbilical width, proportionate height, rib count, and rib frequency are so large that no tests of statistical significance were made. The much more closely spaced ribs of *R. atanuiensis* are clearly shown in Figure 112c. Similarly, the intermediate nature of the hybrid populations is adequately shown by the tabular data and does not require extensive discussion.

Rhysoconcha variumbilicata, new species. Figures 64f, g; 110-112.

Diagnosis. — Shell very small, diameter 1.74-2.37 mm. (mean 2.00 mm.), with 4¼ - 5⅜ tightly coiled whorls. Apex and early spire moderately to strongly elevated, usually rounded above, last whorl descending slightly more rapidly, H/D ratio 0.474-0.587 (mean 0.535). Umbilicus strongly constricted internally, last whorl decoiling slightly to moderately more rapidly, columellar wall usually concave, contained 5.91-19.0 times (mean 10.1) in the diameter. Postnuclear sculpture of prominent, lamellar, rather widely spaced, slightly protractively sinuated radial ribs, 53-82 (mean 63.6) on the body whorl, whose interstices are 4-6 times their width. Microsculpture of fine radial riblets, six to nine between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above, slightly compressed laterally on outer margin, with flattened and inward extension of baso-columellar margin, umbilical margin strongly rounded. Aperture ovate, slightly compressed laterally and on baso-columellar margin, inclined about 10° from shell axis. Parietal barriers 4, extending posteriorly almost one-quarter whorl, 2nd and 4th deeply recessed: upper parietal high and bladelike, expanded and serrated above on posterior quarter, with very gradual anterior descension until just before termination; 2nd parietal greatly reduced in height, less than one-quarter length of upper lamella, weakly expanded and serrated above, with sharp anterior descension; 3rd parietal nearly equal in height posteriorly to upper, expanded and serrated above on posterior quarter, with rather sharp descension to a raised lamellar blade, about half the height of 1st parietal, that occupies anterior half of barrier, with gradual anterior descension and termination slightly beyond end of upper parietal; 4th parietal equal in height and length to elevated portion of 3rd parietal, deeply recessed, very short, without any anterior extension. Columellar barrier deeply recessed, bladelike, expanded and serrated above posteriorly, with gradual anterior descension. Major palatal barriers 5, very rarely 6 (2 per cent), short, extending posteriorly about one-eighth whorl, upper 2 reduced to short threadlike traces: lower moderately raised, very broadly expanded above and serrated, with relatively sharp anterior descension almost to lip margin; 2nd equal or subequal in height to 1st, somewhat less broadly expanded above, with more gradual anterior descension; 3rd equal in height to 2nd, less broadly expanded above, with more gradual anterior descension; 4th reduced to a very short, deeply recessed threadlike ridge, lying below plane of upper parietal; 5th equal in height and length to 4th, deeply recessed, lying above plane of upper parietal; 6th, when present, located between 2nd and 3rd major barriers.

TABLE LXXXII. - DIFFERENCES BETWEEN RHYSOCONCHA VARIUMBILICATA AND R. ATANUIENSIS

Mean Diameter	2.00 mm.	2.33 mm.
Mean H/D Ratio	0.535	0.445
Mean D/U Ratio	10.1	2.96
Mean Rib Count	63.5	93.8
Mean Ribs/mm.	10.38	13.53
Number of Parietals	4	3
Columellar Lamella	DEEPLY RECESSED	NEAR LIP EDGE
Upper Palatals	GREATLY REDUCED	SLIGHTLY REDUCED
Lower Palatals	BROADLY EXPANDED ABOVE	NORMALLY EXPANDED
Body Whorl	LATERALLY COMPRESSED	EVENLY ROUNDED

The narrow umbilicus, widely spaced ribbing, smaller size, presence of 4 parietal barriers, and higher spire combine to separate *Rhysoconcha variumbilicata* from *R. atanuiensis*. The other Rapan species with 4 parietals, *Opanara duplicidentata*, is more than twice its size (mean diameter 4.32 mm.) and has a widely open umbilicus (mean D/U ratio 3.03). All other Rapan species normally have only 2 or 3 parietals.

Description. — Shell very small, with 5⅛ tightly coiled whorls. Apex and spire moderately elevated, rounded above, last whorl descending slightly more rapidly, H/D ratio 0.574. Apical whorls 1⅜, sculpture of fine radial riblets, interspersed by two or three microradials and crossed by extremely fine spiral riblets. Postnuclear sculpture of prominent, lamellar, widely spaced, slightly protractively sinuated radial ribs, 59 on the body whorl, whose interstices are 4-6 times their width. Microsculpture of fine radial riblets, six to nine between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures deep, whorls strongly rounded above, slightly compressed laterally, basal margin inwardly extended and slightly concave, columellar margin strongly rounded. Color light yellow-white, with broad, regularly spaced, reddish flammulations that tend to coalesce below periphery of body whorl. Umbilicus narrow, last whorl decoiling slightly more rapidly, contained 6.78 times in the diameter. Aperture ovate, compressed laterally and on baso-columellar margin, inclined about 10° from shell axis. Parietal barriers 4, extending posteriorly slightly less than one-quarter whorl, 2nd and 4th shortened and very deeply recessed, with a single accessory trace situated just below upper parietal: upper parietal high and bladelike, expanded and serrated above on posterior quarter, with very gradual anterior descension until just before termination; 2nd parietal equally high and elevated, about one-quarter length of upper parietal, without anterior extension; 3rd parietal equal in height and length to posterior elevated portion of upper parietal, sharply descending to a slender raised lamella, about half the height of upper parietal, with gradual anterior descension, terminating just beyond anterior end of upper parietal; 4th parietal equal in height and length to elevated posterior portion of 3rd parietal, without anterior extension. Columellar barrier a low lamellar blade, broadly expanded above, deeply recessed within aperture, with gradual anterior descension. Palatal barriers 5, short, extending posteriorly about one-eighth whorl, upper 2 greatly reduced in prominence: lower palatal high and bladelike, very broadly expanded and serrated above with rather sharp anterior descension; 2nd and 3rd palatals equal in height to 1st, progressively less broadly expanded above, with more gradual anterior descension; 4th and 5th palatals shortened, greatly reduced in prominence, situated respectively above and below level of upper parietal, reduced to threadlike traces. Height of holotype 1.15 mm., diameter 2.06 mm.

Holotype. — Austral Islands: Rapa Island, Station 403, west slope of the northeast ridge, Mt. Mangaoa, at 800-900 ft. elevation. Collected under stones by Donald Anderson on July 16, 1934. BPBM 144376.

Range. — Mt. Mangaoa and Maitua area at 500-900 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: west slope of northeast ridge (Stations 403, 485), Mt. Mangaoa, under stones at 800-900 ft. elevation (90 specimens, BPBM 138337-40, BPBM 138342, BPBM 138345, BPBM 144376-7, BPBM 144379, BPBM 144380); northeast ridge (Station 527) of Mt. Mangaoa under stones at 800 ft.

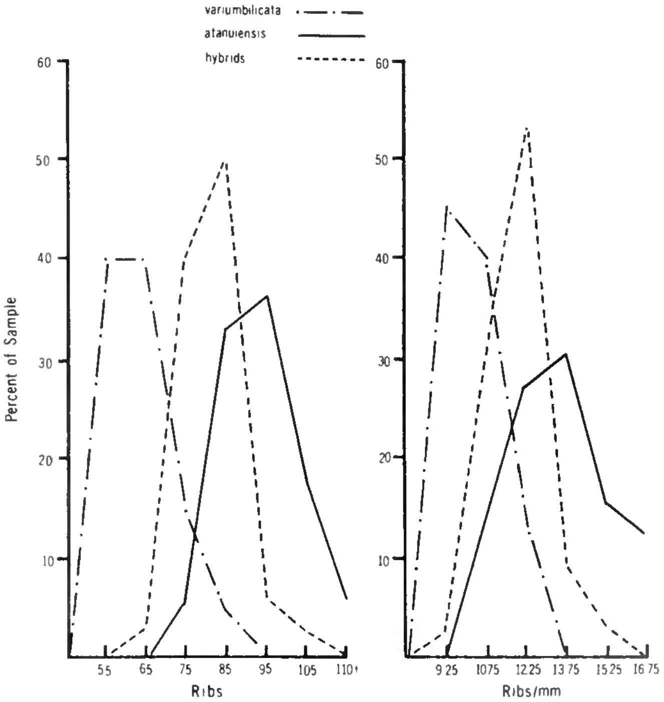

FIG. 110. Frequency distribution of ribs and rib spacing in *Rhysoconcha atanuiensis*, *R. variumbilicata*, and hybrid populations.

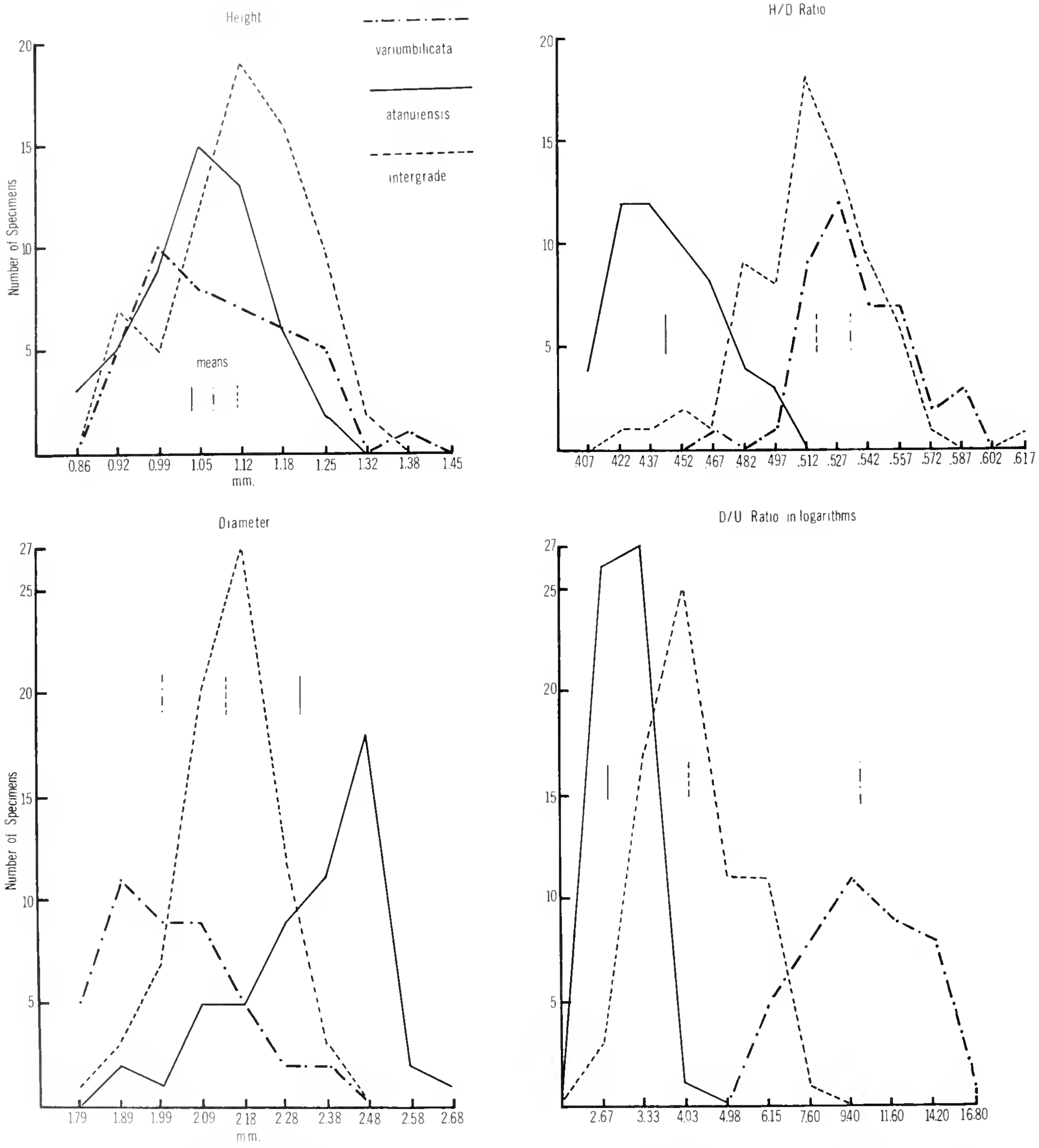

FIG. 111. Size and shape frequency distribution in *Rhysoconcha atanuiensis*, *R. variumbilicata*, and hybrid populations. Class intervals for D/U ratio determined from an equal arithmetic measurement of a logarithmic scale to avoid overemphasizing degrees of narrowing above 5.50.

elevation (9 specimens, BPBM 138405-6); Maitua in native forest with a sprinkling of coffee trees (Station 427) under stones at 575 ft. elevation (12 specimens, BPBM 135525-8); in native forest (Station 305B) under stones (= Station 293) (7 specimens, BPBM 137849); Maitua area (Station 304) under stones (11 specimens, BPBM 137818-8).

Remarks. — *Rhysoconcha variumbilicata* has a much more restricted distribution than does *R. atanuiensis*, being known only from Mt. Mangaoa at 800-900 ft. elevation and several stations in the Maitua area (fig. 109). On Mt. Mangaoa, both species were collected together without sign of intergradation — at Station 485 there were 10 *atanuiensis* and 56 *variumbilicata;* at Station 527 there were one *atanuiensis* and nine *variumbilicata*. In the Maitua area, *R. variumbilicata* was collected in an ecotonal area between the coffee plantation and native forest

TABLE LXXXIII. - LOCAL VARIATION IN RHYSOCONCHA ATANUIENSIS, R. VARIUMBILICATA AND HYBRID POPULATIONS

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
variumbilicata						
BPBM 138337, -8, -9 Sta. 485	20	0.99±0.013 (0.89-1.09)	1.88±0.020 (1.76-2.09)	0.526±0.0045 (0.474-0.571)	4 3/4+ (4 1/4-5 1/4)	10.88±0.749 (6.30-19.00)
BPBM 137849 Sta. 305B	5	1.13±0.023 (1.06-1.19)	2.07±0.031 (1.99-2.15)	0.543±0.0089 (0.508-0.557)	4 7/8+ (4 3/4-5 1/8)	10.96±0.649 (9.15-12.60)
BPBM 137817 Sta. 304	8	1.17±0.043 (0.99-1.39)	2.16±0.054 (1.89-2.38)	0.540±0.0074 (0.523-0.583)	5- (4 1/2-5 1/8)	8.29±0.916 (5.91-13.20)
BPBM 135525 Sta. 427	4	1.21±0.022 (1.16-1.26)	2.21±0.058 (2.09-2.35)	0.548±0.0155 (0.515-0.587)	5 1/4 (5 1/8-5 3/8)	9.37±0.715 (7.90-11.32)
atanuiensis-variumbilicata hybrids						
BPBM 140018 Sta. 353	11	0.94±0.015 (0.89-1.03)	1.95±0.023 (1.82-2.05)	0.482±0.0089 (0.436-0.525)	4 5/8- (4 3/8-4 3/4)	3.30±0.100 (2.95-3.93)
BPBM 137639 Sta 291A	18	1.11±0.017 (0.99-1.23)	2.20±0.020 (2.09-2.35)	0.508±0.0057 (0.476-0.570)	5- (4 1/2-5 1/4)	4.09±0.177 (3.23-6.40)
BPBM 142536 Sta. 358	4	1.12±0.016 (1.09-1.16)	2.14±0.022 (2.09-2.19)	0.523±0.0085 (0.508-0.547)	5- (4 7/8-5)	4.83±0.525 (4.20-6.40)
BPBM 144518, -19, -22, -23 Sta. 426	35	1.14±0.012 (1.03-1.29)	2.17±0.015 (2.02-2.35)	0.525±0.0036 (0.477-0.562)	5- (4 1/2-5 1/4)	4.84±0.170 (2.82-6.88)
atanuiensis						
BPBM 138431 Sta. 485	4	0.86±0.013[1] (0.82-0.89)	2.02±0.055[1] (1.88-2.11)	0.424±0.0103[1] (0.406-0.444)	4 5/8-[1] (4 3/8-4 7/8)	2.93±0.060[1] (2.77-3.04)
BPBM 142616 Sta. 435	8	1.02±0.032 (0.89-1.19)	2.29±0.043 (2.12-2.52)	0.444±0.0071 (0.420-0.473)	5+ (4 7/8-5 1/4)	2.74±0.053 (2.47-2.92)
BPBM 146161, -6, -7 Sta. 367	26	1.09±0.013 (0.99-1.23)	2.42±0.016 (2.28-2.58)	0.450±0.0049 (0.412-0.500)	4 3/4+ (4 5/8-5 1/4)	3.06±0.043 (2.61-3.67)
BPBM 144652 Sta. 474	4	1.15±0.025 (1.09-1.19)	2.53±0.051 (2.45-2.68)	0.455±0.0115 (0.434-0.487)	 (4 3/4-5 1/4)	2.93±0.125 (2.62-3.22)

1. Subadult examples

(Station 304), in native forest with a sprinkling of coffee trees (Station 427) and in pure native forest (Station 305B). Typical *R. atanuiensis* was collected in the coffee plantation (Station 318) and "100 yards from the base of cliff in forest" on the northeast side of Mt. Tautautu (Station 435). Apparently hybrid populations were taken in the coffee plantation (Stations 291A, 303, and 426), native forest (Station 305A), and "native forest alongside and just west of marae" (native temple) (Stations 319 and 353). There is no simple pattern concerning the ecological distribution of the two species and their hybrids.

Specimens of *R. variumbilicata* showed little variation. One adult had a 6th palatal barrier, but otherwise there was no apertural variation. The constricted umbilicus with concave columellar margin (fig. 112b) also was found in the Mangarevan *Anceyodonta constricta* (fig. 82b). Variation in rib spacing and frequency (table LXXXIV) is minor, while the differences between the two species are large and obvious.

Description of soft parts. — Foot and tail about two-thirds shell diameter in length, all material squashed laterally so that details of foot and tail shape could not be observed. Sole undivided. Pedal grooves quite prominent, relatively high on foot. No caudal horn or middorsal groove. Slime network typical. Head protruding in front of foot. Ommatophores long, light brown eyespots present. Gonopore located below and behind right ommatophore.

Body color light yellow-white, without darker markings.

Mantle collar typical, no glandular extension onto pallial roof.

Pallial region extending somewhat more than three-quarters whorl apically. Lung roof clear, a very few scattered granules located near kidney. Kidney about 0.75 mm. long, very slender, somewhat sinuated. Ureter originating below kidney anterior end, reflexing along and terminating just anterior of rectal kidney anterior end. Heart more than one-half length of kidney, almost parallel to hindgut. Principal pulmonary vein typical. Hindgut following parietal-palatal margin for one-eighth whorl above pallial cavity, quite slender.

Ovotestis imbedded in first half whorl above stomach reflexion, composed of four or five bi- or trifurcate long alveoli that occupy almost entire area of whorl and parallel the plane of coiling rather than being radiately oriented. Hermaphroditic duct (fig. 64f, GD) rather wide above, moderately expanded and very long medially, very abruptly reflexing into talon. Albumen gland (GG) quite small, slender, short, individual acini not reduced in actual size. Talon (GT) almost equal in length to albumen gland, proportionately quite large, with expanded head and narrowed shaft. Prostate (DG) of one row, doubled only in middle, of large acini opening into narrow duct. Uterus (UT) typically divided into two sections.

Vas deferens (VD) a continuation of prostate duct, entering almost apically into penis opposite point where two penial pilasters unite. Penial retractor (PR) long, slender, originating from diaphragm, inserting directly onto penis head. Penis (P) about 1.50-1.95 mm. long, without fleshy head extension, tapering apically, inter-

TABLE LXXXIV. - RIB VARIATION IN RHYSOCONCHA VARIUMBILICATA, R. ATANUIENSIS AND HYBRID POPULATIONS

Name	Number of Specimens	Ribs	Ribs/mm.	Diameter
variumbilicata				
BPBM 144376-7 Sta. 403	7	60.0±1.92 (53-67)	9.84±0.412 (8.63-11.47)	1.95±0.038 (1.86-2.14)
BPBM 138337-8 Sta. 485	8	62.1±2.12 (56-78)	10.36±0.368 (9.28-11.99)	1.91±0.028 (1.81-2.07)
All	20	63.6 (53-82)	10.38 (8.63-12.18)	
atanuiensis-variumbilicata hybrids				
BPBM 137639 Sta. 291A	16	79.9±2.25 (68-104)	11.83±0.324 (10.27-15.05)	2.15±0.026 (1.99-2.34)
BPBM 137639 Sta. 291	6	81.5±3.48 (73-94)	11.71±0.377 (10.61-13.18)	2.21±0.040 (2.07-2.34)
BPBM 144518, -23 Sta. 426	8	85.8±2.13 (75-96)	12.22±0.309 (10.29-13.17)	2.24±0.030 (2.11-2.34)
All	33	81.3 (68-104)	11.93 (9.41-15.05)	
atanuiensis				
BPBM 140161 Sta. 367	6	88.3±1.26 (85-93)	11.66±0.253 (10.95-12.38)	2.41±0.027 (2.32-2.47)
BPBM 142616-7 Sta. 435	20	94.3±2.23 (79-113)	13.91±0.354 (11.23-17.05)	2.16±0.040 (1.88-2.52)
All	33	93.8 (79-132)	13.53 (10.95-17.05)	

nally (fig. 64g) with two narrow, slender, rather closely set pilasters that merge apically, are slightly higher than wide in the central section and fade out basally. Atrium (Y) long and slender.

Free oviduct (UV) much longer than prostate. Spermatheca (S) with elongated and narrow head lying between base of albumen gland and apex of pallial cavity, very slender shaft following normal endodontid pattern, inserting on penial side of peniovidual angle. Vagina absent.

Free muscle system typical. Right ommatophoral retractor passing through peniovidual angle. Buccal retractors not split, uniting posteriorly with tail fan just prior to termination of columellar muscle. Esophagus and buccal mass typical, stomach occupying slightly more than one whorl, intestinal looping typical, occupying one-eighth whorl above pallial cavity. Digestive gland reduced to single narrow strand in region of ovotestis, otherwise typical. Salivary glands as in *Endodonta*.

Radula with very small teeth, centrals about 8μ long and 6μ wide, laterals 5 or 6 in number, more than 9 marginals, but no complete rows obtained on mounts. Jaw lost in preparation.

(Based on BPBM 138337, adult specimen 2.14 mm. in diameter with 5¼ whorls, five individuals dissected.)

Rhysoconcha atanuiensis, new species. Figures 110-112.

Diagnosis. — Shell quite small, diameter 1.88-2.67 mm. (mean 2.33 mm.), with 4⅜ - 5¼ rather tightly coiled whorls. Apex and early spire flat to weakly elevated, last two whorls descending much more rapidly, H/D ratio 0.406-0.500 (mean 0.445). Umbilicus broadly open, U-shaped, whorls regularly decoiling, contained 2.47-3.67 times (mean 2.96) in the diameter. Postnuclear sculpture of narrow, prominent, rather crowded, slightly protractively sinuated radial ribs, 79-132 (mean 93.8) on the body whorl, whose interstices are 3-4 times their width. Microsculpture of very fine radial riblets, four to six between each pair of major ribs, crossed by very fine and crowded spiral riblets. Sutures impressed, strongly rounded above and on umbilical margin, almost evenly rounded on outer margin. Aperture ovate, almost evenly rounded on outer margin, inclined about 15° from shell axis. Parietal barriers 3, rarely (2 per cent) 4, extending posteriorly less than one-quarter whorl: upper parietal high and bladelike, serrated and expanded above on posterior third, with very gradual anterior descension until just before termination; 2nd parietal slightly reduced in height posteriorly, expanded and serrated portion shorter, with rather sharp descension to a raised lamellar ridge that terminates slightly beyond anterior end of upper parietal; 3rd parietal with posterior elevated portion equal in height to 2nd but reduced in length, rather sharply descending to an anterior threadlike portion of varying length that terminates normally almost one-third of length of 2nd parietal behind anterior end, but may extend almost opposite anterior end of upper parietal. Columellar barrier narrow, bladelike, lying almost parallel to plane of coiling, with sharp anterior descension, almost reaching lip margin. Palatal barriers 5, rarely 6 (4 per cent), extending posteriorly more than one-eighth whorl: lower palatal slender, high and bladelike, expanded and serrated above on posterior half, with abrupt anterior descension; 2nd and 3rd palatals longer than 1st, expanded and

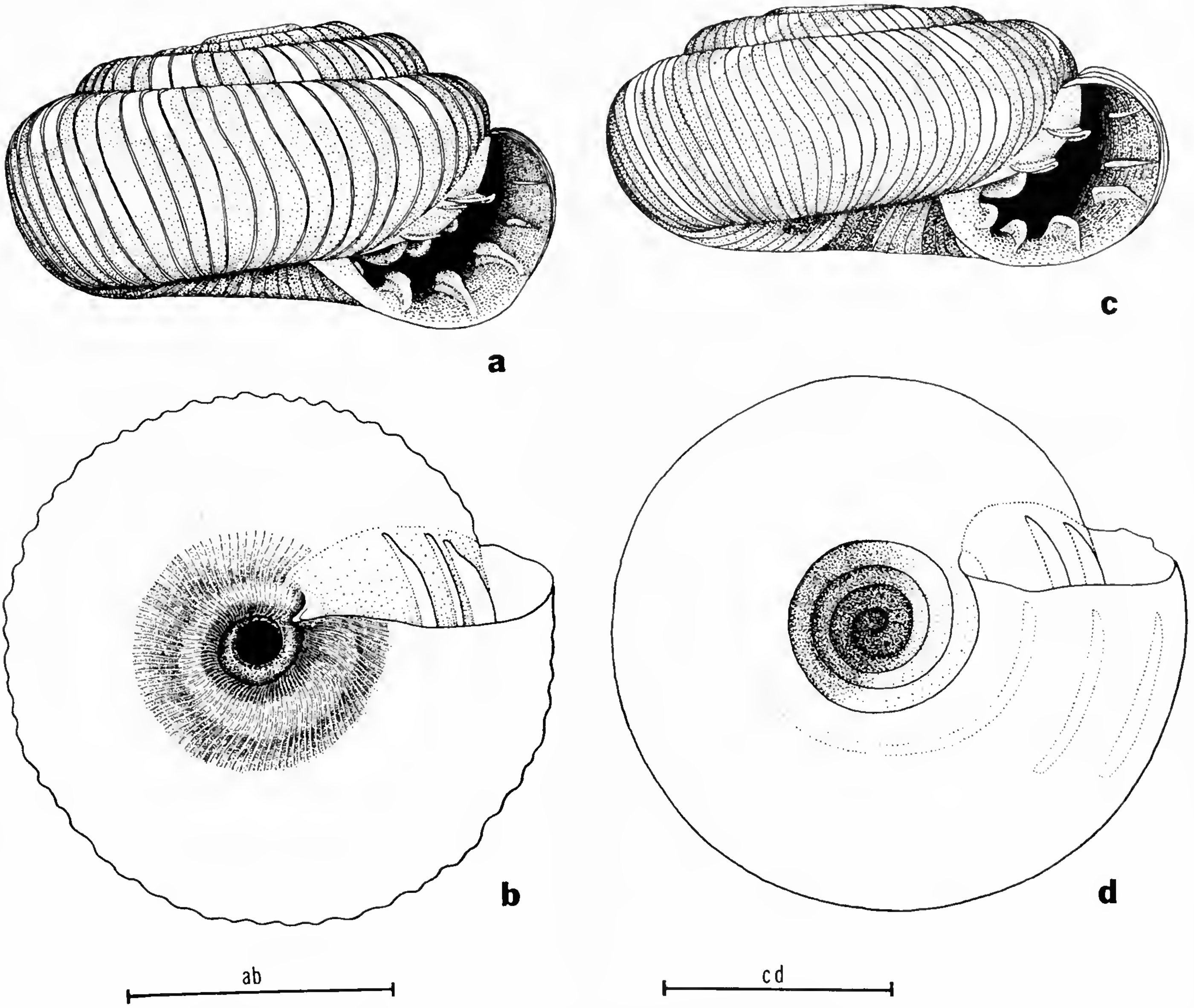

FIG. 112. **a-b**, *Rhysoconcha variumbilicata*, new species. Station 403, Mt. Mangaoa, Rapa Island, Austral Islands. Holotype. BPBM 144376; **c-d**, *R. atanuiensis*, new species. Station 367, Atanui Bay, Rapa Island, Austral Islands. Holotype. BPBM 140161. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

serrated above on posterior half, with progressively more gradual anterior descension; 4th and 5th palatals markedly reduced in height, low lamellar blades, slightly recessed, with very gradual anterior descension; 6th palatal, when present, located between 2nd and 3rd.

The wide umbilicus, much more crowded ribbing, lower spire, presence of 3 parietals, close approach of the columellar barrier to the lip edge, and much larger size of the upper 2 palatals combine to immediately separate specimens of *Rhysoconcha atanuiensis* from *R. variumbilicata*. All other Rapan species are considerably larger, mean diameter at least 2.82 mm., and usually have only 4 palatal barriers.

Description. — Shell quite small, with 5¼ rather tightly coiled whorls. Apex and early spire flat, last two whorls descending progressively more rapidly, H/D ratio 0.494. Apical whorls 1⅜, with sculpture of strongly retractive radial riblets, interspersed by one or two microradials and crossed by tiny microspiral riblets. Postnuclear whorls with low, prominent, rather crowded, slightly protractively sinuated radial ribs, 98 on the body whorl, whose interstices are 3-4 times their width. Microsculpture of extremely fine radial riblets, four to six between each pair of major ribs, with a distinctly finer and more crowded sculpture of spiral riblets. Sutures deep, whorls strongly rounded above and on umbilical margin, almost evenly rounded on outer margin. Apex and spire light yellow-white, lower whorls with broad and irregular, reddish flammulations that tend to coalesce near periphery and on shell base. Umbilicus broadly open, U-shaped, regularly decoiling, contained 3.12 times in the diameter. Aperture ovate, evenly rounded on outer margins, inclined less than 15° from shell axis. Parietal barriers 3, extending posteriorly almost one-quarter whorl: upper parietal high, thin, bladelike, expanded and serrated above on posterior third, with very gradual anterior descension until just before termination; 2nd parietal equally high posteriorly with expanded portion slightly shorter and sharply descending to a lower bladelike portion that extends anteriorly slightly beyond end of upper parietal; 3rd parietal with posterior elevated portion slightly lower and shorter than 2nd parietal, deeply recessed, with anterior margin 0.36 mm. behind edge of 2nd parietal. Columellar barrier a thin bladelike lamella, extending quite far posteriorly (fig. 112c), almost parallel to plane of coiling, stopping just short of lip margin. Palatal barriers 5, short and high, extending about one-eighth whorl: lower parietal thin, narrowly expanded and serrated above on posterior half, with abrupt anterior descension;

2nd and 3rd palatals equal in height to 1st, slightly longer, expanded and serrated above on posterior half, with progressively more gradual anterior descension; 4th palatal markedly reduced in height, but still low and bladelike, expanded and serrated above, with very gradual anterior descension, lying below plane of upper parietal; 5th palatal similar in shape to 4th, more deeply recessed, reduced in height, lying above plane of upper parietal. Height of holotype 1.22 mm., diameter 2.46 mm.

Holotype. – Austral Islands: Rapa Island, Station 367, hillside on south end of Atanui Bay at 300-400 ft. elevation. Collected under stones in a coffee plantation by Donald Anderson on July 12, 1934. BPBM 140161.

Range. – Widely dispersed at low to intermediate elevations, with higher records on Mt. Mangaoa and Mt. Perahu, Rapa Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Rapa Island: Tapui Islet (Station 442) at 20 ft. elevation on dead kukui twigs and leaves (1 specimen, BPBM 142681); hillside at Pake Bay (Station 321) (1 specimen, BPBM 137971); Titikaveka Valley (Station 414) at 500 ft. elevation (1 specimen, BPBM 140558); above cemetery at Ahurei (Station 504) (1 specimen, BPBM 143658); northwest of Mt. Tepiahu (Station 330) at 500-600 ft. elevation under stones in a forest with coffee trees predominating (4 specimens, BPBM 138072-4); hillside on south side of Atanui Bay (Station 367) at 300-400 ft. elevation under stones in a coffee plantation (62 specimens, BPBM 140161-8); hillside above Area (Stations 383, 474) at 250-450 ft. elevation under stones and on dead leaves (6 specimens, BPBM 140508, BPBM 144652-3); hillside and valley west of Tavaitahu (Stations 346, 347) at 750 ft. elevation under stones in forest (10 specimens, BPBM 142471, BPBM 142183, BPBM 142502-4); valley northwest of Mt. Tautautu (Station 342) at 600-700 ft. elevation under stones (4 specimens, BPBM 142406); hillside northeast of Mt. Tautautu, east Maitua area (Station 435) under stones and on dead leaves (33 specimens, BPBM 142616-9); hillside back of Maitua (Station 318) under stones and in moist wood in a coffee plantation (10 specimens, BPBM 144084-6); northeast ridge of Mt. Mangaoa (Stations 485, 526, 527) at 800-1,100 ft. elevation under stones and on dead leaves (12 specimens, BPBM 138341, BPBM 138343, BPBM 138408, BPBM 143740); southeast valley of Mt. Orangi hillside (Stations 296, 299) at 550-700 ft. elevation (14 specimens, BPBM 137783, BPBM 138486-7); east ridge of Mt. Perahu (Stations 453, 512) at 1,500-1,900 ft. elevation (3 specimens, ex BPBM 135483, ex BPBM 135485, BPBM 142905).

Remarks. – The appearance of typical *Rhysoconcha atanuiensis* has been outlined above. Populations from Atanui, Area, and Mt. Orangi do not deviate from the basic pattern. Others show some characters typical of *R. variumbilicata*. One set from the Maitua area (Station 435, BPBM 142616-9) has the columellar barrier deeply recessed and the upper two palatals reduced to traces, but the shape (table LXXXIII) and ribbing (table LXXXIV) of typical *atanuiensis*. In size (tables LXXXI, LXXXII), this population is intermediate between the two forms. The single shells from Ahurei and Pake Bay, plus some of the Tavaitahu and the four Mt. Tepiahu examples have a very weak 4th parietal located between the 1st and 2nd. All of the above, plus two of the three Mt. Perahu shells, and some of the Mangaoa and Maitua specimens have the columellar barrier deeply recessed. All of the above have the shape, size, and ribbing of *atanuiensis*.

Most *R. atanuiensis* were taken at 250-700 ft. elevation, but some individuals were taken on Mt. Mangaoa at 800-1,100 ft. and Mt. Perahu at 1,500-1,900 ft. elevation. Two individuals had a 6th palatal located between the 2nd and 3rd palatals. Otherwise barrier variation included only characters tending toward the *variumbilicata* condition.

Description of soft parts. – Foot and much of head region in all available material had been pulled off during original field processing, with only tip of tail remaining. Sole undivided, pedal grooves high on side of foot, tail slightly tapering and rounded posteriorly.

Body color yellow-white, without darker markings.

Pallial region extending five-eighths to three-quarters whorls apically. Lung roof clear, no trace of granulations. Kidney very narrow, about 0.90 mm. long, sinuated, rectal arm about one-third length of pericardial. Ureter typical. Heart over one-half length of kidney, nearly parallel to hindgut, very large in proportion to kidney size. Principal pulmonary vein very inconspicuous. Hindgut typical, following parietal-palatal margin well above pallial cavity apex.

Ovotestis imbedded in first half to three-quarters whorl above stomach reflexion, lying parallel to sides of whorl rather than being radiately oriented, nearly filling whorl, composed of four to five bi- or trifurcate long alveoli. Hermaphroditic duct slender, medially expanded, sharply reflexed before entering talon shaft, proportionately much longer than usual. Albumen gland very narrow, small, scarcely longer than talon, acini as large as in normal species. Talon typical in shape and form, proportionately very large. Prostate mainly with one row of acini, doubled in middle, opening into slender duct. Uterus typical.

Vas deferens typical, reflexing at penioviducal angle, entering apically into penis on opposite side from pilaster union. Penial retractor arising from diaphragm, inserting directly onto penis head without fleshy extension, relatively long. Penis about 1.6-1.9 mm. long, tapering apically, internally with two narrow, rather closely set pilasters, medially slightly higher than wide, merging at penis apex, decreasing in prominence near end of broken specimens. Lower part of penis, spermatheca, free oviduct and all of atrium missing in available material. Spermatheca with narrow and elongated head lying between apex of pallial cavity and base of albumen gland, remaining part of shaft in normal position.

Stomach, esophagus and intestinal coiling as in *R. variumbilicata*.

Radula with very small teeth, centrals about 8-10μ long, 6μ wide. Mounted individuals with 6 laterals, 11 marginals with edge turned under slightly. Jaw lost in processing.

(Based on BPBM 142616, adult specimens 2.11 and 2.17 mm. in diameter with, respectively, 4¾- and 4⅞ whorls. Six examples dissected at least in part.)

Rhysoconcha atanuiensis-variumbilicata hybrids. Figures 110, 111.

Material. – Rapa Island: Maitua, in a coffee plantation (Stations 291A, 303, 426) at 500-600 ft.

elevation under stones (81 specimens, BPBM 135796, BPBM 137639-40, BPBM 144518-23); Maitua, in native forest (Station 305A) at 700 ft. elevation near cliff (15 specimens, BPBM 137838-42); Maitua, unlocalized area (Station 358) at 550 ft. elevation (9 specimens, BPBM 135701, BPBM 142536); Maitua, in native forest alongside and just west of marae (native temple) (Stations 319, 353) at 750 ft. elevation (26 specimens, BPBM 138534, BPBM 140018-20.)

Remarks. – In the Maitua area of Rapa there is a complex of populations that shows various types of intergradation between *R. atanuiensis* and *R. variumbilicata*. Each of the Maitua populations shows a relatively stable umbilical form (table LXXXIII), but populations that apparently are less than 200 ft. apart can differ widely in umbilical size and ribbing. Ten stations of the Mangarevan Expedition were located from the coffee plantation up to the base of the cliff at Maitua. It is difficult to determine the precise geographic relationship of the stations, but they are apparently placed approximately as indicated below. Stations 291, 303, and 426 are all designated as specifically within the coffee plantation at about 500-600 ft. elevation. Eighteen adults from Station 291A (BPBM 137639) had the D/U ratio varying from 3.23-6.40 (mean 4.09). A single juvenile shell from Station 303 (BPBM 135796) had the umbilicus within the same size range. A larger series of shells from Station 426 (BPBM 144518-23) had the D/U ratio varying from 2.82-6.88 (mean 4.84). Station 427 (BPBM 135525, 135527) is stated as being located about 50 yd. south of Station 292 which is located 100 yd. above and about 75 ft. higher in elevation than Station 291. Stations 292 and 427 were located in essentially native forest with a sprinkling of coffee trees. The four adults of *variumbilicata* from Station 427 had a D/U ratio from 7.90-11.32 (mean 9.37). Station 305B (BPBM 137849) is the same as Station 293, which is located above Station 292 and about 100 yd. below the cliff in native forest. The five adults of *variumbilicata* from Station 305B had a D/U ratio of 9.15-12.60 (mean 10.96). Station 305A (BPBM 137838-42) is located just above Stations 305B and 293. The two adults from Station 305A have D/U ratios of 4.33 and 6.19. Station 304 (BPBM 137817) is stated to lie on the hillside between Stations 291 and 293 and the collection was made under a single pile of stones. The D/U ratio of eight *variumbilicata* adults ranges from 5.91-13.20 (mean 8.29). Presumably Station 304 is ecologically equivalent to Station 292; i.e., being located on the ecotonal area between the coffee plantation and the native forest. Station 319 (BPBM 138534) is at 750 ft. elevation, about 20 ft. west of the marae (native temple) in moist native forest. The two adults have a D/U ratio of 2.86 and 3.39. Shells from Station 353 (BPBM 140018-20) are from essentially the same population as the material from Station 319, since the locality is given as "alongside of Marae which is just below Mangaoa (a little to the west)." The 11 adult shells had a D/U ratio of 2.95-3.93 (mean 3.30). Specimens from Station 358 (BPBM 142536), an unlocalized place at Maitua (elevation 550 ft.), have a D/U ratio of 4.20-6.40 (mean 4.83).

As indicated above, *R. variumbilicata* was collected at Stations 304, 305B, and 427. The remaining stations had specimens that were intermediate in different ways. The specimens from Stations 319 and 353 were more similar to *atanuiensis* in shape (mean H/D ratio 0.478) and umbilical width (mean D/U ratio 3.27), although with the size (mean height 0.94 mm., mean diameter 1.96 mm.) of *variumbilicata* and almost precisely intermediate in rib count (mean 76.0) and rib spacing (mean ribs/mm. 12.10). All checked specimens had 4 parietals, the 2 upper palatals reduced to threads, but the columellar barrier recessed in some, reaching the lip edge in others.

Specimens from Stations 291A, 303, 305A, 358, and 426 were similar to *atanuiensis* in shape (mean H/D ratio 0.522), intermediate in size (mean diameter 2.16 mm.), umbilical width (mean D/U ratio 4.63), rib count (mean ribs 82.7), and rib spacing (mean ribs/mm. 11.96). From Stations 291 and 426, in the checked examples, there were 12 with 3 parietals and 24 with 4 parietals; 15 had the columellar barrier reaching the lip edge, while in 21 examples it was deeply recessed; and all had the 2 upper palatals reduced to threads.

Providing the more than 40 years since the Mangarevan Expedition collections have not seen destruction of these populations, the Maitua area offers what may be a unique opportunity to study snail evolution in action. Efforts by Harald Rehder to collect material in this area were unsuccessful in the last few years and I am not optimistic concerning their survival (see p. 100).

Genus **Ruatara**, new genus

Endodontidae having typical apical and microsculpture, major radial sculpture normally spaced or rather crowded. Apex and spire slightly to moderately elevated, sometimes rounded above, body whorl descending only slightly more rapidly, periphery rounded or obtusely angulated. Whorls about 5½, rather tightly coiled, number reduced in *Ruatara koarana*, greatly reduced in *Ruatara oparica oparica*. Umbilicus barely perforate to closed in both juveniles and adults, columellar wall essentially parallel to shell axis. Parietal barriers usually 2 or 3, rarely more, prominent, greatly shifted in *R. koarana*. Columellar barrier twisted onto basal lip (*R. koarana*); prominent and deeply recessed; or slanting partway across columellar callus. Palatal barriers 0-5, usually 3 or 4, reduced to absent in *R. oparica reductidenta*. Hermaphroditic duct highly convoluted. Penis with near apical insertion of vas deferens and without fleshy extension to penis head, internally with one very large and transversely rugose pilaster. Spermatheca and free oviduct uniting well above atrium, producing a clearly marked vaginal region. Anatomy otherwise typical of the Endodontidae.

Type species. – *Ruatara oparica normalis,* new subspecies.

The convolution of the hermaphroditic duct, presence of only one rugose pilaster in the penis, clear

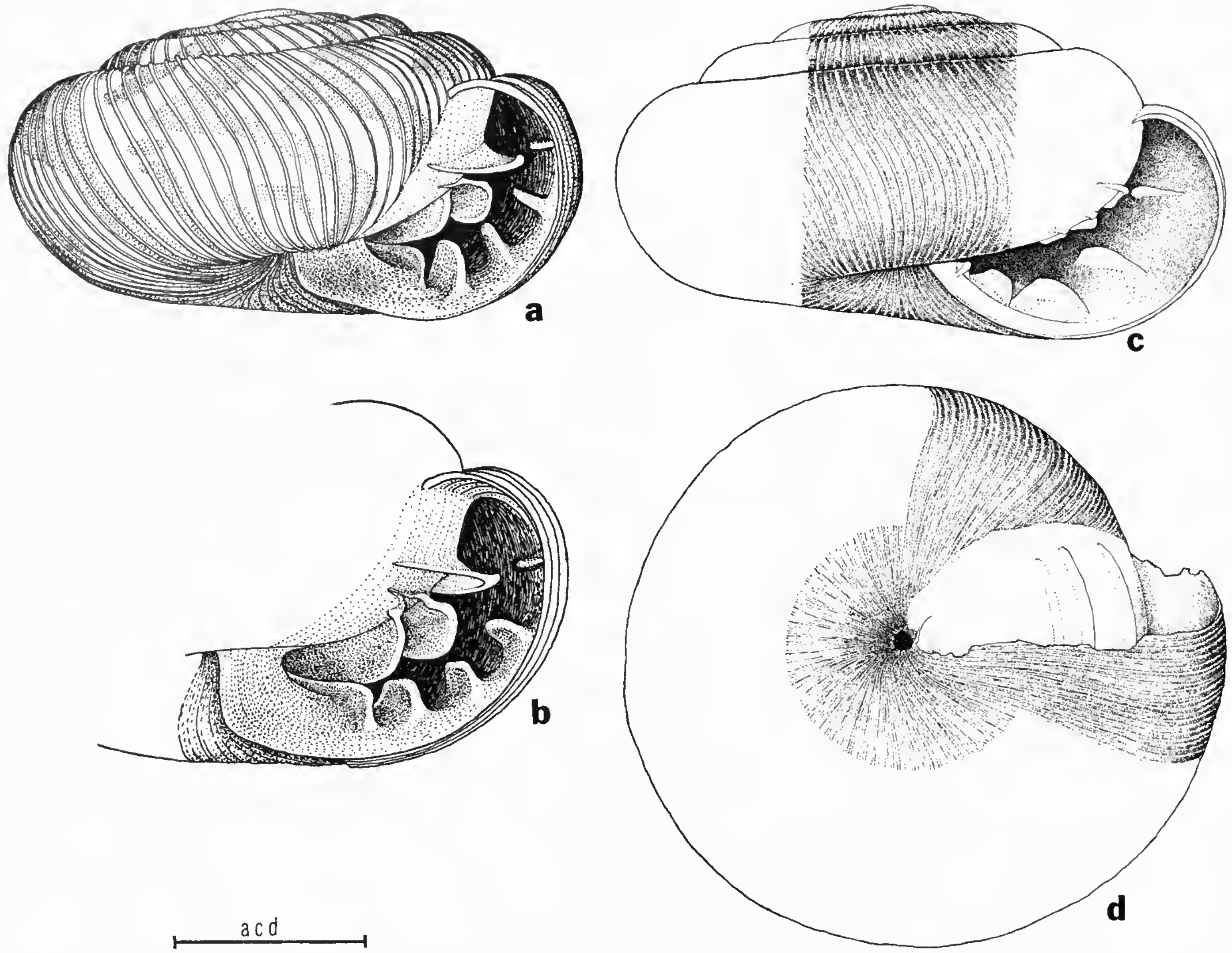

FIG. 113. **a-b**, *Ruatara koarana*, new species. Station 357, Mt. Koara, Rapa Island, Austral Islands. Holotype. BPBM 142521; **c-d**, *R. oparica oparica* (Anton). Opana (=Opara, Rapa) Island. Probably paratype. FMNH 46378 ex W. F. Webb, Gerard Gude. Scale lines equal 1 mm. Figures *a-b* by YK reproduced through the courtesy of Bernice P. Bishop Museum; *c-d* (MM).

demarcation of a vaginal region, near apical penial insertion of the vas, and absence of an umbilical opening in juvenile shells combine to separate *Ruatara* from the other Rapan genera. Anatomically, it is one of the most clearly differentiated Eastern Polynesian genera. The first three characters separate it from all other genera in the family.

Inclusion of *Ruatara koarana* is based on general conchological similarities, since no anatomical material of that species suitable for dissection was available. Quite possibly it is an aberrant *Opanara*, but until dissected, it can be classified here. The great alteration of the columellar region in *R. koarana*, resulting in staggered recession of the parietal barriers (fig. 113b), is unique among the known Endodontidae, as is the change in position of the columellar barrier from parallel to the plane of coiling in juveniles, to deflected onto the basal lip in adults. While the apertural barriers are much larger than those found in *R. oparica*, the character of the sculpture and general shell shape are more similar to that species than to any other Rapan taxon.

Ruatara oparica is widely distributed on Rapa and has been divided into three subspecies. *R. koarana* has been found only at a single station on Mt. Koara. The two species are readily separable by characters of the parietal barriers. The following comparison substitutes for a formal key:

Ruatara koarana – parietal barriers strongly and progressively more deeply recessed within aperture;

Ruatara oparica – parietal barriers with at least 2nd terminating slightly in front of anterior end of upper parietal.

Ruatara koarana, new species. Figure 113a-b.

Diagnosis. – Shell small, diameter 2.80-3.03 (mean 2.93 mm.), with 4¾ - 5½ rather tightly coiled whorls. Apex and spire slightly and almost evenly elevated, a trifle rounded above, last whorl descending a little more rapidly, H/D ratio 0.567-0.670 (mean 0.612). Umbilicus barely perforate to closed. Postnuclear sculpture of narrow, prominent, lamellar, protractive radial ribs, 79-81 (mean 80) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, three to six between each pair of major ribs, crossed by extremely fine and crowded spiral riblets.

Sutures impressed, whorls flatly rounded down to obtusely angulated periphery, with evenly rounded lower palatal and basal margin. Aperture ovate, slightly flattened laterally above obtusely angulated periphery, inclined about 20° from shell axis. Parietal barriers 3, high and bladelike, irregularly situated within aperture: upper very high and bladelike, weakly expanded and serrated above on posterior half, rather sharply descending to anterior end; 2nd parietal set back almost three-sixteenths of a whorl from anterior end of 1st, equally high and expanded posteriorly, with more gradual anterior descension to a short and threadlike segment that terminates well behind anterior end of upper parietal; 3rd parietal recessed almost one-quarter whorl from anterior end of upper, visible portion equally high, with very sharp anterior descension, entire barrier strongly twisted from plane of coiling. Columellar barrier a high bladelike ridge, lying almost perpendicular to shell axis in juveniles, twisted downward onto basal lip in adults and almost touching lower palatal barrier. Palatal barriers 4, very high, extending posteriorly about one-eighth whorl: lower palatal markedly displaced from normal position by deflection of columellar, not lying parallel to plane of other palatals, deeply recessed, with sharp anterior descension to middle of baso-columellar callus; 2nd palatal slightly displaced from normal position, more strongly expanded and serrated above, less deeply recessed, with more gradual anterior descension; 3rd palatal nearly normal in position, slightly lower than 2nd, with even more gradual anterior descension; 4th palatal peripheral, deeply recessed, greatly reduced in height, a crescentic or V-shaped ridge situated slightly above level of upper parietal.

The extreme recession of the lower parietals coupled with displacement of the columellar and lower palatal barriers is unique in the Endodontidae. Of the other Rapan species, it is most likely to be confused with *R. oparica oparica,* which has much more crowded ribbing and the columellar barrier on the columellar lip. *Opanara perahuensis* has regularly spaced parietals, a much different ribbing pattern and more whorls. Other Rapan species with narrow or closed umbilici have only 2 parietals.

Description. — Shell small, with 5 rather tightly coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a trifle more rapidly. H/D ratio 0.567. Embryonic whorls 1½, sculpture eroded. Postnuclear whorls with narrow, crowded, lamellar, protractive radial ribs, 81 on the body whorl, whose interstices are 3-4 times their width. Microsculpture of fine radial riblets, three to six between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures shallow, whorls flatly rounded down to very weakly and obtusely angulated periphery, lower palatal margin evenly rounded, becoming slightly flattened basally. Color light yellow horn with irregular, zigzagged, reddish flammulations. Umbilicus minutely perforate, contained 45 times in the diameter. Columellar wall with exceedingly thick and extensive callus, extending well on to basal margin. Aperture ovate, slightly flattened laterally above periphery, with evenly rounded lower palatal margin, basal margin somewhat sinuated. Parietal barriers 3, very high and thin, irregularly situated within aperture: upper parietal extending slightly more than one-quarter whorl, expanded and serrated above on posterior visible half, with gradual anterior descension; 2nd parietal deeply recessed, posteriorly equal in height to upper parietal, elevated portion twisted diagonally downward from front to rear, with slightly sharper anterior descension to a threadlike portion that stops just anterior of upper parietal end; 3rd parietal set back almost one-quarter whorl, equally high posteriorly, twisted diagonally downward from plane of coiling, without threadlike anterior portion. Columellar barrier a moderately elevated bladelike ridge, deflected downward onto basal margin, deeply recessed within aperture, reaching slightly past apex of heavy basal columellar callus, with its anterior end almost touching side of 1st palatal. Palatal barriers 4, short, very high, displaced from normal position: 1st palatal high and bladelike, weakly expanded posteriorly, with sharp anterior descension to middle of callus, less recessed, less deflected from plane of coiling, with more gradual anterior descension; 3rd palatal equal in height to 2nd, situated slightly below level of upper parietal, with more gradual anterior descension; 4th palatal peripheral in position, greatly reduced in height, an elevated, weakly crescentic ridge, deeply recessed within aperture and situated above level of upper parietal. Height of holotype 1.68 mm., diameter 2.96 mm.

Holotype. — Austral Islands: Rapa, Station 357, Oromange, Mt. Koara at 800 ft. elevation on a hillside under stones in native forest. Collected by Harold St. John on July 11, 1934. BPBM 142521.

Range. — Only known from near Oromange, Mt. Koara at 800 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: Mt. Koara (Station 357) near Oromange at 800 ft. elevation (4 specimens, BPBM 142521-2).

Remarks. — Only four specimens of this remarkable shell were found. The single juvenile, 2.10 mm. in diameter with 3⅜ whorls, has a slightly open umbilicus and the columellar barrier is perpendicular to the shell axis. In the adult specimens, the columellar twists down and occupies a basal position, roughly paralleling the lower palatal. The extreme development of the baso-columellar callus and consequent gross displacement of the 2 lower parietals, the columellar and first 2 palatal barriers are unique. Even in the juvenile shell, the deep recession of the lower parietals, and the sideways twisting of the lower palatal barriers is evident. Unfortunately, it was impossible to dissect this species and reference of it to *Ruatara* much be considered tentative.

The crowding of the radial ribs, mean ribs/mm. is 8.91, is slightly greater than in the much larger *R. oparica normalis* and much, much less than in *R. o. oparica,* which is essentially identical in height, although much more depressed.

Ruatara oparica (Anton, 1839)

Ruatara oparica is the only species of endodontid previously known from Rapa, and the second most frequently encountered species collected by the Mangarevan Expedition. It shows considerable variation in apertural barriers, ribbing and umbilical opening. As with most other species for which very large samples were available, the following analysis is based on only part of the material. Time did not permit measuring all specimens. Recognition of three subspecies, *R. oparica oparica, R. o. normalis,* and *R. oparica reductidenta,* is conservative. Division into four subspecies is logically defensible, but would not be consistent with taxonomic treatment elsewhere in this study.

Barrier variation concerns both actual numbers and relative prominence. Considering all specimens studied, the number of parietals varied from 1 - 5, but only 8 (2 per cent of 402 examples checked) had 1 or 5; 35 (8.7 per cent) had 4; 99 (24.6 per cent) had 2; and

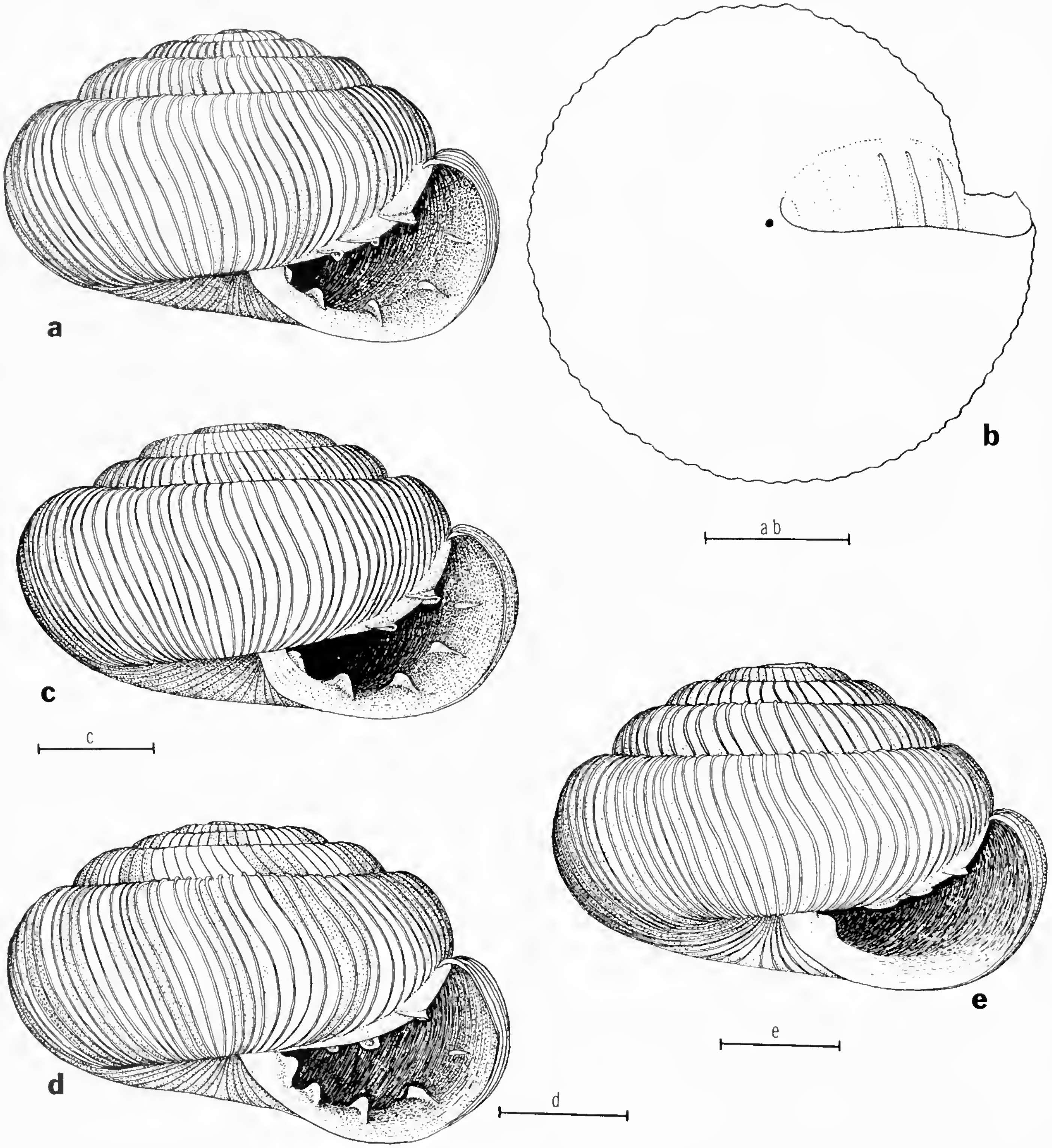

FIG. 114. **a-d**, *Ruatara oparica normalis,* new subspecies. *a-b,* form with 3 parietals, Morongoto, Rapa Island, Austral Islands. BPBM 53246; *c,* form with 2 parietals. Station 490, Mt. Ruatara, Rapa Island, Austral Islands. Paratype. BPBM 143492; *d,* form with prominent barriers. Station 360, Morongoto, Rapa Island, Austral Islands. Paratype. BPBM 144246; **e**, *R. o. reductidenta,* new subspecies. Station 291, Maitua, Rapa Island, Austral Islands. Holotype. BPBM 137609. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

259 (64.7 per cent) had 3 parietals. Specimens from the northern part of Rapa (Mt. Perahu and Mt. Ruatara) usually have only 2 parietals, while those from the southern part of the island generally have 3 parietals (fig. 115). Using the contingency table comparison, this difference is highly significant ($\chi^2 = 8.69$). Visual inspection of Figure 115 indicates that there is no difference in parietal barrier frequency distributions between both *oparica oparica* and *oparica normalis* from the southern part of Rapa and *oparica reductidenta* from the Mt. Tautautu region.

Palatal barrier counts are equally variable, the number ranging from 0-5, with considerably different frequencies observed. Specimens from the Mt. Tautautu-Maitua area (*reductidenta*) normally lack all palatals. Even though one or two palatal traces are often present (16 per cent), they are reduced in size to tubercular nodules and are in no sense truly comparable to the large 1st and 2nd palatals seen in *R. oparica oparica*. Hence Figure 115 tends to mask the gross differences between the Mt. Tautautu-Maitua populations and those from other areas by failing to reflect the size difference in the 1st and 2nd palatals. Although there seems to be a difference in proportions between the north Rapan populations and the non-Mt. Tautautu south Rapan populations in the frequency of 3 and 4 palatals (fig. 115), the difference does not reach a significant level ($\chi^2 = 2.56$). Further study of the north Rapan material may show that a significant difference exists. Numerical reduction in the palatals was, without exception, orderly, the upper being lost before the 3rd, 3rd before the 2nd, etc.

Rib variation was equally complicated. The type material, all specimens in old collections, and the few examples from Station 466 on the south side of Mt. Tanga at 700-800 ft. elevation agreed in having a large number of very crowded ribs (tables LXXXI and LXXXV). Specimens from the Mt. Tautautu-Maitua area had relatively few, much less crowded ribs, while the remaining specimens taken by the Mangarevan Expedition were approximately intermediate in rib count (table LXXXVI), but tending closer to the Mt. Tautautu-Maitua type in rib frequency (table LXXXVII). Specimens taken from Mt. Ruatara (Station 491) and south Rapa (exclusive of the *reductidenta* and *oparica* populations) were virtually identical in ribbing and rib frequency, since the means for all *normalis* taken by the Mangarevan Expedition (table LXXXI) and those from Station 491 (table LXXXVI) are essentially the same. Differences in rib count and ribs/mm. between *normalis* and *reductidenta* are highly significant, with 53 df, "t" = 8.469 for rib count and "t" = 6.481 for ribs/mm. The differences between *reductidenta* and the nominate race are so large that no test of statistical significance was necessary.

Umbilical closure is most advanced in *R. o. reductidenta*, with only 1 of 93 examples having a

TABLE LXXXV. - FREQUENCY DISTRIBUTION OF RIBS/MM. IN RUATARA OPARICA

Ribs/mm.	oparica oparica	oparica normalis	reductidenta
5.71-6.70		3	12
6.71-7.70		13	16
7.71-8.70		20	1
8.71-9.70		13	
9.71-10.70		1	
10.71-11.70	1	1	
11.71-12.70	7		
12.71-13.70	2		
13.71-14.70	3		
14.71	2		
Number	15	51	29
Mean	12.96	8.12	6.85
Range	(10.75-14.83)	(6.01-10.83)	(5.71-8.04)

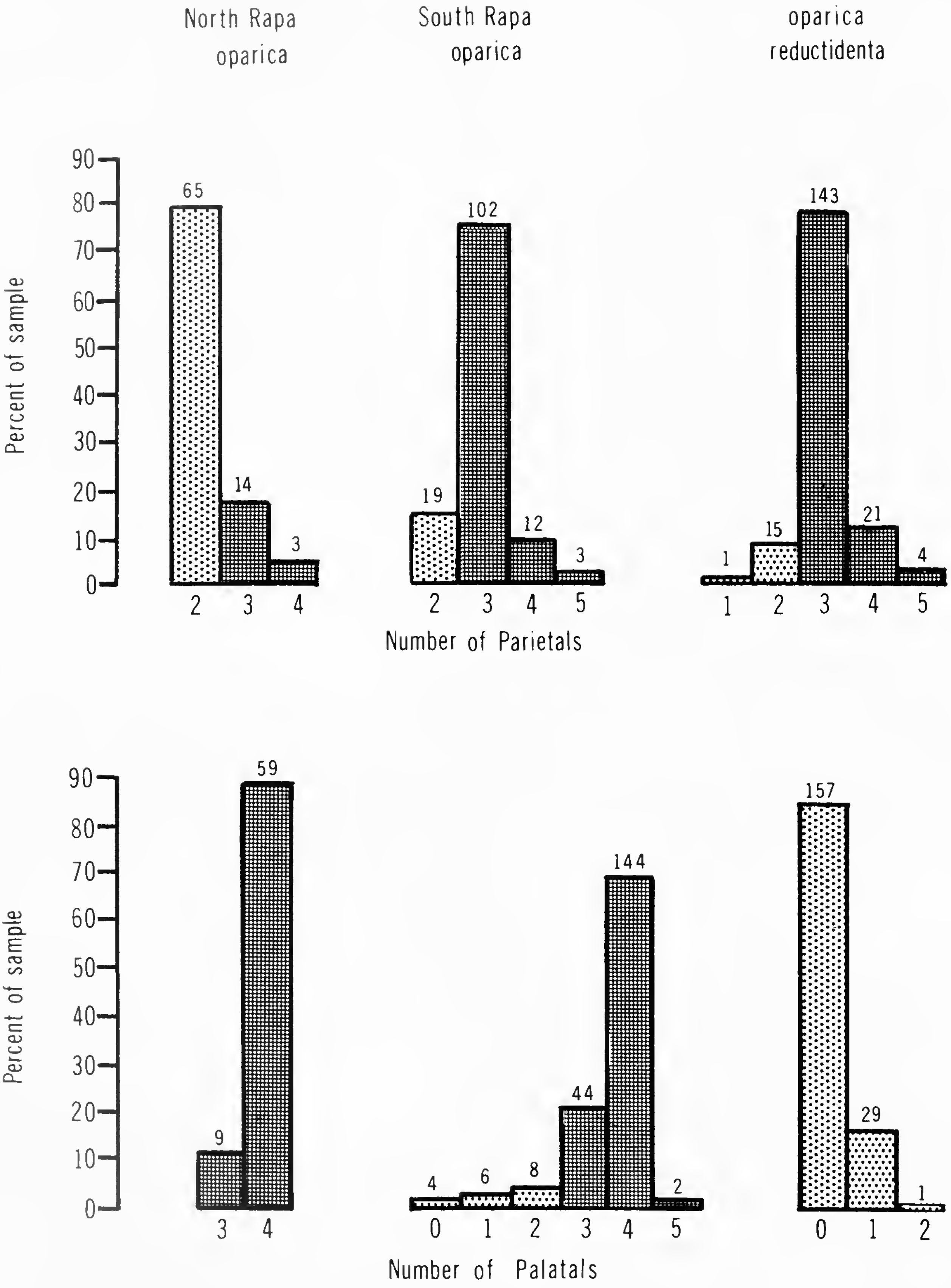

FIG. 115. Parietal and palatal barrier number variation in *Ruatara oparica*.

TABLE LXXXVI. - RIB VARIATION IN RUATARA OPARICA

Form	Number of Specimens	Rib Count	Ribs/mm.	Diameter
oparica				
Cuming	13	119.8±3.60 (101-150)	12.73±0.304 (10.75-14.83)	2.99±0.052 (2.80-3.39)
normalis				
Sta.491	30	99.8±1.86 (77-121)	8.22±0.167 (6.01-9.76)	3.88±0.055 (3.22-4.44)
reductidenta				
Sta. 291	25	78.4±1.64 (66-93)	6.93±0.085 (6.33-8.04)	3.59±0.046 (3.26-4.08)

perforate umbilicus. It is least advanced in *R. o. oparica,* with only 5 of 24 having a closed umbilicus. *R. oparica normalis* is intermediate, with 72 specimens having a perforated umbilicus and 82 a closed umbilicus. When open, the umbilicus still was so minute that no meaningful measurements were possible.

The importance of local size variation (table LXXXVII) cannot be determined from present data. This was one of the first species measured and inclusion of some paraneanic individuals in smaller sets and presence of essentially only gerontic individuals in other sets (Station 490, table LXXXVII) certainly biased measurements, particularly in respect to height and diameter. The much greater size of the specimens from Station 490 almost certainly is the result of sample bias. On the other hand, the small size of individuals from Station 399 may have biological significance. These shells were collected from a ridge on open ground under dead leaves. The habitat would be much drier than from a forest with a greater degree of moisture retention and a local "dwarfing" effect would be a reasonable expectation. Whether the lower H/D ratio of Station 399 examples is correlated with the small size (compare with the H/D ratios of *R. oparica oparica*) or reflects a genetically caused lowering of the spire is unknown. Similarly, I have no explanation concerning the greater H/D ratio of the few Mt. Perahu examples.

When the variations discussed above are correlated, a division into three subspecies seems most reasonable:

Ruatara oparica oparica (Anton, 1839) from Mt. Tanga is quite small with very numerous and crowded radial ribs, apertural barriers as in the south Rapan populations of *R. o. normalis;*

Ruatara oparica normalis, new subspecies from north Rapa and most of south Rapa (except Mt. Tanga, Maitua and Mt. Tautautu) is rather large with fewer and more widely spaced radial ribs, generally (73.6 per cent) with 4 palatals and most frequently with 3 parietals on south Rapa and 2 parietals on north Rapa.

Ruatara oparica reductidenta, new subspecies from Maitua and Mt. Tautautu is insignificantly smaller than *R. oparica normalis* and has fewer and more widely spaced radial ribs, but differs most significantly in having normally no palatal barriers; even when 1 or 2 are present, they are reduced to extremely small tubercular nodules.

Within *R. oparica normalis* there is the north-south dichotomy in parietal barrier frequency, but since the populations agree in all other respects, I attach no systematic recognition to this variation. The three subspecies are geographically isolated (fig. 116) and readily separable on a population basis. Although the loss of palatal barriers that distinguished *R. o. reductidenta* is a more dramatic alteration, there is a greater amount of change required in altering either of the other two subspecies into *R. oparica oparica.*

Ruatara oparica oparica (Anton, 1839). Figures 113c, d; 115; 116.

Helix (Helicodonta) opanica (sic) Anton, 1839, Verzeich. d. Conchol., p. 39, no. 1443 – "Opana in Amerika" (error).

Helix oparica Anton, Pfeiffer, 1842, Sym. Hist. Helic., **2,** p. 92 – Rapa (= Opara) Island (necessary emendation); Pfeiffer, 1848, Monog. Helic. viv., **1,** p. 186; Deshayes, 1850, Hist. Nat. Moll. terr. fluv., **1,** p. 191, no. 257, pl. 55, fig. 12 (plate issued in 1841); Pfeiffer, 1852, Syst. Conchyl. Cab., 1, **12,** (2), p. 199, pl. 100, figs. 16-20 (plate issued in 1850); Pfeiffer, 1853, Monog. helic. viv., **3,** p. 144; Pfeiffer, 1868, *Ibid.,* **5,** p. 221; Pfeiffer, 1876, *Ibid.,* **7,** p. 259.

Helix (Endodonta) oparica (Anton), Tryon, 1887, Man. Conchol., (2), **3,** p. 67, pl. 12, figs. 37-39 (copied from Syst. Conchyl. Cab.).

Endodonta (Thaumatodon) opanica (sic) (Anton), Pilsbry, 1893, Man. Conchol., (2), **9,** p. 26.

Diagnosis. – Shell quite small, diameter 2.80-3.39 mm. (mean 2.98 mm.), with 4¾ - 5¼ normally coiled whorls. Apex and spire moderately and evenly elevated, very slightly rounded above, last whorl descending a trifle more rapidly, H/D ratio 0.488-0.597 (mean 0.565). Umbilicus usually minutely perforate, too narrow to measure, frequently (20.8 per cent) closed. Postnuclear sculpture of narrow, lamellar, crowded, protractively sinuated radial ribs, 101-154 (mean 122.9) on the body whorl, whose interstices are less than twice their width. Microsculpture of fine radial riblets, two to three between each pair of major ribs, crossed by barely visible and extremely crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on outer margin, with basal margin slightly flattened and extended inwardly. Aperture ovate, with strongly rounded margins, inclined about 15° from shell axis. Parietal barriers variable in

TABLE LXXXVII. - LOCAL VARIATION IN RUATARA OPARICA

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls
oparica oparica					
British Museum	13	1.68±0.037 (1.49-1.95)	3.00±0.049 (2.81-3.41)	0.559±0.0080 (0.488-0.590)	4 1/4+ (4 1/2-5)
BPBM 143113 Sta. 466	10	1.71±0.057 (1.52-1.92)	2.96±0.068 (2.72-3.34)	0.572±0.0046 (0.553-0.597)	4 5/8+ (4 1/2-5 1/8)
oparica normalis					
BPBM 140385, -7 Sta. 399	22	1.93±0.027 (1.69-2.15)	3.40±0.036 (3.11-3.74)	0.563±0.0052 (0.522-0.614)	5 (4 3/4-5 1/4)
BPBM 142936 Sta. 455	8	2.12±0.056 (1.85-2.32)	3.48±0.081 (3.25-3.97)	0.607±0.0099 (0.571-0.660)	5 3/8 (5 1/8-5 5/8)
BPBM 138402, -4 Sta. 527	13	2.18±0.063 (1.92-2.54)	3.51±0.069 (3.15-3.94)	0.611±0.0061 (0.579-0.646)	5 1/2- (5-6)
BPBM 143747, -9 Sta. 526	5	2.19±0.060 (1.99-2.35)	3.68±0.038 (3.58-3.77)	0.596±0.0148 (0.540-0.628)	5 3/8+ (5-5 3/4)
Mt. Perahu Sta. 376, 446, 451-2, 509, 512-3	10	2.41±0.044 (2.19-2.62)	3.77±0.038 (3.58-3.94)	0.636±0.0108 (0.589-0.690)	5 5/8+ (5 3/8-6)
BPBM 144246, -7, -50 Sta. 360	14	2.25±0.062 (1.99-2.81)	3.78±0.060 (3.48-4.30)	0.597±0.0100 (0.545-0.654)	5 1/2- (5-6 1/8)
BPBM 143492 Sta. 490	39	2.50±0.024 (2.19-2.88)	4.17±0.034 (3.71-4.87)	0.599±0.0037 (0.524-0.638)	5 5/8+ (5 1/4-6 1/4)
oparica reductidenta					
BPBM 137686 Sta. 292	8	2.05±0.048 (1.89-2.35)	3.56±0.072 (3.38-4.01)	0.577±0.0074 (0.545-0.607)	5 1/8+ (5-5 1/2)
BPBM 137609, 12, -15 Sta. 291	50	2.18±0.025 (1.92-2.72)	3.69±0.027 (3.31-4.24)	0.591±0.0049 (0.528-0.728)	5 3/8+ (5-6 1/8)

number, 2 (21.1 per cent), 3 (71.0 per cent), or 4 (7.9 per cent), extending posteriorly about three-sixteenths of a whorl: upper parietal high and bladelike, expanded and serrated above on posterior quarter, with gradual anterior descension until just before anterior end; 2nd parietal normally with elevated posterior portion slightly shorter and higher, sharply descending to an anterior threadlike two-thirds that terminates slightly beyond anterior end of upper parietal; 3rd parietal, when present, similar in structure to 2nd, usually slightly reduced in height and length of posterior elevated portion; 4th parietal, when present, a low threadlike trace, not elevated posteriorly, situated below 3rd parietal. Columellar barrier a raised threadlike ridge, lying parallel to plane of coiling posteriorly, slanting slightly downward anteriorly, moderately recessed within aperture. Palatal barriers normally 4 (86.8 per cent), occasionally 3 (7.9 per cent) or 2 (5.3 per cent), relatively short, extending about one-eighth whorl: lower basal in position, high and crescentic, with rather sharp anterior descension, moderately recessed within aperture; 2nd palatal normally slightly higher, longer, with more gradual anterior descension; 3rd palatal, when present, moderately reduced in height, with much more gradual anterior descension, more deeply recessed within aperture; 4th palatal, when present, greatly reduced in height, a raised lamellar or threadlike ridge, very short, deeply recessed within aperture, lying slightly below level of upper parietal.

The very crowded and numerous radial ribs, smaller diameter, usually barely perforate umbilicus, and well-developed palatal barriers combine to separate the nominate subspecies from both *Ruatara oparica reductidenta* and *Ruatara oparica normalis.* The former differs most obviously in having no palatal barriers or at most one or two small tubercules on the basal and lower palatal margins, while *R. oparica normalis* differs in its larger size, fewer and less crowded radial ribs, and generally more elevated spire. The progressively recessed parietals and massive columellar callus separate *Ruatara koarana.* All *Orangia* and the barely perforate *Opanara* differ in their much larger and more prominent palatal barriers.

Description. – Shell slightly larger than average, with 5 relatively tightly coiled whorls. Apex and spire strongly elevated, broadly rounded above, last whorl descending slightly more rapidly, H/D ratio 0.577. Embryonic whorls 1⅜, sculpture eroded except for faint traces of radial ribbing in sutures. Postnuclear whorls with prominent, broad, lamellar, slightly protractively sinuated radial ribs, 119 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of prominent, moderately widely spaced radial riblets crossed by exceedingly fine and crowded spiral riblets. Sutures moderately impressed, slightly channeled on portions, whorls almost evenly rounded on outer margins with somewhat flattened basal margin. Color light yellowish-horn with very vague, irregular, light reddish-brown flammulations. Umbilicus barely perforate, contained more than 30 times in the diameter. Aperture elongately ovate with evenly rounded outer margin, somewhat flattened basal margin, inclined about 5° from shell axis. Parietal barriers 3, extending three-sixteenths of a whorl: upper a bladelike ridge with relatively sharp anterior descension, only slightly higher and expanded on posterior third; 2nd lamella with anterior half threadlike, extending further

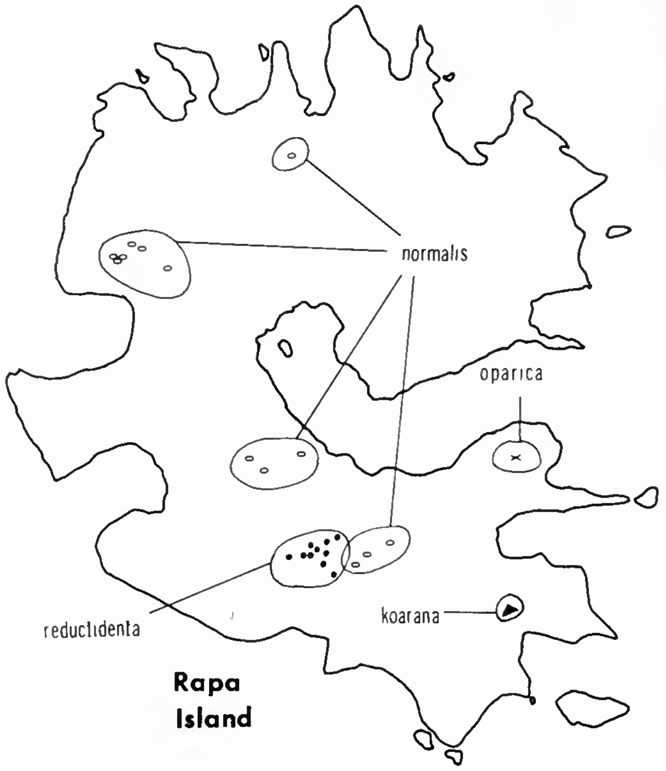

FIG. 116. Geographical distribution of *Ruatara oparica*.

past lip edge than upper, the posterior third high and almost crescent shaped; lower parietal similar to 2nd, but slightly deflected downward on posterior portion and not quite as high. Columellar barrier a prominent, narrow ridge, slanting downward at a 45° angle across heavy baso-columellar callus. Palatal barriers 4: lower, a small nodular ridge at baso-columellar margin, slightly protruding above heavy basal callus; 2nd and 3rd high, prominent, rounded, crescentic, extending about one-eighth whorl; 3rd more gradually descending anteriorly; upper palatal very low, ridgelike, slightly crescent shaped, narrow, much less prominent than others, situated opposite upper parietal. Height of lectotype 1.84 mm., diameter 3.19 mm.

Lectotype. – Austral Islands: Rapa (= Opara). Collected by Hugh Cuming. BMNH 1962705/1.

Range. – Slopes of Mt. Tanga, Rapa Island, Austral Islands.

Paratypes. – BMNH 1962704/2-5.

Material. – Rapa (17 specimens, BMNH 1962704/1-5, BMNH, FMNH 46378 ex Webb, Gude); south Mt. Tanga (Station 466) at 700-800 ft. elevation under stones and on dead leaves (25 specimens, BPBM 143113-5).

Remarks. – The Hugh Cuming expedition through Polynesia is known to have been on Rapa from May 13, 1828 to May 17, 1828 (St. John, 1940, p. 88). Specimens of *Ruatara oparica* in the British Museum (Natural History) from the Cuming collection and all material from old collections (several individuals were not listed) agreed with the population from Station 466 on south Mt. Tanga (table LXXXVII), with 10 df, for the diameter "*t*" = 0.4593 and for the H/D ratio "*t*" = 1.1844. While possibly material from the Anton collection may still exist in Europe, although currently unrecognized, I have selected a lectotype from the Cuming specimens. It differs from the figured example primarily in having the columellar barrier more sharply deflected downward.

It is of passing interest to note that recent studies have managed to localize many of Cuming's species quite precisely. Thus Cooke and Kondo (1960, pp. 97, 106) show that *Pitys pagodiformis* (E. A. Smith, 1892) (= *Helix bilamellata* Pfeiffer, 1845, not Sowerby, 1844), *Lamellovum globosum* (Petit, 1843), and the assimineid *Electrina succinea* (Sowerby, 1832) came from the slopes leading to Mt. Morongoto. In the same paper (pp. 59-62, 191-192) they placed *Antonella trochlearis trochlearis* (Pfeiffer, 1842) on Mt. Tanga and speculated as to the original sites for various *Strobilus*. These could not be positively localized by Cooke and Kondo as no Cuming material was available to them. H. B. Baker (1938b, p. 62) suggested that the helicarionid *Microcystis ornatella* (Beck, 1837) came from near Area, but later (H. B. Baker, 1940, pp. 175-177) made no attempt to deal with local variation in the helicarionid *Hiona orbis* (Beck, 1837).

Pfeiffer's emendation of "*opanica*" to "*oparica*" is accepted here, although strict adherence to nomenclatural technicalities (Article 32 (a)) would require a return to "*opanica.*" At the time of description and during the middle 1800's, Opana and Opara were recognized alternative spellings for Rapa Island. Hence Pfeiffer's change could be considered an invalid emendation. I prefer the more usual *oparica* spelling as applied to many other molluscan species and as used in the great majority of references cited above.

As discussed elsewhere (p. 492), the syndrome of size reduction accompanied by sculptural crowding is commonly encountered on Rapa, with *Opanara areaensis*, probably *O. megomphala*, and *Orangia cookei* having exactly analogous cases.

The distinction between *Ruatara oparica oparica* and *R. o. normalis* was not recognized during the initial survey of material. Hence no soft parts of the Mt. Tanga specimens were borrowed and the anatomy of the nominate race has not been studied. Probably specimens suitable for dissection are present in the Bishop Museum.

Ruatara oparica normalis, new subspecies. Figures 64h, i; 114a-d; 115; 116.

Diagnosis. – Shell relatively large, diameter 2.70-4.84 mm. (mean 3.81 mm.), with 5 - $6\frac{1}{4}$ normally coiled whorls. Apex and spire moderately and evenly elevated, sometimes rounded above, last whorl generally descending somewhat more rapidly, H/D ratio 0.524-0.690 (mean 0.601). Umbilicus either minutely perforate (contained more than 30 times in the diameter) or completely closed, about equal in frequency. Postnuclear sculpture of prominent, narrow, protractively sinuated, relatively widely spaced to crowded radial ribs, 77-133 (mean 98.5) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of prominent radial riblets, three to six between each pair of major ribs, with barely detectable traces of exceedingly fine spiral ribbing. Sutures impressed, whorls strongly rounded above, with almost evenly rounded outer and basal margins, with gradually curved inward columellar extension. Aperture ovate, strongly rounded above, evenly rounded on outer margins, inclined about 15° from shell axis. Parietal barriers normally 2 in the Mount Perahuan and Mount Ruataran populations, normally 3 in specimens from South Rapa, sometimes (less than 11 per cent) with a fourth or fifth threadlike trace, extending posteriorly somewhat more than one-eighth whorl: upper parietal a moderately elevated lamellar blade, expanded and serrated above on posterior quarter, with either gradual anterior descension or rather sharp anterior descension to a raised threadlike ridge; 2nd parietal with posterior quarter elevated, equal in height to upper, expanded and serrated above, with sharp descension to threadlike anterior half that terminates at, before, or slightly beyond end of upper parietal; 3rd parietal, when present, with same structure as 2nd, sometimes situated below 2nd parietal, sometimes between 1st and 2nd; 4th or 5th parietals, when present, low and threadlike traces situated below or between lower barriers. Columellar barrier a broad and rounded lamellar ridge, either deeply recessed within aperture and abruptly descending, lying parallel to plane of coiling, or extending further anteriorly and slanting diagnoally downward partway across columellar callus. Palatal barriers variable in size and number, normally with 4 (73.6 per cent), often with 3 (19.2 per cent), only rarely with 0, 1, 2 or 5 palatals (7.2 per cent), barriers when present small to moderate in size, short crescentic ridges: lower palatal basal in position, usually the highest, rarely flattened above, with sharp anterior descension; 2nd slightly reduced in height, sometimes weakly flattened above, generally with more gradual anterior descension; 3rd still lower, usually slightly flattened above, generally with quite gradual anterior descension; 4th, when present, greatly reduced in height, a very short threadlike trace to weakly elevated ridge, lying distinctly below level of upper parietal.

Ruatara oparica normalis differs from the subspecies *Ruatara o. reductidenta* in almost always having 3 or 4 distinct palatal barriers; *R. o. reductidenta* generally lacks all palatal barriers, although often (16 per cent) having 1 or 2 very small palatal tubercles. *R. o. oparica* is much smaller and with much more crowded radial ribbing.

Description. — Shell large, with slightly less than 6⅛ normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.632. Apical whorls 1½, sculpture eroded. Postnuclear whorls with narrow, prominent, protractively sinuated, rather widely spaced radial ribs, 81 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine radial riblets, four to seven between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above, evenly rounded on outer margins, with basal margin slightly flattened. Color partly leached from shell, remaining portions light yellow horn, without traces of reddish flammulations. Umbilicus minutely perforate. Aperture ovate, with evenly rounded outer margins, slightly flattened basally, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly three-sixteenths of a whorl: upper parietal high and bladelike, weakly expanded and serrated above on posterior third, with gradual anterior descension; 2nd parietal with posterior portion slightly reduced in length and height, rather sharply descending to a short threadlike portion that terminates well before anterior end of upper parietal. Columellar barrier a broad lamellar ridge, parallel to plane of coiling posteriorly, that slants downward across columellar callus near recessed anterior end. Palatal barriers 4, low, short, moderately recessed within aperture; 1st basal in position, flattened, serrated and expanded above, with sharp anterior descension; 2nd reduced in height and length, flattened above, with more gradual anterior descension; 3rd higher than 2nd, sinuated on top, with more gradual anterior descension; 4th greatly reduced in height, deeply recessed, very short, lying slightly below level of upper parietal. Height of holotype 2.83 mm., diameter 4.47 mm.

Holotype. — Austral Islands: Rapa Island, Station 490, northeast slope of Mount Ruatara at 750 ft. elevation. Collected by Yoshio Kondo on July 26, 1934. BPBM 143492.

Range. — Mt. Perahu, Mt. Ruatara, Mt. Mitiperu, Morongoto, Kopenena valley, Maraia and Mt. Mangaoa, Rapa Island, Austral Islands at various elevations.

Paratypes. — Same as list of material.

Material. — Rapa: Kopenena valley (Stations 468, 469) at 200-600 ft. elevation (5 specimens, BPBM 143187-90); Maraia at 500 ft. elevation (Station 399) on dead leaves (30 specimens, BPBM 140385-7); one-half way up Mt. Mitiperu (Station 454) under stones and in dirt (7 specimens, BPBM 142926-9); two-thirds way up Mt. Mitiperu (Station 455) under stones (18 specimens, BPBM 142936-9); northeast slope of Mt. Ruatara (Stations 490, 491, 492) at 750-800 ft. elevation (448 specimens, BPBM 135714-6, BPBM 143492-6, BPBM 143526, BPBM 143550); Morongoto at 800 ft. elevation (Stations 360, 400) in dead fern fronds and under stones (39 specimens, BPBM 53246, BPBM 144246-50, BPBM 144339-40); northeast ridge of Mt. Mangaoa (Stations 526, 527) at 800-1,100 ft. elevation under stones and on dead leaves (30 specimens, BPBM 138400, BPBM 138402-4, BPBM 143747-9); south slope of Mt. Perahu (Station 376) at 900-1,000 ft. elevation under moss on ground (5 specimens, BPBM 140253, BPBM 140255); east ridge of Mt. Perahu (Stations 446, 451, 452, 509, 512, 513) at 1,200-1,850 ft. elevation (21 specimens, BPBM 135442, BPBM 135482, BPBM 135569-72, ex BPBM 135488, BPBM 140254, BPBM 142749, BPBM 142823, BPBM 142831, BPBM 142877, BPBM 142879).

Remarks. — *Ruatara oparica normalis* has a scattered distribution (fig. 116) interrupted on south Rapa by the populations of *R. o. reductidenta* in the Maitua and Mt. Tautautu region. On south Rapa it was taken at low-to-intermediate elevations, only on Mt. Mangaoa reaching more than 1,000 ft. elevation. The Mt. Ruatara samples were taken at lower heights, but on Mt. Perahu it occurred sparsely at 900-1,850 ft. elevation.

Much of the general variation has been discussed above, including the dichotomy in parietal barrier frequency between north Rapa (Mt. Perahu and Mt. Ruatara) and south Rapa (fig. 115). Size and shape variation was moderate (table LXXXVII). The specimens from Maraia (Station 399) were distinctly smaller than most examples seen, while the sample from Mt. Ruatara (Station 490) contained very large shells. The large number collected at Mt. Ruatara (448 specimens) certainly introduced a bias when only the 39 specimens sorted out by the Bishop Museum staff as gerontic and adult were measured, but the much larger maximum size indicates that this is a real difference. Other samples were approximately evenly incremental in diameter, with a jump of 0.39 mm. from

Station 360 (Morongoto) to the large Mt. Ruatara (Station 490) population. Depressed shells were taken at Maraia (Station 399) (mean H/D ratio 0.563) while those from Mt. Perahu were markedly elevated (mean H/D ratio 0.636). The remaining five samples had mean H/D ratios of 0.596-0.611. These extremes are significantly different from their nearest mean. Comparing Station 399 (mean 0.563) with Station 526 (mean 0.596), with 25 df, "*t*" = 2.5798; comparing Station 527 (mean 0.611) with the Mt. Perahu shells (mean 0.636), with 21 df, "*t*" = 2.1391. The possible meaning of these differences has been discussed above.

Rib variation did not depart from a normal distribution (table LXXXV). Specimens from north Rapa and south Rapa had virtually identical rib counts and frequency (respectively, 99.8 and 96.6 ribs, 8.12 and 7.98 ribs/mm.). The minor difference probably was caused by the greater mean diameter (3.88 mm.) of the north Rapa, Mt. Ruatara population and its higher percentage of gerontic individuals with crowded ribbing on the last quarter whorl. Rib counts and rib frequencies overlapped those of the other two subspecies (tables LXXXV, LXXXVI), but the differences in means are obviously significant (table LXXXVI). Since the selected population data in Table LXXXVII so closely approximated the means from the subspecies, SEM's were not calculated for the entire samples.

The name *normalis* refers to the generalized appearance of those shells compared with the probable derivatives *R. oparica oparica* and *R. oparica reductidenta.*

Description of soft parts. — Foot and tail partly retracted, tapering posteriorly, rounded behind. Sole undivided, pedal grooves typical, no caudal horn or middorsal groove visible. Slime network inconspicuous.

Body color yellow-white, without darker markings.

Mantle collar (MC) elongated, with thickened edges, no glandular extension onto pallial roof.

Pallial region extending apically about five-eighths of a whorl. Lung roof clear except for thick clusters of white granules on top of kidney. Kidney about 1.78-2.14 mm. long, narrow anteriorly, with broadly expanded rectal arm about one-third to one-half of length depending on degree of contraction. Ureter typical, opening just beyond termination of rectal kidney arm. Heart about one-third length of kidney, not parallel to hindgut. Principal pulmonary vein slender, unbranched, fading out just before hindgut. Hindgut following palatal-parietal margin just above apex of pallial cavity, then slanting downwards.

Ovotestis (fig. 64h, G) of many palmately clavate alveoli imbedded in first whorl above stomach reflexion, more than in *Opanara areaensis.* Hermaphroditic duct (GD) slender at first, markedly expanded and convoluted medially, narrowing abruptly before reflexing onto talon shaft. Albumen gland (GG) small, compact, typical. Talon (GT) with expanded head, narrow neck just before junction with hermaphroditic duct, base expanded. Prostate (DG) with one or two rows of large acini opening into a narrow tube, shorter than free oviduct. Uterus (UT) with normal two parts.

Vas deferens (VD) very slender, reflexing at peniovidueal angle, entering penis just below apex of penis at top of pilaster. Penial retractor (PR) arising from diaphragm, inserting directly onto penis head just before entrance of vas deferens, no fleshy extension to penis head. Penis (P) about 3.3 mm. long, gradually tapering apically, internally with a large, complexly corrugated pilaster (fig. 64i) becoming bifurcated basally, terminating at penis apex. Atrium (Y) broad, short.

Free oviduct (UV) slightly longer than prostate, tapering to vagina. Spermatheca (S) with very slender shaft, expanded head buried in albumen gland. Vagina (V) clearly separable, but short.

Free muscle system typical. Right ommatophoral retractor passing through peniovidueal angle.

Buccal retractors not split, uniting with tail fan just before termination of columellar muscle. Esophagus typical. Stomach extending almost one whorl, starting one-eighth whorl above pallial cavity apex. Intestinal looping typical.

Jaw lost in processing. Radula with large teeth, central 14μ long and 13μ wide, laterals 4 to 6, with more than 10 marginals.

(Based on BPBM 143492, whole specimens 4.18 mm. in diameter with 5½ whorls and 4.28 mm. with 5⅝+ whorls, additional fragmentary specimens and BPBM 140385, 3.42 mm. with 5 whorls.)

Ruatara oparica reductidenta, new subspecies. Figures 64j; 114e; 115; 116.

Diagnosis. — Shell relatively large, diameter 3.29-4.34 mm. (mean 3.74 mm.), with 5 - 6⅛ normally coiled whorls. Apex and spire moderately and evenly elevated, occasionally slightly rounded above, last whorl generally descending a little more rapidly, H/D ratio 0.528-0.698 (mean 0.563). Umbilicus completely closed, rarely narrowly perforate. Postnuclear whorls with narrow, prominent, often lamellar, protractively sinuated radial ribs, 66-95 (mean 78.4) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, with barely visible traces of spiral microribbing. Sutures impressed, whorls strongly rounded above, with almost evenly rounded outer and basal margins. Aperture ovate, strongly rounded above, inclined about 15° from shell axis. Parietal barriers variable in number, normally 3 (77.7 per cent) or 4 (11.4 per cent), sometimes 2 (8.2 per cent) and very rarely (2.7 per cent) only 1 or 5, generally quite low, extending posteriorly less than three-sixteenths of a whorl: upper parietal sometimes weakly expanded and serrated above on posterior quarter, with gradual anterior descension, other times a raised threadlike ridge for entire length; 2nd parietal usually raised and expanded above slightly on posterior quarter, with quick descension to a low threadlike ridge terminating slightly in front of upper parietal; 3rd parietal normally a low threadlike ridge equal in length to 2nd parietal; 4th parietal, when present, either a shortened trace between one of the upper pairs, or a threadlike trace lying below 3rd parietal. Columellar barrier a deeply twisted, broadly rounded lamellar ridge, normally slightly twisted downward at anterior end. Normally the palatal wall bears only a weak callus that terminates near basal lower palatal margin (84.0 per cent), often there is a short, low tubercle occupying the position of the 1st palatal (15.5 per cent) and very rarely (0.5 per cent) there is a weak trace of a 2nd palatal.

The normal complete absence of palatal barriers is the primary character separating *Ruatara oparica reductidenta* from the nominate subspecies. The latter form normally has a higher percentage of individuals with a measurably perforate umbilicus.

Description. — Shell relatively large, with 6⅛ normally coiled whorls. Apex and spire strongly and almost evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.661. Apical whorls 1⅜, sculpture eroded. Postnuclear sculpture of narrow, prominent, protractively sinuated radial ribs, 92 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, with exceedingly vague traces of spiral ribbing. Sutures deep, whorls strongly rounded above, with evenly rounded outer margins, basocolumellar margin gently extended inward. Color light yellow horn, without traces of reddish flammulations. Umbilicus completely closed. Aperture ovate, with evenly rounded outer margins, inclined about 15° from shell axis. Parietal barriers 3, extending posteriorly less than three-sixteenths of a whorl, greatly reduced in size; upper parietal a moderately elevated lamellar blade, very weakly expanded and serrated above on posterior quarter, with gradual anterior descension; 2nd parietal almost equally elevated on posterior quarter, with sharp anterior descension to a low threadlike ridge that terminates anteriorly in front of upper parietal; 3rd parietal barely expanded and serrated above on posterior quarter, anterior five-eighths a low threadlike ridge. Columellar wall with a deeply recessed, broadly rounded lamellar ridge, whose anterior end twists slightly downward. Palatal wall without trace of barriers, a moderately heavy callus extending from columellar-parietal margin and gradually weakening to union of basal and lower palatal walls. Height of holotype 2.70 mm., diameter 4.08 mm.

Holotype. — Austral Islands: Rapa Island, Station 291, back of Aurei at Maitua, 500-600 ft. elevation. Collected under stones by Donald Anderson and C. M. Cooke, Jr. on July 12, 1934. BPBM 137609.

Range. — Maitua and northwest of Mt. Tautautu at 450-800 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material

Material. — Rapa: Maitua at lowest coffee patch (Station 302), 100 yd. below Station 291 at 450 ft. elevation (1 specimen, BPBM 137807); coffee plantation (Stations 291, 426) in Maitua area at 500-600 ft. elevation (275 specimens, BPBM 137609-21, BPBM 137641-2, BPBM 137643-5, BPBM 137669-71, BPBM 144524-7); from coffee patch to cliff base, one-quarter mile (Station 316) east of Station 292 at 500-700 ft. elevation (6 specimens, BPBM 137948, BPBM 144023-4); 100 yd. below cliff base, Maitua, about 75 yd. (Stations 292, 293, 305A, 427, 429) above Station 291 at 700-800 ft. elevation (59 specimens, BPBM 135523-4, BPBM 137686-91, BPBM 137730, BPBM 137843, BPBM 143885-8, BPBM 144566-7); Maitua, between cliff (Station 306) and Station 305 (1 specimen, BPBM 137869); Maitua area (Stations 317, 318) at 700-750 ft. elevation (18 specimens, BPBM 144041-2, BPBM 144087-9); Maitua area, along marae (Station 353) below Mangaoa (5 specimens, BPBM 140012-6); Maitua area (Station 307) at unspecified elevation (1 specimen, BPBM 143917); under one log (Station 358) in Maitua area at unspecified altitude (29 specimens, BPBM 135697, BPBM 135700, BPBM 142534-5); northwest of Mt. Tautautu (Station 342) at 600-700 ft. elevation (15 specimens, BPBM 142407-12).

Remarks. — Specimens of *Ruatara oparica reductidenta* were found in forest, ecotonal (Station 353) and plantation (Stations 291, 426) areas in the Maitua region, with one record (Station 342) from the adjacent Mt. Tautautu. No differences were noted between the native forest and coffee plantation specimens. While examples from Station 292 averaged slightly smaller (table LXXXVII) than those from Station 291 (with 56 df, "*t*" = 1.7821) and were insignificantly lower ("*t*" = 1.1258), this difference probably is the result of measuring bias. As can be seen from Figure 115, a few specimens of *R. oparica normalis* approach the barrier condition of *R. o. reductidenta.* These are scattered through several populations and in both size and ribbing agree with *R. o. normalis.*

The name *reductidenta* refers to the reduced palatal barriers.

Description of soft parts. — Only fragmentary extracted specimens were available for dissection. Most parts of the genitalia were observed and corresponded exactly with *Ruatara oparica normalis.* Only the penis is figured (fig. 64j). Varying in length from 2.6-3.4 mm., internally it was identical with that of *Ruatara oparica normalis.*

Radula with very large teeth, central 16μ long, 13μ wide. Laterals 4 or 5 in number, marginals 10 or 11 with edge turned under.

(Based on BPBM 137609, fragmentary examples.)

Genus **Orangia,** new genus

Endodontidae having typical apical sculpture, with (*sporadica* and *maituatensis*) or without (*cookei*) secondary spiral cording, normal spiral microsculpture greatly reduced, major sculpture of widely spaced (*sporadica*) to very crowded (*cookei tautautuensis*), protractively sinuated radial ribs. Apex and spire moderately elevated, last whorl usually not descending much more rapidly, periphery markedly angulated (*sporadica* and *cookei cookei*) or protruded (*maituatensis*) to evenly rounded (*cookei tautautuensis*). Whorls about 6, reduced in number slightly in *cookei tautautuensis* and *maituatensis.* Umbilicus narrowly open in juveniles, barely perforate or usually closed in adults (fig. 118). Parietal barriers 2, upper lamellate for entire length, lower with threadlike anterior portion terminating opposite or before anterior end of upper. Columellar barrier reaching lip margin (*cookei tautautuensis*) to deeply recessed (*cookei cookei, sporadica,* and *maituatensis*). Palatal barriers normally 4, rarely 5, variable in height. Genitalia with a fleshy extension of penis head merging with penial retractor, markedly subapical insertion of the vas deferens, internally with two pilasters that become high, thin lamellar ridges apically. Penial retractor originating from diaphragm. Anatomy otherwise typical of Endodontidae.

Type species. — *Orangia cookei cookei,* new species and subspecies.

The generally angulated periphery, normal presence of a supraperipheral sulcus, large size, strong color patterns, prominent and protractive radial ribs, and the fleshy extension of the penis head into the penial retractor are all characters that *Orangia* shares with *Australdonta.* The differences are many. *Orangia* has a secondary microsculpture of spiral cords (or none); *Australdonta* spiral grooves (fig. 124). *Orangia* has 2 parietals; *Australdonta* usually 3 or 4, often more. *Orangia* has a prominent columellar barrier; *Australdonta,* except rarely, lacks a columellar. *Orangia* has 4 palatals; most *Australdonta* have 5, although *A. pseudplanulata, A. raivavaeana,* and *A. tubuaiana* have 3 or 4 palatals and they are absent in *A. radiella. Orangia* has the umbilicus closed or barely perforate in adults; *Australdonta* has the umbilicus rather widely open. The penial pilasters in *Orangia* are narrowed and greatly elevated apically (fig. 121c); in *Australdonta* the pilasters are grossly expanded and thickened above (fig. 125b, e), never elevated into narrow blades. *Orangia* species average nearly six whorls; all *Australdonta* species average

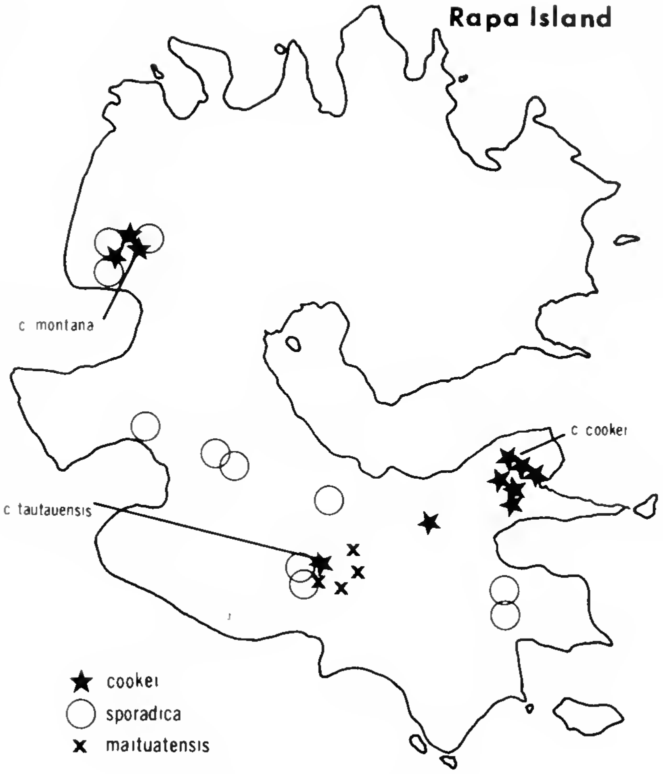

FIG. 117. Distribution of *Orangia*.

much less than six whorls and thus show more rapid increase in whorl width.

Orangia and *Australdonta* seem to be parallel in their shared conchological features, although they probably both were derived from the *Mautodontha* series. The penial pilaster pattern of *Orangia* is seen in the other Rapan genera and is quite distinct from the *Mautodontha-Australdonta* pattern. I consider that *Orangia* is a specialized, local derivative of the *Opanara* complex endemic to Rapa.

Speciation within the genus is simple and uncomplicated. *O. cookei,* which I consider is the most generalized species, lacks the secondary spiral cording, has a rounded or obtusely angulated periphery, more crowded ribbing, and occurs as three geographically isolated subspecies (fig. 117). *O. maituatensis,* which has secondary spiral cording above and below the body whorl periphery, a right-angled periphery, much more depressed spire, less crowded ribbing (mean ribs/mm. 6.78), and a prominent supraperipheral sulcus is restricted to the Maitua area. It is much more similar in appearance to *O. cookei cookei* than to *O. cookei tautautuensis* that lives in the same region. *O. sporadica* is less sharply angulated than *O. maituatensis,* has a very prominent supraperipheral sulcus, widely spaced radial ribbing (mean ribs/mm. 4.35), a prominent secondary microsculpture below the body whorl periphery, and occurred at scattered localities

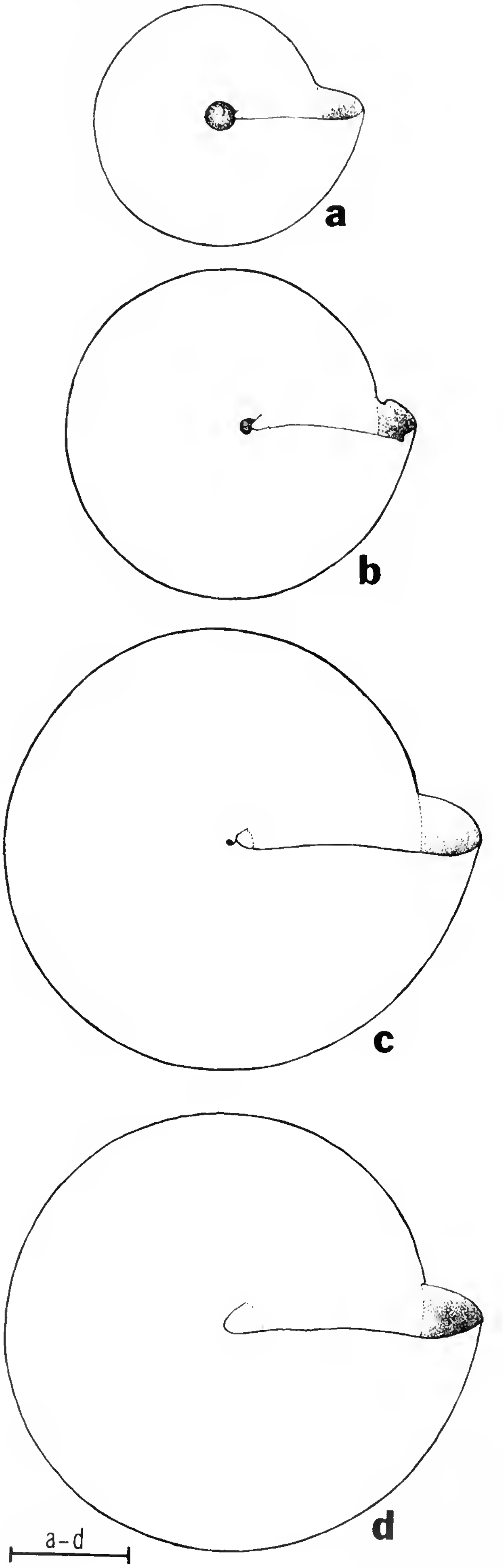

FIG. 118. Umbilical closure in *Orangia cookei cookei*. **a-b**, juveniles; **c**, subadult, **d**, adult. Station 312, Mt. Tepiahu, Rapa Island, Austral Islands. Scale line equals 1 mm. (MM).

over large areas of Rapa (fig. 117). It was not taken at the same localities as *O. cookei cookei*, *O. c. tautautuensis*, or *O. maituatensis*, but there is a possibility that *O. c. montana* inhabits the same stations on Mt. Perahu. At Station 451, which extends over 300 ft. vertically and an unknown distance horizontally, 16 *montana* and one *sporadica* were collected. Stations on Mt. Perahu were much less rigorously localized than in the Maitua area, so that the two taxa may be ecologically separated.

Umbilical closure in *Orangia* is accomplished differently than in *Ruatara*. In the latter (fig. 113d), the umbilicus is essentially minutely perforate from the apical whorls onward, with the columellar wall straight or only slightly curved inward until adulthood, when heavy callus formation apparently (fig. 114a, c) alters the columellar configuration. In *Orangia* the umbilicus is narrowly open during early growth stages, with a curved inward growth of the columellar region (fig. 118) providing complete or nearly complete umbilical closure. The proportions of closed *versus* perforate umbilici differ between taxa (fig. 119). Except in *O. maituatensis*, more than 60 per cent of each form have the umbilicus completely closed. In the latter species, one-fifth have a closed umbilicus, four-fifths a perforate umbilicus contained an average of 26.7 times in the diameter.

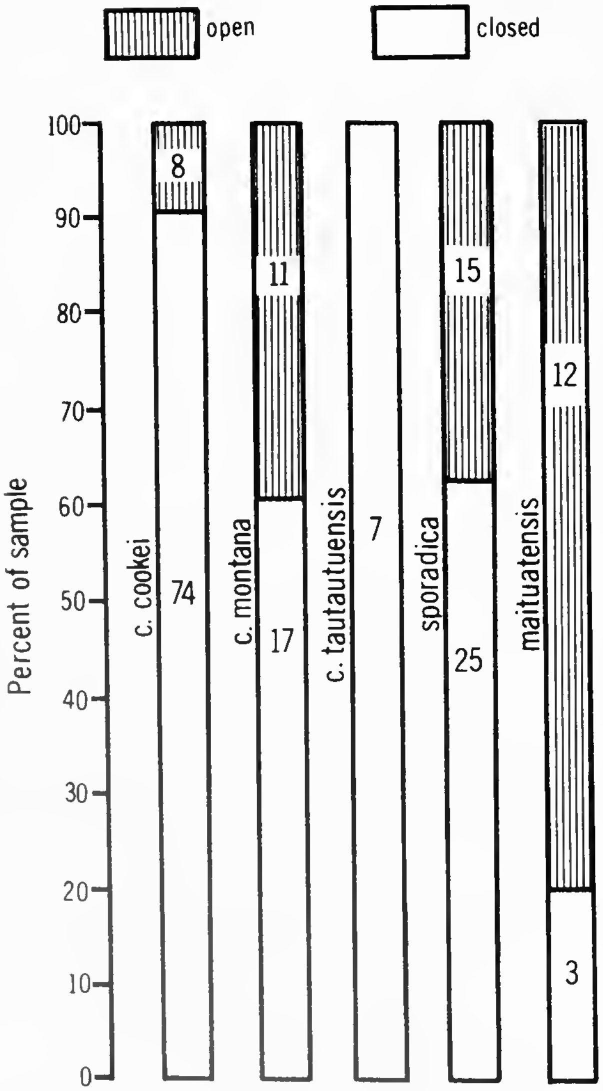

FIG. 119. Relative proportions of closed and barely perforate umbilici in *Orangia*.

Size variation is quite minor (table LXXXI), with *Orangia cookei tautautuensis* being conspicuously (14.5 per cent) smaller, *O. cookei montana* slightly (6 per cent) larger, and the other taxa virtually identical. Variation in H/D ratios is similarly minor, with the greater depression of *O. maituatensis* (8.6 per cent) attributable to a 5.9 per cent decrease in shell height. The comparatively great elevation of *O. cookei tautautuensis* correlates with the reduction in diameter (14.5 per cent), which far exceeds the reduction in height (7.3 per cent).

Sculptural variation is rather large. *O. sporadica* is sharply differentiated in both rib count and spacing (see table LXXXVIII), and is immediately separable visually by these characters alone (fig. 123f). The other taxa show substantial overlap in both characters although displaying mean differences. The character of the sculpture is the same, but the spacing differs. A scatter diagram (fig. 120) of ribs plotted against ribs/mm. showed that *O. sporadica*, *O. maituatensis*, and *O. cookei cookei* have the same pattern, while *O. cookei montana* and *O. cookei tautautuensis* are offset, respectively, to the left and right of the main pattern. Regression lines were not plotted for the other taxa, since only for *O. cookei* were there many observations.

Anatomical variation within *Orangia* was minor. *O. maituatensis* had a much longer penis and longer free oviduct (see fig. 121) than the other species, with corresponding slight alterations in penial pilaster patterns. Only fragmented specimens of *O. sporadica* were available and no material adequate for dissection was seen of *O. cookei tautautuensis*.

KEY TO THE GENUS *Orangia*

1. Adult shells with more than 70 ribs; ribs/mm. more than 5.60. 2
Adult shells usually with much less than 70 ribs; ribs/mm. usually much less than 5.25......*Orangia sporadica*, new species
2. Body whorl rounded or obtusely angulated, not protruded; no secondary spiral cording; mean H/D ratio more than 0.500. 3
Body whorl right angled, keel protruded; secondary spiral cording present; mean H/D ratio less than 0.475. *Orangia maituatensis*, new species
3. Columellar barrier extending well in front of callus apex; periphery obtusely or evenly rounded; rarely a supraperipheral sulcus present...4
Columellar barrier reaching just to top of callus apex; periphery usually obtusely angulated; a supraperipheral sulcus normally present.............................*Orangia cookei cookei*, new subspecies
4. Mean diameter about 3.50 mm.; mean H/D ratio about 0.550; ribs very crowded, about 10.00 ribs/mm.; Mt. Tautautu. *Orangia cookei tautautuensis*, new subspecies
Mean diameter about 4.25 mm.; mean H/D ratio about 0.515; ribs much less crowded, about 7.58 ribs/mm.; Mt. Perahu. *Orangia cookei montana*, new subspecies

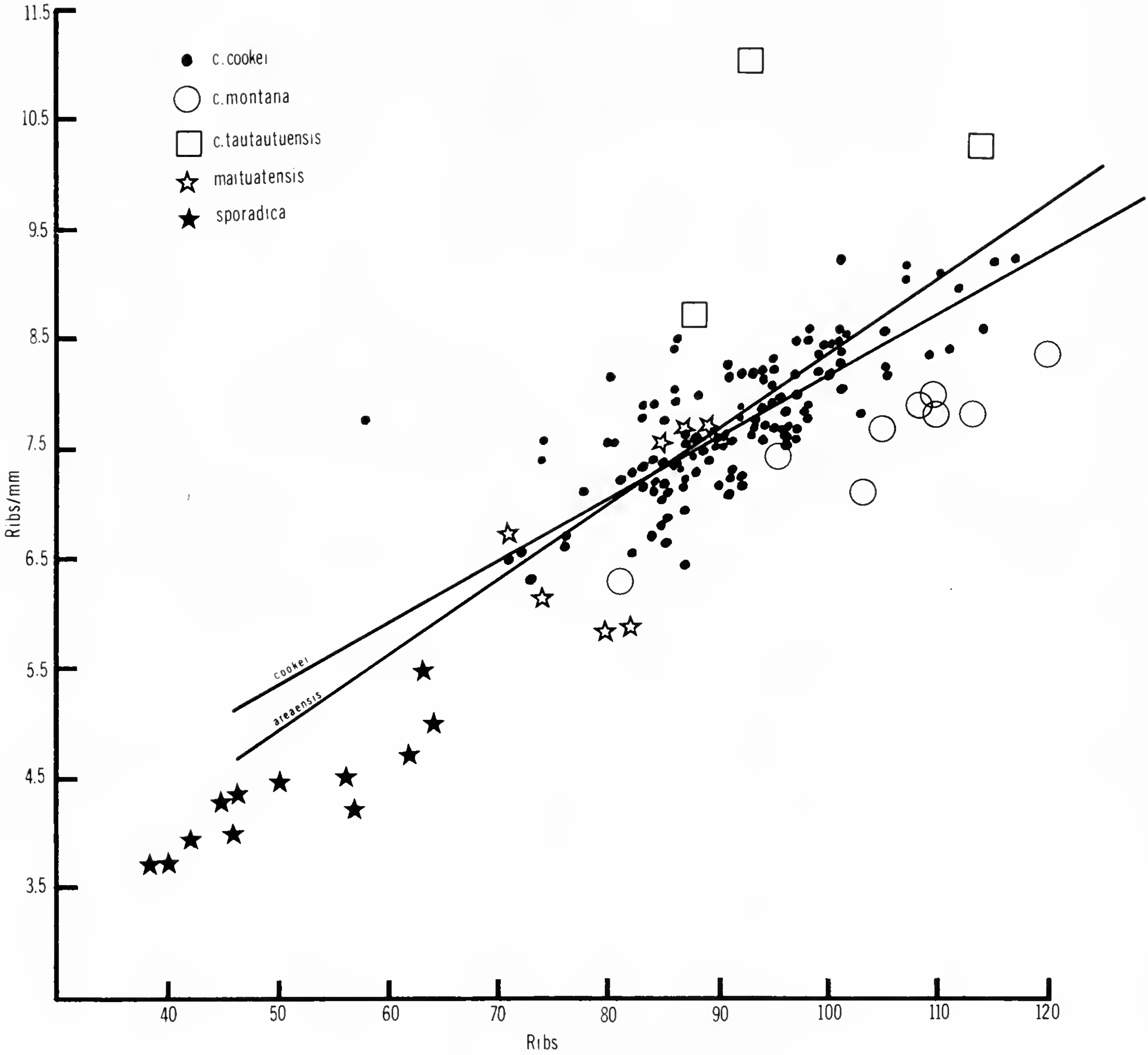

FIG. 120. Correlation of ribs and ribs/mm. in the endodontinine genus *Orangia.*

Orangia cookei, new species.

Differences between the three morphs grouped here are constant. No intergradation was observed. Despite this, the similarities are so many that subspecific designations have been adopted. The forms are geographically isolated, with the nominate subspecies from the Orangi-Tepiahu-Tanga region more closely resembling the Mt. Perahu *Orangia cookei montana* than its neighboring form from Mt. Tautautu, *O. c. tautautuensis.* Only nine specimens of the latter from one station were available, and I have chosen a conservative course in treating it as a subspecies.

The subspecies are as follows:

O. c. cookei has the columellar barrier reaching only slightly past the columellar callus apex; the periphery usually is obtusely angulated and with a noticeable supraperipheral sulcus; the parietals extend almost one-quarter whorl and the palatals about one-eighth whorl; 1st palatal distinctly smaller than 2nd and 3rd; there are about 7.75 ±0.012 ribs/mm. on the body whorl.

O. c. montana has the columellar barrier extending about half way across the columellar callus; the periphery usually is obtusely rounded and lacks a supraperipheral sulcus; the parietals extend about one-quarter whorl and the palatals about one-eighth whorl; 1st palatal subequal or equal to 2nd palatal; there are about 7.57 ±0.20 ribs/mm. on the body whorl.

O. c. tautautuensis has the columellar barrier reaching almost to the lip margin; the periphery is

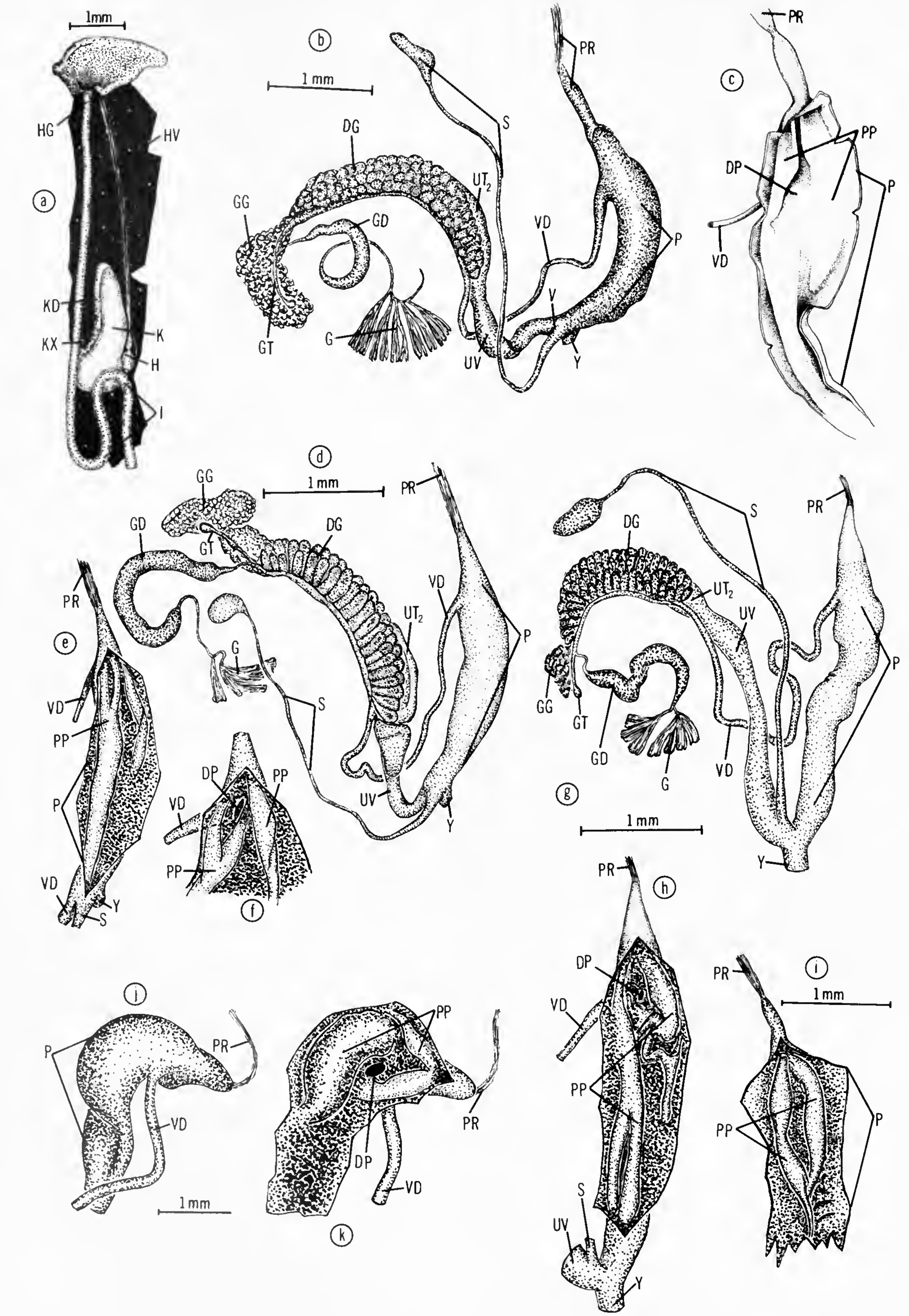

FIG. 121. Anatomy of *Orangia*: **a-c**, *Orangia cookei cookei*, BPBM 143116. *a*, pallial region, *b*, genitalia with most of ovotestis omitted, *c*, interior of penis; **d-f**, *Orangia cookei montana*, BPBM 135433. *d*, genitalia with most of ovotestis omitted, *e-f*, details of penis interior; **g-i**, *Orangia maituatensis*, BPBM 144044, -568. *g*, genitalia with most of ovotestis omitted, *h-i*, interior of penis region; **j-k**, *Orangia sporadica*, BPBM 140404. *j*, exterior of penis, *k*, interior of penis. Scale lines equal 1 mm.

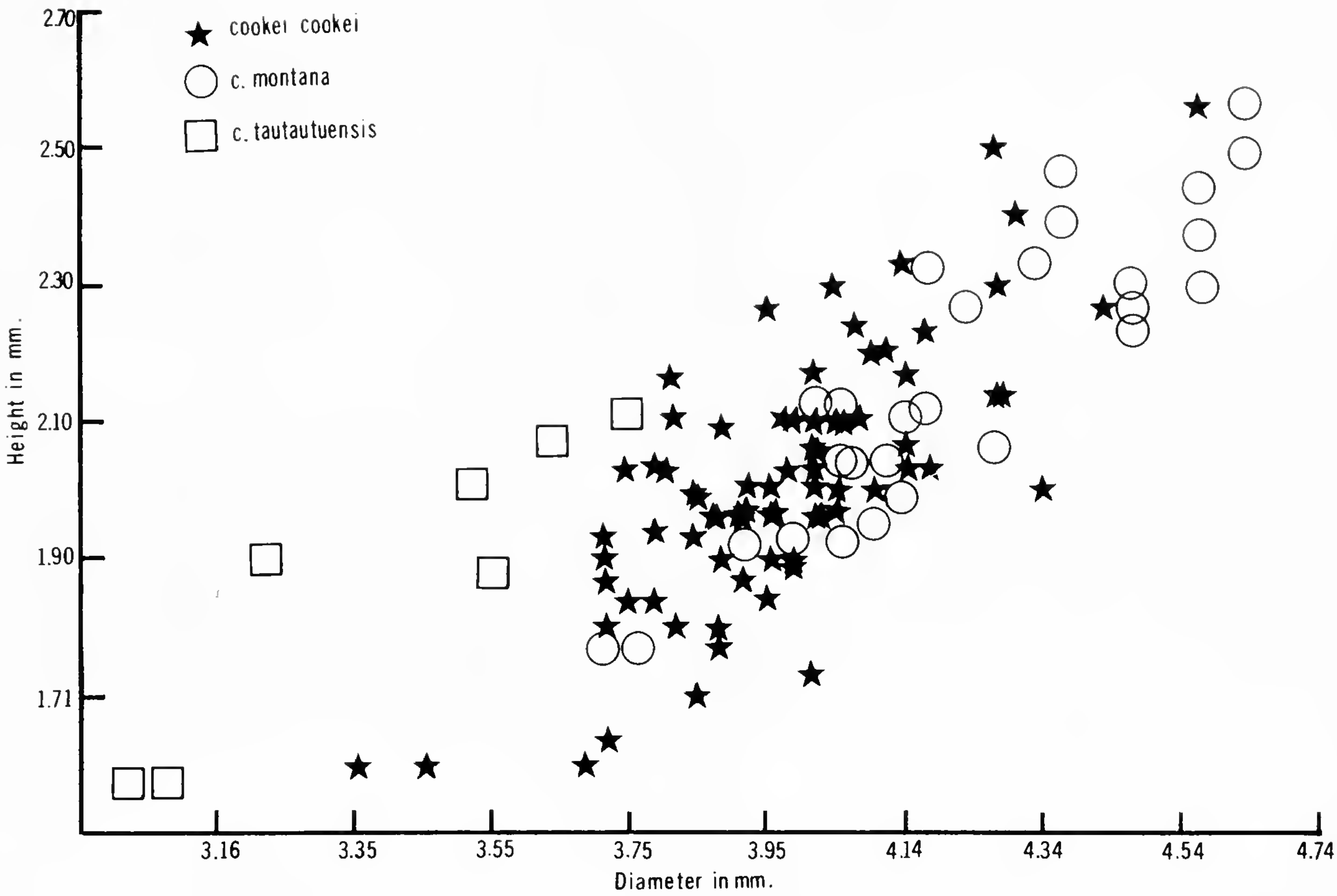

FIG. 122. Scatter diagram showing relationship of height to diameter in subspecies of *Orangia cookei.*

rounded and there is no supraperipheral sulcus; the parietals extend to or beyond the line of vision and the palatals about one-quarter whorl; all the palatals are reduced in height and the 1st is distinctly smaller than the 2nd; there are about 10.05 ± 0.67 ribs/mm. on the body whorl.

Size and shape differences are noticeable, but with quite considerable overlap. Thus, *O. c. cookei* and *O. c. montana* are identical in H/D ratios, but *montana* is significantly larger (comparing the diameter of Station 466 adult *cookei cookei* with Station 509 adult *cookei montana,* with 37 df, "*t*" = 2.5000). A scatter diagram using all adult specimens of the two subspecies (fig. 122) shows that *O. c. montana* clusters at the upper end of the range and *O. c. cookei* at the middle portion, although the largest *O. cookei cookei* is only a trifle smaller than the largest *O. cookei montana.* Since the H/D ratios are identical, the regression lines would be the same and have not been calculated. *Orangia cookei tautautuensis* is obviously smaller and higher (fig. 122).

The changes involved in deriving *montana* from *cookei* — lengthening of the columellar barriers, decrease in peripheral angulation, increase in barrier size and slight size increase — are minor. Considerably more change is required to alter *cookei* into *tautautuensis* — the columellar barrier is greatly lengthened, both parietal and palatal barriers are lengthened by 50-100 per cent with the latter decreased in height; the whorl count is lowered, diameter reduced 14.5 per cent, but the height only 7.3 per cent, resulting in a 8.2 per cent increase in H/D ratio; rib count increased by 5.7 (6.2 per cent) on the body whorl with the ribs/mm. increasing from 7.78 to 10.05 (29.2 per cent). The increase is rib number is not statistically significant, since with 45 df, "*t*" = 1.0048, when specimens of *O. cookei cookei* from Station 466 are compared with specimens of *O. c. tautautuensis* in respect to rib count. The difference in rib spacing for the same sets is significant (with 45 df, "*t*" = 2.038), as are the differences in diameter and H/D ratios for adults from Station 478 (*c. tautautuensis*) and Station 466 (*c. cookei*), since with 30 df, "*t*" = 7.5763 for diameter and "*t*" = 3.2091 for H/D ratio.

As discussed below *Orangia cookei tautautuensis* is one of several Rapa Island taxa characterized by diminution in size, crowding of ribs, and changes in proportions.

Orangia cookei cookei, new species and subspecies. Figures 118; 121a-c; 122; 123a-b.

Diagnosis. — Shell of average size, diameter 3.36-4.57 mm. (mean 4.00 mm.), with 5¼ - 6¼ normally coiled whorls. Apex flat or weakly elevated, spire moderately elevated, last whorl descending much more rapidly in gerontic individuals, normally slightly deflected below periphery in adults, H/D ratio 0.424-0.585 (mean 0.510). Umbilicus narrowly open in juveniles, barely perforate or closed in

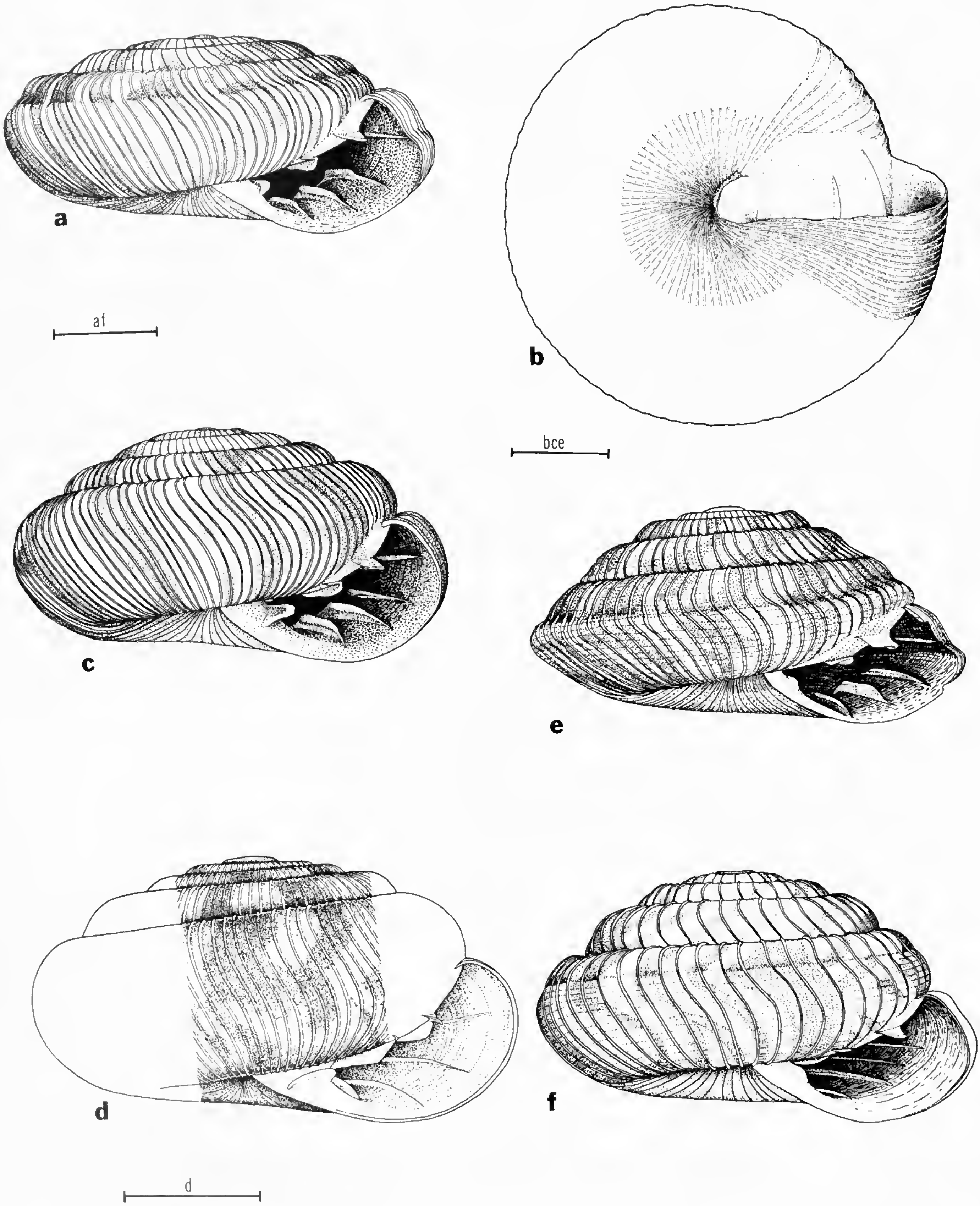

FIG. 123. a-b, *Orangia cookei cookei*, new species and subspecies. *a*, Station 466, Mt. Tanga, Rapa Island, Austral Islands. Holotype. BPBM 143116; *b*, Station 325, Mt. Orangi, Rapa Island, Austral Islands. Paratype. BPBM 139938; **c**, *O. cookei montana*, new subspecies. Station 509, Mt. Perahu, Rapa Island, Austral Islands. Holotype. BPBM 135433; **d**, *O. cookei tautautuensis*, new subspecies. Station 478, Rapa Island, Austral Islands. Holotype. BPBM 143300; **e**, *O. maituatensis*, new species. Station 308, Maitua, Rapa Island, Austral Islands. Holotype. BPBM 143940; **f**, *O. sporadica*, new species. Station 340, Mt. Tautautu, Rapa Island, Austral Islands. Holotype. BPBM 144151. Scale lines equal 1 mm. Figures *a*, *c*, *e-f* by YK reproduced through the courtesy of Bernice P. Bishop Museum; *b*, *d* (MM).

TABLE LXXXVIII. - RIB VARIATION IN ORANGIA

Name	Number of Specimens	Ribs	Ribs/mm.	Diameter
sporadica				
	12	50.8±2.69 (38-64)	4.35±0.147 (3.71-5.45)	3.68±0.109 (3.26-4.31)
maituatensis				
	7	81.1±2.52 (71-89)	6.79±0.321 (5.81-7.70)	3.84±0.156 (3.36-4.44)
cookei cookei				
All	110	92.6 (72-135)	7.78 (6.31-10.80)	3.78 (3.13-4.31)
Sta. 466	44	91.3±1.76 (71-135)	7.77±0.119 (6.31-10.80)	3.74±0.032 (3.13-4.24)
Sta. 534	50	92.2±1.39 (72-117)	7.75±0.086 (6.51-9.21)	3.79±0.036 (3.13-4.24)
Sta. 312	7	103.4±3.42 (88-115)	8.54±0.205 (7.79-9.20)	3.86±0.085 (3.52-4.21)
cookei montana				
	9	104.8±3.74 (81-120)	7.58±0.201 (6.27-8.36)	4.40±0.067 (4.08-4.64)
cookei tautautuensis				
	3	98.3±7.97 (88-114)	10.05±0.672 (8.78-11.06)	3.41±0.110 (3.19-3.52)

adults. Postnuclear sculpture of narrow, prominent, strongly protractively sinuated radial ribs, 72-135 (mean 92.6) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, five to nine between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls moderately rounded above, somewhat flattened to level of weak supraperipheral sulcus, which is occasionally absent. Periphery obtusely angulated (rounded in gerontic individuals), base of shell evenly rounded, with flattened inward extension of columellar region, a heavy columellar callus present. Aperture ovate, with obtusely angulated periphery, inclined slightly more than 15° from shell axis. Parietal barriers 2, extending posteriorly almost one-quarter whorl: upper high and bladelike, posterior third to half markedly expanded and serrated above, with very gradual anterior descension that accelerates during last eighth of length; 2nd parietal with posterior elevated portion equal in height and superior expansion, slightly shorter, sharply descending anteriorly to a low threadlike portion that stops before anterior end of 1st parietal. Columellar barrier high and crescentic, twisting slightly downward to top of columellar callus. Palatal barriers 4, very rarely 5, extending posteriorly about one-eighth whorl: lower basal in position, expanded, serrated, and flattened above on posterior third with very gradual anterior descension, moderately recessed within aperture; 2nd and 3rd palatals slightly higher posteriorly, with equally gradual anterior descension, not recessed more deeply within aperture; 4th palatal supraperipheral, reduced in height, equally expanded above, with very gradual anterior descension, reaching slightly further anteriorly.

Both *Orangia sporadica* and *O. maituatensis* have a prominent microsculpture of spiral cording visible below body whorl periphery. *O. sporadica* also differs in having fewer radial ribs on the body whorl (38-64) and the apertural barriers greatly reduced in size. *O. maituatensis* has somewhat more widely spaced ribbing (71-89 on the body whorl), a more depressed shape (mean H/D ratio 0.466), and very strongly developed apertural barriers. The nominate subspecies differs from *O. cookei tautautuensis* by its larger size, lower H/D ratio, deeply recessed columellar, and angulated periphery. *O. cookei montana* is a much less angulated shell with an extremely long columellar, and much more prominent parietal and palatal barriers.

Description. — Shell large, with 5¾ normally coiled whorls. Apex slightly elevated, lower whorls and spire descending more rapidly, body whorl slightly deflected below periphery, H/D ratio 0.488. Apical and early postnuclear whorls with sculpture eroded. Postnuclear whorls with narrow, lamellate, protractively sinuated radial ribs, 91 on the body whorl, whose interstices are about 3 times their width. Microsculpture of fine radial riblets, five to nine between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification. Sutures impressed, whorls moderately rounded above, slightly flattened laterally above distinct supraperipheral sulcus, periphery obtusely rounded, lower palatal margin evenly rounded, columellar margin extended inwardly. Color light yellow-white, with almost regularly spaced, irregularly shaped, zigzagged, reddish flammulations that tend to decrease in prominence below periphery of body whorl. Umbilicus completely closed. Aperture compressedly ovate, a slight supraperipheral indentation, inclined about 20° from shell axis. Columellar wall with thick white callus. Parietal barriers 2, extending posteriorly one-quarter whorl: upper high and lamellate, with posterior half strongly expanded and serrated above, with very gradual descension anteriorly; 2nd with posterior portion equal in height and expansion, slightly shorter, with sharp anterior descension

TABLE LXXXIX. - LOCAL VARIATION IN ORANGIA

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls
cookei cookei					
BPBM 140068 Sta. 354	5	1.98±0.068 (1.72-2.12)	3.95±0.060 (3.81-4.14)	0.501±0.0183 (0.444-0.543)	5 3/4+ (5 3/4-5 7/8)
BPBM 137968 Sta. 321	17	1.99±0.023 (1.76-2.15)	3.98±0.028 (3.81-4.30)	0.501±0.0048 (0.434-0.524)	6- (5 1/2-6 1/8)
BPBM 143116 Sta. 466	25	2.03±0.032 (1.82-2.52)	3.98±0.027 (3.74-4.30)	0.510±0.0062 (0.466-0.585)	5 7/8 (5 5/8-6 1/8)
BPBM 144792, -5 Sta. 534	19	2.11±0.046 (1.79-2.58)	4.02±0.057 (3.74-4.60)	0.527±0.0069 (0.457-0.575)	6+ (5 3/4-6 1/4+)
BPBM 139938-9 Sta. 325	10	2.10±0.048 (1.82-2.42)	4.12±0.058 (3.84-4.37)	0.505±0.0120 (0.424-0.557)	6- (5 5/8-6 1/4)
cookei montana					
BPBM 135433 Sta. 509	14	2.10±0.060 (1.79-2.48)	4.13±0.064 (3.74-4.60)	0.507±0.0075 (0.474-0.564)	5 7/8+ (5 1/2-6 1/4)
BPBM 142827-8 Sta. 451	12	2.27±0.056 (2.02-2.58)	4.36±0.070 (4.03-4.67)	0.519±0.0072 (0.485-0.560)	6 (5 3/4-6 1/4)
cookei tautautuensis					
BPBM 143300-2 Sta. 478	7	1.89±0.083 (1.59-2.12)	3.42±0.109 (3.05-3.77)	0.552±0.0110 (0.517-0.592)	5 5/8 (5 1/8-6)
sporadica					
BPBM 144151 Sta. 340	7	2.09±0.065 (1.89-2.35)	3.83±0.057 (3.64-4.04)	0.547±0.013 (0.491-0.589)	6 (5 3/4-6 1/4)
BPBM 140404, -6 Sta. 401	6	2.30±0.063 (2.12-2.48)	4.12±0.064 (3.91-4.30)	0.559±0.0086 (0.524-0.580)	6 1/8+ (6-6 3/8+)
maituatensis					
BPBM 143940 Sta. 308	3	1.99±0.166 (1.82-2.32)	4.25±0.205 (3.84-4.47)	0.451±0.0341 (0.411-0.519)	5 3/4+ (5 5/8-6)

to threadlike portion that stops before end of upper parietal. Columellar barrier high and crescentic, slightly twisted downward to upper edge of columellar callus. Palatal barriers 4, extending posteriorly about one-eighth whorl: lower slightly reduced in height, expanded and serrated above on posterior half with gradual anterior descension; 2nd and 3rd palatals higher, equally expanded and serrated above, with very gradual anterior descension, not recessed further within aperture; 4th palatal supraperipheral, greatly reduced in height, expanded and serrated above, with gradual anterior descension, reaching slightly nearer lip margin. Height of holotype 2.01 mm., diameter 4.11 mm.

Holotype. — Austral Islands: Rapa Island, Station 466, hillside on south side of Mt. Tanga at 700-800 ft. elevation. Collected under stones by Donald Anderson on July 23, 1934. BPBM 143116.

Range. — Vicinity of Mt. Tanga, Mt. Tepiahu, and Mt. Orangi at 300-850 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: Mt. Tanga (Stations 466, 532, 534) at 300-800 ft. elevation under stones (1,091 specimens, BPBM 143116-23, BPBM 143800, BPBM 144792-8); Pake Bay (Station 321) (39 specimens, BPBM 137968-70); Mt. Tepiahu (Stations 311, 312, 354, 462) from sea level to 850 ft. elevation (140 specimens, BPBM 137924-6, BPBM 139900-1, BPBM 140068-76, BPBM 143053-7); south side of Mt. Orangi (Station 325) at 850 ft. elevation under stones (15 specimens, BPBM 139938-9).

Remarks. — There was comparatively little size and shape variation in local populations (table LXXXIX). The few recorded differences probably reflect selection from the very large set of this species in the Bishop Museum. The 1,285 specimens of the nominate race represented the second largest sample available for a species. Only for *Australdonta degagei* (Garrett) was there a greater number of specimens. Only part of the *Orangia cookei* adults were measured. While a large part of the nearly 1,300 specimens were juvenile, discussions of the ribbing and size variations are based on measurements of about 110 specimens, perhaps one-third of the adult specimens.

Ribbing variation was minimal, except for Station 312 (table LXXXVIII), where there was a sharp increase in rib count and degree of crowding. The differences from Station 534 are statistically significant, but since only seven of 67 specimens were measured (with 55 df, "t" = 2.8497 for rib count and 3.2588 for rib spacing), this easily could be a strongly biased sample. I doubt there is any biological significance to the difference.

Most specimens were taken in the Mt. Tanga-Mt. Tepiahu area, but 15 specimens were taken on Mt. Orangi. Variation in the barrier structure is summarized in the diagnosis above.

Description of soft parts. — Foot slightly shorter than shell diameter, not tapering posteriorly, tail bluntly rounded. Sole undivided, without corrugations. Pedal grooves and slime network typical. Head projecting slightly in front of foot. Gonopore located below and behind right ommatophore.

Body color yellow-white, without darker markings.

Mantle collar (MC) with bluntly rounded, thickened anterior edge, no distinct lappets, grossly expanded around pneumostome, distance from edge of collar to pneumostome large, no glandular extension into mantle cavity. Pneumostome normal, masked by thickening of mantle collar. Anus continued by a slight crease through mantle collar.

Pallial region (fig. 121a) extending apically for one-half to five-eighths whorls. Lung roof clear in central section, scattered white granules around and near kidney and ureter. Kidney (K) slender, about 2.27 mm. long, posteriorly reaching hindgut, tapering anteriorly. Ureter (KD) arising opposite apex of kidney, not enlarging on way to reflexed opening just anterior of rectal kidney arm termination. Heart (H) slightly more than one-third kidney length, angled from hindgut. Principal pulmonary vein (HV) simple, unbranched, fading out near mantle collar. Hindgut (HG) extending about one-sixteenth whorl above apex of pallial cavity before deflecting downward on palatal wall, continuing one-eighth whorl above cavity before reflexing in "S" loops.

Ovotestis (fig. 121b, G) of palmately clavate clumps of alveoli strung along a single collecting tubule for almost three-quarters whorl above stomach apex. Hermaphroditic duct (GD) very slender at anterior end, grossly expanded in middle, sharply reflexed to junction with talon. Albumen gland (GG) well developed, figured example poorly preserved with outlines obscured. Talon (GT) very slender, more elongated than in *Endodonta*, tip slightly expanded. Prostate (DG) usually three to four rows of large acini opening into a slender tube appressed to uterus. Head of prostate and uterus capped with a small patch of glandular tissue, composed of finer acini than found in albumen gland. Preservation did not allow determination of the connections. Uterus (UT) with thin-walled, normally expanded upper chamber occupying two-thirds of prostate length, entering usually greatly expanded, thick-walled, lower chamber that gradually tapers into free oviduct, internally smooth.

Vas deferens (VD) a slender continuation of prostate duct, reflexed at peniovidùcal angle, entering laterally on penis between main part and a branch of one pilaster (fig. 121c). Penial retractor (PR) short, arising from diaphragm just above apex of pallial cavity, fusing with a fleshy extension of penial head without sharp differentiation. Penis (P) long, tapering to atrium and above entrance of vas deferens, internally sculptured with two large pilasters, one or both (usually) narrow and greatly elevated on apical half, broadening and lowering drastically near atrium, larger of two split with an arm cupping entrance of vas deferens (fig. 121c). Atrium (Y) very short.

Free oviduct (UV) distinctly shorter than prostate-uterine portion, tapering gradually, irregularly pustulose internally, differentiating it from lower uterine chamber. Spermatheca (S) with slender duct appressed to prostatic tube-uterine margin until just before head expansion, head lying in groove between base of albumen gland and head of expanded prostate. Vagina (V) very short, not structurally differentiated.

Free muscle system typical. Right ommatophoral retractor passing through peniovidùcal angle.

Buccal mass compact, buccal retractors not split, attaching in U-shaped fan slightly behind midpoint of buccal mass. Esophagus slender, arising just behind midpoint of buccal mass, extending above level of spermathecal head. Stomach occupying slightly less than one full whorl, typical in form. Intestine with normal S-loop pattern, abutting on base of kidney. Hindgut only reaching parietal-palatal margin slightly above apex of pallial cavity, following normal course forward to anus.

Digestive and salivary glands normal in size and position.

Jaws not successfully mounted.

Radula with 5 laterals and about 13 marginals, central approximately 8μ wide and 13μ long. Marginals with basal plates much wider than long, ectocone typically fragmented.

(Based on BPBM 139938, whole specimen 4.21 mm. in diameter with 6⅛ whorls, other whole and partial examples.)

Orangia cookei montana, new subspecies. Figures 121d-f; 122; 123c.

Diagnosis. — Shell larger than average, diameter 3.72-4.64 mm. (mean 4.24 mm.), with 5½-6¼ normally coiled whorls. Apex flat or barely elevated, lower whorls of spire descending more rapidly, last whorl slightly deflected below periphery, H/D ratio 0.474-0.564 (mean 0.513). Umbilicus narrowly open in juveniles, barely perforate or closed in adults. Postnuclear sculpture of narrow, lamellate, prominent, protractively sinuated radial ribs, 81-120 (mean 104.8) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, four to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets that are barely visible under 96× magnification. Sutures impressed, whorls strongly rounded above, slightly flattened laterally above very obtusely rounded periphery, lower palatal margin less compressed than in the nominate subspecies, umbilical margin strongly extended inwardly. Aperture ovate, periphery strongly rounded or at most with a very weak obtuse angulation, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly one-quarter whorl: upper high and bladelike, expanded and serrated above on posterior half, with very gradual anterior descension that accelerates in last eighth of length; 2nd parietal with posterior portion shorter, equally elevated and expanded above, with sharp descension to threadlike anterior portion that stops slightly short of anterior end of 1st parietal. Columellar barrier a high crescentic blade that twists slightly downward across top of heavy columellar callus, reaching midway to lip margin. Palatal barriers 4, extending posteriorly a little more than one-eighth whorl; first 3 high bladelike lamellae, expanded and serrated above on posterior half with progressively more gradual anterior descension and slightly more deeply recessed within aperture; 4th palatal reduced in height, expanded and serrated above, with very gradual anterior descension, slightly less recessed within aperture.

The longer columellar barrier reaching halfway across the columellar callus, much more rounded peripheral and apertural margins, and larger parietals and palatals combine to separate *Orangia cookei montana* from the nominate subspecies. *O. c. tautautuensis* is a smaller, higher shell with even longer columellar and the palatal barriers greatly reduced in size.

Description. — Shell larger than average, with 6¼ normally coiled whorls. Apex and spire moderately and almost evenly elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.564. Apical whorls 1⅜, sculpture typical. Postnuclear whorls with narrow, high, lamellate, protractively sinuated radial ribs, 109 on the body whorl, whose interstices are 2 - 3 times their width. Microsculpture of fine radial riblets, four to eight between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Suture impressed, whorls strongly rounded above and on outer margins, with very faint indications of obtuse angulation at the periphery, lower palatal wall evenly and rather strongly rounded. Color light yellow-white, with irregular, reddish flammulations, that become zigzagged and reduced in prominence on shell base. Umbilicus closed by inward growth of basal and umbilical lip areas. Aperture ovate, with very obtusely rounded outer margins, inclined about 20° from shell axis. Apertural barriers as outlined above in diagnosis. Height of holotype 2.47 mm., diameter 4.37 mm.

Holotype. — Austral Islands: Rapa Island, Station 509, east ridge of Mt. Perahu at 1,300-1,550 ft. elevation. Collected under stones by Yoshio Kondo, Donald Anderson, and natives on July 28, 1934. BPBM 135433.

Range. — East ridge of Mt. Perahu at 1,200-1,800 ft. elevation, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa: east ridge of Mt. Perahu (Stations 446, 451, 509, 521) at 1,200-1,800 ft. elevation (40 specimens, BPBM 135433-4, BPBM 135443, BPBM 135904, BPBM 142748, BPBM 142827-30).

Remarks. — One of the 28 measured specimens had a 5th palatal. Otherwise there was no significant variation in the apertural barriers. The holotype of *Orangia cookei montana* is atypical in being the most elevated specimen known. Most specimens have the spire distinctly lower.

Specimens from Station 451 at 1,200-1,500 ft. elevation were distinctly larger than those from Station 509 at 1,300-1,500 ft. elevation (table LXXXIX). With 24 df, "*t*" = 2.4206 for the diameter. This is not the same pattern of variation seen in *Opanara bitridentata* where material from Stations 451 and 509 is *smaller* than material from higher stations. Careful study of variation in the Mt. Perahu area would be well worthwhile.

Only a single specimen was taken above 1,550 ft. elevation (Station 521), suggesting that *montana* is a form of lower elevations on Mt. Perahu.

Description of soft parts. — Foot and tail almost completely retracted into pallial region, rounded behind, not tapering. Sole undivided. Pedal grooves and slime network typical.

Body color yellow-white, without darker markings.

Mantle collar as in nominate subspecies. Pneumostome in normal position, mantle lobes absent.

Pallial region extending apically for less than three-quarters whorl. Lung roof with widely scattered white granules, clumped near kidney surface. Kidney about 2.34 mm. long, same shape as in nominate subspecies. Ureter typical. Heart about one-third kidney length, not lying parallel to hindgut. Principal pulmonary vein typical.

Ovotestis (fig. 121d, G) imbedded in digestive gland, extending three-quarters whorls above stomach reflexion, composed of palmately-clavate alveoli. Hermaphroditic duct (GD), albumen gland (GG), and talon (GT) as in nominate subspecies. Prostate (DG) with one to three rows of acini opening into small tube. Uterus (UT) as in nominate subspecies.

Vas deferens (VD) typical, opening laterally into penis well below penis apex, between arms of main pilaster (fig. 121e, f). Penial retractor (PR) arising from diaphragm, inserting on fleshy head extension of penis. Penis (P) about 2.11 mm. long, tapering slightly basally, internally with two pilasters, both rounded basally, becoming slender elevated flaps apically, larger of two split into two lobes, smaller of which cups the vas opening (fig. 121f, DP). Atrium (Y) very short.

Free oviduct (UV) and spermatheca (S) as in nominate subspecies. Vagina (V) not structurally differentiated due to low insertion of spermathecal stalk.

Free muscle system and digestive system as in *O. cookei cookei.*

Jaw not successfully mounted.

Radula with 6 laterals and more than 9 marginals, central about 6μ wide and 10μ long. Shape of teeth as in *Orangia cookei cookei.*

(Based on BPBM 135433, two whole individuals, 4.11 and 4.18 mm. in diameter, with 6+ and 61.8- whorls and several extracted specimens.)

Orangia cookei tautautuensis, new subspecies. Figures 122; 123d.

Diagnosis. — Shell relatively small, diameter 3.03-3.75 mm. (mean 3.42 mm.), with 5⅛-6 normally coiled whorls. Apex and spire strongly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.517-0.592 (mean 0.552). Umbilicus completely closed. Postnuclear sculpture of narrow, prominent, lamellate, protractively sinuated radial ribs, 88-114 (mean 98.3) on the body whorl, whose interstices are about twice their width. Microsculpture of very fine radial riblets, five to nine between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are visible only under 96× magnification. Sutures impressed, whorls strongly rounded above, sometimes with a weak supraperipheral sulcus present, periphery strongly rounded, lower palatal margin flatly rounded. Aperture ovate, sometimes with sinuated upper palatal margin, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly more than one-quarter whorl, to or slightly beyond line of vision; upper high and bladelike, expanded and serrated above on visible posterior half, with very gradual anterior descension; 2nd with visible posterior portion equally expanded and serrated above, sharply descending to anterior threadlike portion which stops opposite anterior end of upper parietal. Columellar barrier high and crescentic posteriorly, sharply descending to a raised threadlike ridge twisting slightly downward across columellar callus and almost reaching lip margin. Palatal barriers 4, reduced in height compared to other subspecies, extending posteriorly almost one-quarter whorl: lower palatal partially hidden in front view by strong development of columellar barrier and callus, weakly elevated posteriorly, expanded and serrated above, moderately recessed within aperture; 2nd and 3rd palatals slightly higher posteriorly, recessed within aperture, with extremely gradual anterior descension; 4th palatal supraperipheral, reduced in height, equally recessed within aperture.

The great elongation of the apertural barriers, smaller size and proportionately greater height of the shell at once separate *Orangia cookei tautautuensis* from the other two subspecies. The easiest character for identification is the columellar barrier nearly reaching the lip margin.

Description. — Shell rather small, with 5⅞ somewhat tightly coiled whorls. Apex and spire strongly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.573. Apical whorls 1¼, sculpture mostly eroded, with traces of fine radial ribbing remaining in suture. Postnuclear sculpture of high, prominent, lamellate, protractively sinuated radial ribs, 114 on the body whorl, whose interstices are about twice their width. Microsculpture of extremely fine and crowded radial riblets, four to eight between each pair of major ribs, with barely visible spiral riblets. Sutures impressed, whorls strongly rounded above, with slightly compressed outer and basal margins. Color light yellow-white with irregular, somewhat zigzagged, reddish flammulations that become much less prominent on shell base. Umbilicus completely closed. Aperture ovate, with sinuated lower margins, inclined about 15° from shell axis. Apertural barriers as described above under diagnosis except that upper parietal broken near anterior end. Height of holotype 2.01 mm., diameter 3.52 mm.

Holotype. – Austral Islands: Rapa Island, Station 478, hillside northwest of Mt. Tautautu at 750 ft. elevation. Collected under stones by Yoshio Kondo on July 25, 1934. BPBM 143300.

Range. – Hillside northwest of Mt. Tautautu at 750 ft. elevation, Rapa Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Rapa: hillside northwest (Station 478) of Mt. Tautautu at 750 ft. elevation (9 specimens, BPBM 143300-2).

Remarks. – One example of *Orangia cookei tautautuensis* had a 5th palatal, but no other barrier variation was noticed.

It is quite interesting that Station 478 and its very close neighbor, Station 477, should have produced densely sculptured, elevated subspecies of both *Orangia cookei* and *Opanara areaensis.* The same variation is also seen in *Opanara megomphala megomphala,* which is the high-spired, more densely ribbed subspecies. It was found at Station 427, the coffee plantation at Maitua and Station 477. I have no information as to what local conditions might correlate with this distinctive and parallel variation in three species.

None of this material was in good enough condition for successful dissection.

Orangia maituatensis, new species. Figures 121g-i; 123e.

Diagnosis. – Shell of average size, diameter 3.82-4.44 mm. (mean 4.03 mm.), with 5-6⅛ normally coiled whorls. Apex and spire moderately and almost evenly elevated, occasionally slightly flattened above, body whorl deflected beneath periphery, H/D ratio 0.411-0.519 (mean 0.466). Umbilicus barely perforate, contained more than 19 times in the diameter (mean of perforate shells 26.7), frequently (20 per cent) closed. Postnuclear sculpture of high, narrow, lamellate, protractively sinuated radial ribs, 71-89 (mean 81.1) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of very fine radial riblets, four to eight between each pair of major ribs, crossed by very crowded and fine spiral riblets, with a secondary sculpture of low rounded spiral cording most clearly visible on shell base, but also occurring above periphery. Sutures impressed, whorls flatly rounded down to prominent supraperipheral sulcus, periphery right or obtusely angulated, weakly protruded, lower palatal and basal margins evenly rounded, with inward extension of baso-columellar wall. Aperture ovate, somewhat compressed laterally above and below weakly protruded periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision: upper thin, high, bladelike, expanded and serrated above on posterior visible half, with practically no anterior descension until just before termination; 2nd parietal slightly lower posteriorly, more broadly expanded above, with sharp anterior descension to threadlike anterior third that ends opposite termination of upper parietal. Columellar barrier a high bladelike ridge that sharply descends and twists slightly downwards reaching just across apex of columellar callus. Palatal barriers 4, extending posteriorly about three-sixteenths of a whorl, moderately deeply recessed within aperture: 1st palatal reduced in height, a bladelike ridge, weakly expanded and serrated above with gradual anterior descension; 2nd palatal higher than 1st, with more gradual anterior descension; 3rd palatal moderately reduced in height, higher than 1st, with more gradual anterior descension and deeper recession; 4th palatal supraperipheral in position, a raised threadlike ridge extending nearer to apertural margin.

The much sharper angulation of the periphery, continuation of secondary spiral cording above the periphery, much larger and less deeply recessed palatal barriers, lower spire, and more crowded and numerous radial ribs differentiate *Orangia maituatensis* from the otherwise quite similar *O. sporadica. Orangia cookei* differs in lacking any trace of secondary spiral cording, having a larger and more prominent columellar barrier, is generally more elevated, and normally has the umbilicus closed rather than being minutely perforate.

Description. – Shell large, with 6 normally coiled whorls. Apex and spire strongly elevated, markedly rounded above, last whorl descending slightly more rapidly, H/D ratio 0.519. Apical whorls 1½, sculpture eroded. Postnuclear whorls with narrow, high, lamellate, slightly protractively sinuated radial ribs, 82 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, four to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets, with a secondary sculpture of low, crowded, rounded spiral cords that are most prominent on shell base, but are present in reduced prominence above periphery of body whorl. Sutures impressed, whorls flatly rounded down to prominent supraperipheral sulcus, periphery slightly protruded, almost right-angled, with evenly rounded lower palatal and basal margins. Aperture ovate, flattened laterally with sinuated margin of periphery, inclined less than 20° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper a high bladelike ridge, expanded and serrated above on posterior half, scarcely descending anteriorly until just before termination; 2nd parietal slightly reduced in height on posterior half, more expanded above, sharply descending to threadlike portion that terminates opposite anterior end of upper parietal. Columellar barrier high and crescentic posteriorly, abruptly descending and twisting slightly downward to top of columellar callus. Palatal barriers 4, extending almost three-sixteenths of a whorl: lower palatal reduced in height, expanded and serrated above, with gradual anterior descension; 2nd palatal distinctly higher, slightly more expanded above, a little more deeply recessed within aperture; 3rd palatal slightly lower than 2nd, higher than 1st, with very gradual anterior descension; 4th palatal supraperipheral, greatly reduced in height, only weakly expanded above, with very gradual anterior descension. Height of holotype 2.31 mm., diameter 4.44 mm.

Holotype. – Austral Islands: Rapa Island, Station 308, foot of cliff behind Maitua at 800 ft. elevation. Collected on dead leaves by Donald Anderson and C. Montague Cooke, Jr. on July 4, 1934. BPBM 143940.

Range. – Cliffs near Maitua and Mt. Tautautu at 700-800 ft. elevation, Rapa Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Rapa Island: foot of cliff behind Maitua (Stations 308, 317, 429) at 700-800 ft. elevation

(21 specimens, BPBM 143938-40, BPBM 144043-6, BPBM 144568); foot of cliff on Mt. Tautautu (Station 477) at 800 ft. elevation (1 specimen, BPBM 144719).

Remarks. – Most of the collected material consisted of juvenile and/or dead specimens, with only three adult and five subadult examples. The spiral microsculpture and peripheral angulation is more similar to *O. sporadica;* the ribbing and apertural barriers are like *O. cookei.* All specimens were taken in a limited part of the Maitua area under natural conditions. Differences from the other species are covered in the generic discussion and diagnosis above.

Description of soft parts. – Foot slightly shorter than shell diameter, not tapering posteriorly, tail bluntly rounded. Sole undivided, not corrugated. Pedal grooves typical. Slime network very weak. Head partly retracted in all available specimens.

Body color yellow-white, no darker markings.

Mantle collar with thickened edges, but no distinct lobes or glandular extension into pallial roof. Pneumostome and anus in normal positions.

Pallial region extending five-eighths whorl apically. Lung roof clear except for few scattered white granules near kidney surface. Kidney about 2.10 mm. long, a short rectal arm abutting hindgut, tapering anteriorly. Ureter starting at apex of kidney, reflexing basally, opening just anterior of kidney rectal arm termination. Heart about one-third length of kidney, not parallel to hindgut. Principal pulmonary vein narrow, fading out near mantle collar. Hindgut reaching parietal-palatal margin about one-sixteenth whorl above apex of pallial cavity, running forward to anus without change in diameter.

Ovotestis (fig. 121g, G) of palmately clavate alveoli imbedded in first whorl above stomach reflexion, lower parts faintly iridescent, upper parts with small ova (?). Hermaphroditic duct (GD) large, grossly expanded after first portion, surface irregularly smooth, reflexed and narrowed before inserting on talon shaft. Albumen gland (GG) small, composed of relatively few alveoli. Talon (GT) with slender shaft, expanded head, leading into prostate and uterus. Prostate (G) of one to three rows of large acini opening into narrow tube partly buried in folds of uterus. Uterus (UT) with narrow thinwalled upper section, lower portion broadly expanded with much thicker walls.

Vas deferens (VD) continuation of prostate tube, reflexing from penioviducal angle, inserting subapically on penis. Penial retractor (PR) originating from diaphragm, inserting on fleshy extension of penis head, rather long. Penis (P) elongated, about 3.6 mm. long, tapering basally, internally with two major pilasters. Variously split and elevated (figs. 121h-i), branches of lower section usually greatly enlarged. Atrium (Y) short.

Free oviduct (UV) longer than prostate-uterus, tapering initially, then swollen basally. Spermatheca (S) with expanded head above apex of pallial cavity, shaft inserting on free oviduct just above atrium. Vagina (V) very short, not structurally differentiated.

Free muscle system and digestive system typical.

Jaw not successfully mounted.

Radula with about 6 laterals, marginals missing from mount, central about 8μ wide and 11μ long. Form of teeth as in *Orangia cookei cookei.*

(Based on BPBM 144043-4, whole specimen 4.01 mm. in diameter with 5⅝ whorls, several smashed and partly extracted individuals).

Orangia sporadica, new species. Figures 121j-k; 123f.

Diagnosis. – Shell of average size, diameter 3.65-4.28 mm. (mean 3.99 mm.), with 5⅜ - 6⅜ normally coiled whorls. Apex and spire moderately and evenly elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.475-0.589 (mean 0.520). Umbilicus open in juveniles, generally closed, sometimes barely perforate in adults. Postnuclear sculpture of high, very narrow, lamellate, protractively sinuated radial ribs, 38-64 (mean 50.8) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of very fine radial riblets, six to eleven between each pair of major ribs, crossed by barely visible, extremely crowded spiral riblets, with a secondary sculpture of low, rounded, rather crowded spiral cords developed below periphery of body whorl. Sutures impressed, whorls strongly rounded above right or obtusely angulated periphery, slightly compressed laterally on lower palatal wall, with inward extended baso-columellar margin. A weak to moderate supraperipheral sulcus present. Aperture ovate, slightly compressed laterally below periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision: upper a very high, bladelike ridge, expanded and serrated above on posterior visible half, with extremely gradual anterior descension until just before anterior end; 2nd parietal equally high and expanded above on visible posterior quarter, sharply descending anteriorly to low threadlike trace that terminates opposite anterior end of upper parietal. Columellar barrier a low, deeply recessed crescentic ridge, that stops posterior to apex of heavy columellar callus. Palatal barriers low, generally 4, sometimes 5 (13 per cent) or rarely 6 - 8 (5 per cent), extending posteriorly about three-sixteenths of a whorl, deeply recessed within aperture: lower palatal basal in position, little more than an elevated threadlike ridge; 2nd palatal a high elevated ridge, weakly expanded and serrated above, with gradual anterior descension; 3rd palatal subperipheral, equal in size to 1st, slightly more deeply recessed within aperture; 4th palatal supraperipheral, greatly reduced in height, a low threadlike ridge. Additional palatals, when present, inserted between various pairs.

The presence of secondary spiral cording below the periphery, the very widely spaced and few (38-64) radial ribs, and very long parietal barriers effectively separate *Orangia sporadica* from the closely related *O. cookei. O. maituatuensis* is very similar in size and shape, differing most obviously by its much more numerous (71-89) radial ribs, lower spire (mean H/D ratio 0.466), angulated periphery, and shorter, much higher palatal barriers.

Description. – Shell relatively large, with 6¼ normally coiled whorls. Apex and spire strongly and evenly elevated, slightly rounded above, last whorl descending distinctly more rapidly, H/D ratio 0.582. Apical whorls 1½, sculpture of radial riblets that are interspersed with two or three finer microradial riblets, crossed by slightly finer and about equally spaced spiral riblets. Postnuclear whorls with very narrow, high, flammulate, protractively sinuated radial ribs, 56 on the body whorl, whose interstices are 4-5 times their width. Microsculpture of very fine radial riblets, six to eleven between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. A secondary sculpture of low, rounded, rather crowded spiral cords present on body whorl below periphery. Sutures impressed, whorls strongly rounded above, with indication of a weak supraperipheral sulcus, periphery strongly rounded, lower palatal margin slightly compressed laterally. Basal-umbilical margin directed inwards, columellar wall with heavy callus. Umbilicus completely closed. Color light yellow-white, with irregularly shaped, reddish flammulations zigzagged both above and below shell periphery. Aperture ovate, upper palatal margin weakly sinuated, slightly compressed laterally below periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision: upper parietal high, thin, bladelike, weakly expanded above for posterior visible third, with practically no anterior descension until just before end; 2nd parietal equally high and lamellate for posterior visible quarter, sharply descending to a low threadlike ridge that terminates opposite anterior end of upper parietal. Columellar barrier a high crescentic ridge posteriorly, descending anteriorly to a point just behind columellar callus apex. Palatal barriers 4, reduced in height, greatly recessed within aperture, extending posteriorly about three-sixteenths of a whorl: lower palatal basal in position, only slightly higher than a threadlike trace; 2nd palatal a raised threadlike ridge, expanded and serrated above, with very gradual anterior descension; 3rd palatal equal in height to 1st, subperipheral; 4th palatal reduced in height from 3rd, supraperipheral, only slightly larger than 1st palatal. Height of holotype 2.34 mm., diameter 4.01 mm.

Holotype. — Austral Islands: Rapa Island, Station 340, northwest of Mt. Tautautu at 600-700 ft. elevation. Collected under stones by C. Montague Cooke, Jr. on July 9, 1934. BPBM 144151.

Range. — Scattered localities on Rapa Island at 600-1,800 ft. elevation, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: northwest of Mt. Tautautu (Stations 340, 479) at 800 ft. elevation, under stones and logs (25 specimens, BPBM 143325, BPBM 144151-3); southwest of Morongoto and Morongoto (Stations 360, 400, 401) at 800 ft. elevation under stones (16 specimens, BPBM 140404-6, BPBM 144251, BPBM 144338, BPBM 144341); northeast ridge of Mt. Mangaoa (Stations 403, 485, 527) at 800-900 ft. elevation under stones (32 specimens, BPBM 138346-7, BPBM 138398-9, BPBM 138401, BPBM 144382, BPBM 144385); east ridge of Mt. Perahu (Stations 451, 452, 513) at 1,200-1,800 ft. elevation on logs (4 specimens, BPBM 135574, BPBM 142832, BPBM 142878); east Maitua, northeast of Mt. Tautautu (Station 435) under stones (20 specimens, BPBM 142620-5); southwest of Anatauri Bay (Station 333) at 650-750 ft. under stones (2 specimens, BPBM 138545); slopes of Mt. Koara (Station 357) at 800 ft. in forest under stones (3 specimens, BPBM 142519-20).

Remarks. — Only 23 of the 102 specimens were adult or gerontic. More than any other Rapan species for which a number of specimens were available, *Orangia sporadica* was taken only in limited quantities at widely scattered localities (fig. 117). Other species such as *Ruatara oparica, Opanara areaensis*, and *Rhysoconcha atanuiensis* were as widely distributed, but each had one or more areas of local abundance. The name *sporadica* refers to its scattered distribution.

The minor variation in diameter and H/D ratio (table LXXXIX) probably is not significant in view of the limited numbers available for study. Of 40 measured examples, seven had 5 palatals, one had 6, and one had 8. Otherwise there was no apertural barrier variation. The rather high number of specimens with additional palatals and the great height reduction of the palatals suggests a variational trend paralleling that found in *Oparana* where multiplication of palatal lamellar traces is common.

Description of soft parts. — Only smashed whole or fragmentary extracted specimens were available. Drawings were not prepared of the pallial region or genitalia, except for part of the penial region (fig. 121j). Only differences from other *Orangia* are noted below.

Penis (P) about 2.30 mm. long, more compacted than in other *Orangia*, pilasters (fig. 121k, PP) shorter, broader, less elevated, and with shorter lamellar portion, fleshy head of penis less developed than in *O. cookei*, penial retractor (PR) slenderer and larger. Entrance of vas deferens (VD) in same position.

Other aspects of anatomy showed no differences from structures seen in *O. cookei*, so far as they could be observed.

(Based on BPBM 140404, two smashed, and several fragmentary examples.)

Genus **Australdonta**, new genus

Endodontidae with typical apical sculpture, secondary microsculpture (fig. 124) of spiral grooves (except possibly *pharcata*), major radial ribs moderately to widely spaced, crowded only in *pharcata* and *ectopia*. Apex and spire weakly (*ectopia, pseudplanulata*) to strongly (*tapina, yoshii*) elevated, last whorl descending slightly to much more rapidly. Supraperipheral sulcus present in all but *rimatarana, degagei, pharcata*, and *ectopia;* subperipheral sulcus present in *ectopia, tapina, yoshii, magnasulcata*, and *tubuaiana*. Periphery usually sharply angled or keeled, rounded only in *degagei*. Whorls about 5½, reduced in *pseudplanulata*, increased in *raivavaeana*. Umbilicus widely open in *pharcata* and *ectopia;* moderately open and slightly to moderately decoiling in other species. Parietal barriers generally 3 or 4, extending posteriorly three-sixteenths to more than one-quarter whorl, reduced to 2 in *pharcata*, many threadlike traces in *radiella* and a single faint trace in *ectopia*. Columellar wall without barrier except in *raivavaeana* and rarely in *pseudplanulata*. Palatal barriers 3 to 5, relatively long, absent in *radiella* and *ectopia*. Penial retractor originating from columellar muscle, inserting on fleshy extension to penis head. Vas deferens inserting laterally on penis between two broadly rounded and expanded pilasters that are complexly expanded and split. Spermathecal shaft inserting on oviducal side of peniovidual angle so that a very short and morphologically undifferentiated vagina exists. Jaw of separate elongated plates. Radula typical.

Type species. — *Australdonta raivavaeana*, new species.

The unique secondary microsculpture of spiral grooving (fig. 124) is a fourth sculptural element that characterizes the genus *Australdonta*. While secondary spiral cording has been developed many times. (*Cookeconcha, Endodonta, Taipidon, Planudonta, Anceyodonta, Gambiodonta, Thaumatodon, Aaadonta, Zyzzyxdonta*), no other Pacific Island Endodontidae have the spiral grooving. Under 10-40× magnification, usually only the major ribs and spiral grooves are clearly visible, but under 80-100× inspection the complex nature of the sculpture can be recognized. The sculpture is least developed in *A. pseudplanulata*, most developed in the larger species. *Australdonta pharcata* appears anomalous (fig. 137a-b) since its sculpture can be interpreted as either very strong grooving or development of secondary spiral cording. The specimens are too worn for resolution of this uncertainty. Other generic level differences concern the presence of a fleshy extension to the penis head, the very broad and complex folding of the penial pilasters, and the presence of a short, internally undifferentiated vaginal region caused by the higher insertion of the spermathecal shaft.

The genus most apt to be confused with *Australdonta* on the basis of general similarities is the Rapa

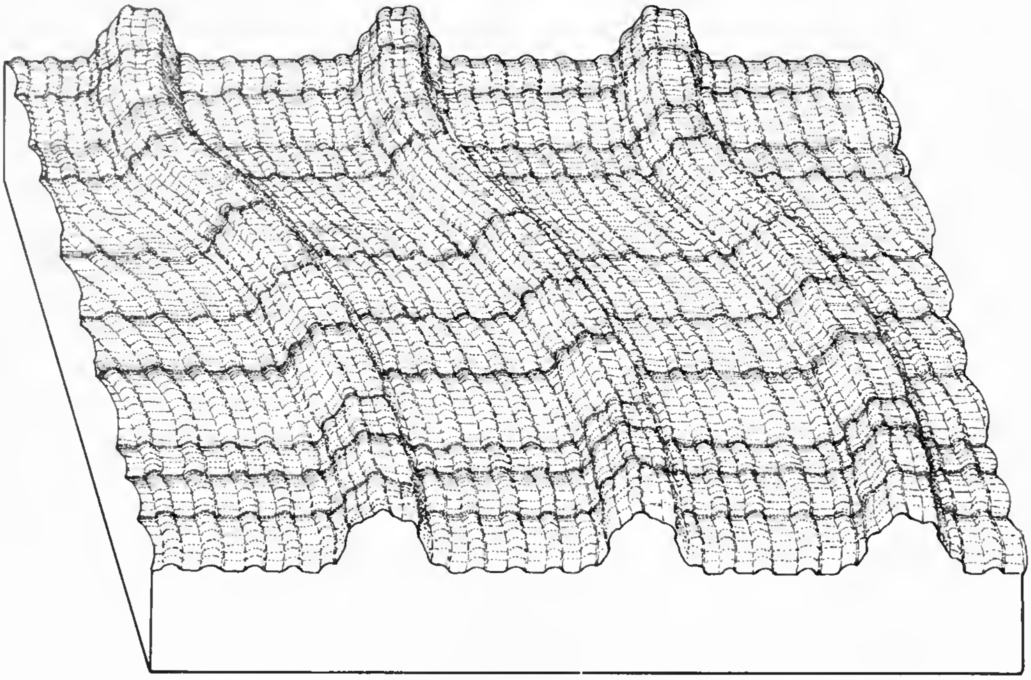

FIG. 124. Microsculpture of *Australdonta raivavaeana*, new species. BPBM 116146, greatly enlarged. (MM).

Island *Orangia*. The angled periphery, large size, supraperipheral sulcus, and secondary spiral cording of the genus give a general appearance very close to that of *Australdonta*. *Orangia* differs in its closed umbilicus, only 2 parietals, high penial pilasters, and the secondary sculpture of spiral cording rather than spiral grooves. The origin of *Orangia* is from the Rapan *Opanara*, while *Australdonta* is a local development from *Minidonta*.

The smaller, more generalized species of *Australdonta, A. pseudplanulata* and *A. rimatarana,* differ from the larger Austral Island *Minidonta, M. planulata, M. anatonuana,* and *M. haplaenopla,* not only in their peculiar sculpture, but in their much wider and regularly decoiling umbilici, much more depressed shape (*planulata* more nearly intermediate), distinct angulation to the periphery (only *M. anatonuana* has an angled periphery), reduced barrier size, and shorter parietals. The structural gap between *Australdonta* and *Minidonta* is significant and involves alteration of several character complexes. Unlike the *Minidonta-Anceyodonta* shift on Mangareva, there are no species known whose generic assignment requires subjective or arbitrary judgment. Besides the sculptural change, umbilical widening, and spire depression, shortening and lowering of apertural barrier size, plus increase in peripheral angulation are the relatively minor shifts in shell structure needed for *Australdonta* to evolve from stock having the characteristics of extant Austral Island *Minidonta*. None of the latter have been dissected, so anatomical comparisons cannot be made.

Previous collections of *Australdonta* were made by Hugh Cuming in 1828 and by Charles De Gage on Rurutu sometime shortly before 1879 (see Garrett, 1879). Only three species level forms were taken, *A. radiella radiella, A. radiella rurutuensis,* and *A. degagei. A. r. rurutuensis* was not found by members of the Mangarevan Expedition despite extensive collections on Rurutu. Possibly the locality is in error, but Garrett was so careful in regard to data that I have accepted his record. All other material was gathered in 1934 during the Mangarevan Expedition.

Within *Australdonta* there are certain clear patterns of variation. Size increase results in stronger peripheral angulation and sulci development. Except for *A. pseudplanulata,* the larger species are more depressed and have a flatter spire (table XC). None of the above are exceptional changes.

Ribbing character is relatively uniform in most species. Only *A. ectopia* and *A. pharcata* have greatly reduced major ribs that are very crowded. *A. magnasulcata* has the individual ribs significantly thickened. *A. yoshii* has the ribs quite widely spaced and reduced in number. There is almost equal spacing in the larger species, *A. radiella,* and the largest species, *A. raivavaeana* and *A. tubuaiana,* have only slightly more crowded ribbing. Since rib spacing normally increases with size, the similarity of rib spacing numbers, 7.44 in *tubuaiana* and 6.02-6.35 in *radiella* and *yoshii,* must be viewed in relation to the much greater size of the first mentioned species. Most species have 5 to 12 microradials between each pair of major ribs. The number is reduced to between four and six only in *A. pseudplanulata* and *A. degagei.* Despite the wide spacing of the major ribs in *A. yoshii,* there is no increase in the number of microradials indicating that

TABLE XC. - RANGE OF VARIATION IN AUSTRALDONTA

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
pseudplanulata	15	96.4(80-120)	1.15(1.06-1.23)	2.74(2.55-2.88)	0.420(0.413-0.430)	4 5/8(4 3/8-4 7/8)	3.56(3.35-3.85)	3-4	0-1	3-4-5
rimatarana	13	115.7(104-127)	1.37(1.18-1.48)	3.08(2.90-3.22)	0.445(0.410-0.479)	5 1/8-(4 7/8-5 3/8)	4.63(4.00-5.87)	3	0	5
degagei	1,866	110.3(83-140)	1.69(1.48-2.04)	3.23(2.86-3.52)	0.540(0.467-0.644)	5 5/8(5 1/8-6 1/4)	6.55(4.86-8.50)	3-4-5	0	3-4-5
tapina	112	131.8(117-156)	1.56(1.38-1.78)	3.51(3.19-3.82)	0.445(0.383-0.500)	5 3/8-(5-6)	5.35(4.34-6.45)	3-4	0	5
yoshii	115	65.9(54-72)	1.62(1.35-1.71)	3.30(2.90-3.55)	0.490(0.463-0.531)	5 1/4+(5-5 1/2)	6.11(5.20-7.39)	3-4	0	5
magnasulcata	5	95	1.41	3.76	0.377	5 3/8	3.36	3-4	0	5
radiella radiella	315	76.5(67-92)	2.09(1.71-2.43)	4.04(3.59-4.61)	0.517(0.468-0.565)	5 3/8+(5-5 7/8)	4.93(3.90-5.90)	4,5,7-11, 12-14	0	0
Cuming adults	11	73.0(67-81)	2.11(1.84-2.43)	4.10(3.85-4.61)	0.514(0.475-0.535)	5-5 5/8	5.02(4.07-5.90)	4-11-12	0	0
Mangarevan adults	8	81.3(68-92)	2.04(1.71-2.30)	3.90(3.59-4.34)	0.522(0.468-0.565)	5-5 7/8	4.81(3.90-5.85)	7-11-14	0	0
radiella rurutuensis	1	73	1.81	3.52	0.514	5	4.86	17	0	0
raivavaeana	882	109.4(81-148)	2.16(1.81-2.67)	4.50(4.08-5.13)	0.479(0.420-0.540)	6(5 1/4-6 1/2)	5.27(4.00-6.50)	3-4	0-1	4-5-6
tubuaiana	17	108.0(95-118)	2.02(1.72-2.45)	4.62(4.17-5.10)	0.437(0.410-0.480)	5 1/2+(5 1/8-6)	5.21(4.70-6.17)	3-4-6	0	3-4
pharcata	2	OVER 200	ca. 1.98	4.61	0.430	----	2.74(2.50-2.97)	2	0	3
ectopia	5	OVER 200	1.63(1.58-1.68)	4.57(4.38-4.77)	0.357(0.331-0.383)	5 3/8	2.26(2.25-2.27)	1	0	0

only a spacing shift is involved in that species. In both *A. pharcata* and *A. ectopia* the major ribs are small and quite crowded. In the former, there are only two to four microradials between each major pair of ribs. The coarsened ribs of *A. magnasulcata* have resulted in no change in spacing or microsculpture.

In most species the spire is comparatively elevated and slightly rounded above. Only in *A. magnasulcata, A. pseudplanulata,* and *A. tubuaiana* is the apex flattened and the later whorls descending relatively rapidly. Both *A. pharcata* and *A. ectopia* have weakly and evenly elevated spires. In general, umbilical size and contour correlate with spire elevation and shape (fig. 130). The wide umbilici in the last two species mentioned above contrast to the very narrow umbilici of the high-spired *A. degagei* and *A. yoshii.* As normal, the smaller species have less sharply angulated peripheries and the largest species the greatest peripheral protrusion. Those species with strongest peripheral protrusion have the greatest development of sulci. Prominent supra- and subperipheral sulci are found in *A. tapina, A. yoshii, A. magnasulcata,* and *A. tubuaiana,* but only a supraperipheral sulcus in *A. raivavaeana, A. radiella,* and *A. pseudplanulata. A. ectopia* has a rather weak subperipheral sulcus, but is flattened above the periphery and thus is without a supraperipheral sulcus.

Whorl count is rather stable, averaging about 5⅜, with only *A. pseudplanulata* (4⅝) significantly reduced and *A. raivavaeana* (6) enlarged.

Apertural barrier variation involves major modifications in only a few cases. Normally there are either 3 or 4 major parietals, with proportions varying between both populations and species (figs. 126, 134, 135). In *A. radiella* (fig. 132a-c) the parietals have split into from four to seventeen traces, usually only one of which is slightly more elevated. Both the columellar and palatal walls lack any barriers in that species. *A. ectopia* and *A. pharcata* have, respectively, 1 very reduced and 2 slightly reduced parietals. A weak columellar barrier is normally found in *A. raivavaeana* and rarely in *A. pseudplanulata.* All other species lack the columellar. Apparently the number of palatals normally is 5, with a reduction to 4 in *A. pseudplanulata* and *A. raivavaeana*, 3 or 4 in *A. tubuaiana,* 3 in *A. pharcata,* and none in *A. radiella* and *A. ectopia.* There is considerable variation as to palatal barrier numbers within species, but a general pattern of reduction with increasing size is quite obvious.

Only *A. raivavaeana* and *degagei* could be dissected. They agree in having a fleshy extension to the penis head, moderately subapical insertion of the vas deferens into the penis, a short vaginal area, and subequal, rather complexly folded pilasters that are larger near the apex (fig. 125). The pallial region (fig. 125c) has no peculiarities and lacks a glandular extension of the mantle collar onto the pallial roof. The presence of a short vaginal region and rather high subequal pilasters effectively separate *Australdonta* from any of the Rapan genera. It is not particularly close in structure to any forms that have been dissected.

Geographical distribution of *Australdonta* is complicated only by the apparent introduction of *A. degagei* from its original home on Rurutu to Rimatara, where it was fantastically abundant at a single station (Station 839), and to Mauke in the Cook Islands. *Australdonta radiella* is reported from both Tubuai, where it was widely distributed and abundant, and Rurutu, based on a record by Garrett (1879). The latter record was not confirmed during the extensive collections by the Mangarevan Expedition. On a northwest to southeast line the islands Rimatara, Rurutu, Tubuai, and Raivavae extend for about 325 miles angling across the Tropic of Capricorn. The smallest and lowest island, Rimatara (5 sq. miles, 315 ft. elevation), had only two species, *A. rimatarana* and *A. degagei,* taken in two days of collecting at three stations. On Rurutu, 5.5 sq. miles and 1,300 ft. maximum elevation, there were five species, *A. degagei, A. pseudplanulata, A. tapina, A. yoshii,* and *A. magnasulcata,* taken from 18 station areas over a nine-day period. Four of the five species, all except *A. yoshii,* were taken together (Station 760), while that species occurred with *A. degagei* and *A. magnasulcata* at Station 748. *A. yoshii* occurred at only the single station, while *A. magnasulcata* was found in only two areas. The other three species seemed widely dispersed on Rurutu.

Tubuai Island, 18 sq. miles and 1,300 ft. maximum elevation, had *Australdonta radiella radiella* widely distributed; *A. tubuaiana* found in limited numbers near Murivai; and the two known examples of *A. pharcata* were taken near Hoopua. There were 289 *radiella*, 17 *tubuaiana*, and 2 *pharcata* collected from the entire island over three days of collecting.

Raivavae Island, 12 sq. miles and 1,434 ft. maximum elevation, had only two species, *A. raivavaeana* and *A. ectopia;* the former common and widely distributed, the latter represented by five specimens at one station. Collections were made on Raivavae over an 11-day period so that the relative paucity of Raivavaean *Australdonta* probably is not a collecting artifact.

There is a quite similar and coherent growth pattern to *Australdonta* that makes separation of species from raw measurements somewhat difficult. Hence *A. degagei, A. rimatarana,* and *A. tapina* show overlap in measurements (table XC), but when height and diameter (fig. 131) or H/D and D/U ratios (fig. 130) are plotted, there is obvious separation of growth patterns. In regard to height and diameter, *A. degagei* and *A. rimatarana* are slightly offset, but parallel in growth; while *A. tapina* has a different slope to the regression line. Separation between *A. raivavaeana*

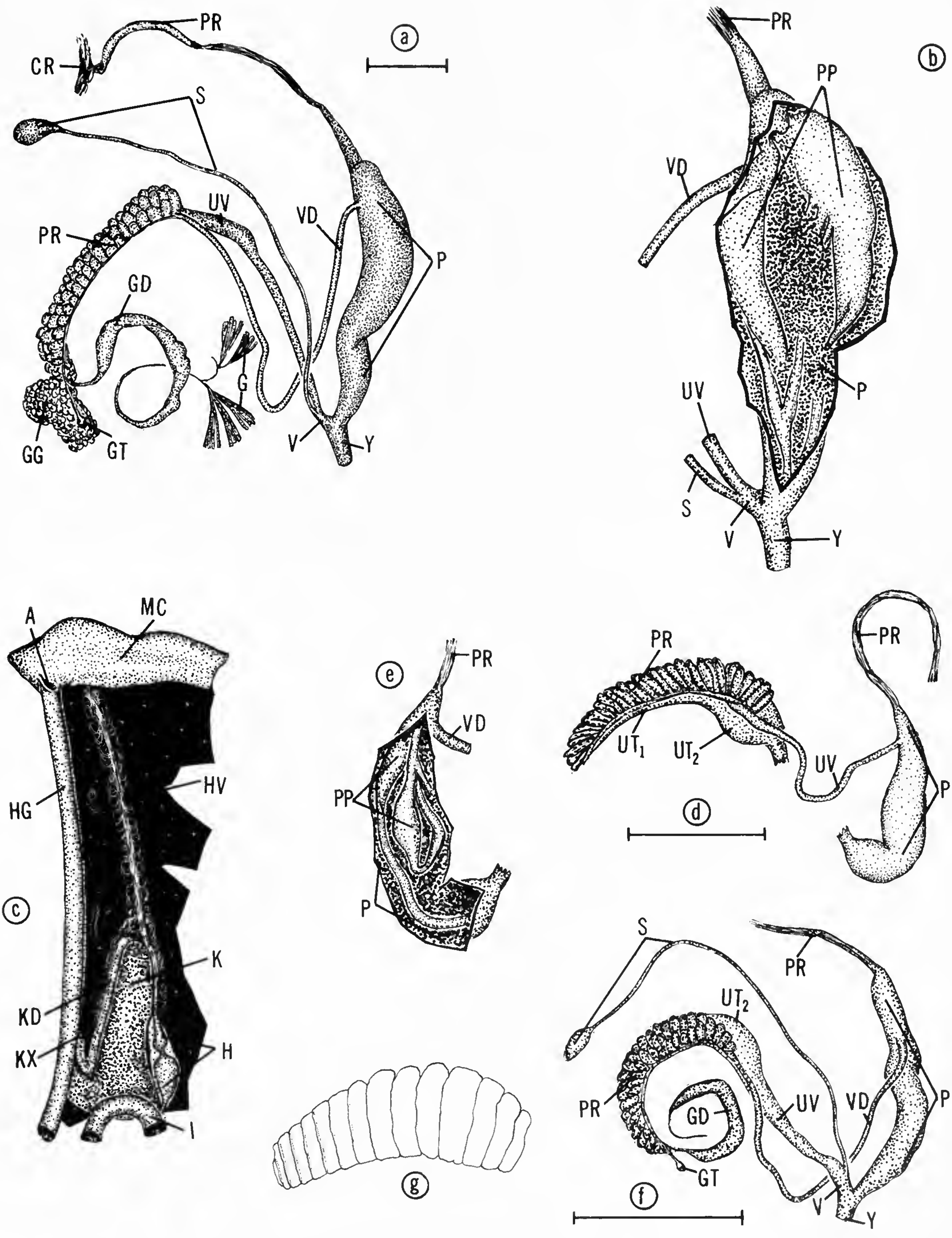

FIG. 125. Anatomy of *Australdonta:* **a-c**, **g**, *Australdonta raivavaeana,* BPBM 147515. *a,* genitalia, *b,* interior of penial region, *c,* pallial region, *g,* jaw; **d-f**, *Australdonta degagei. d,* genitalia, Mauke, Cook Islands, BPBM 95214, *e,* interior of penis, BPBM 95214, *f,* genitalia, Rimatara, Austral Islands. BPBM 149163. Scale lines equal 1 mm.

and *A. tubuaiana* (fig. 136) is less dramatic, but the qualitative differences mentioned under those species enable identification. Variation in apertural barriers is large (fig. 126). Although each species will have a characteristic mean number, sufficient variation exists that caution is required in using the key for identifications of individual specimens.

More than in any other genus of the Endodontidae, *Australdonta* presents a unitary set of species with only minor combinations of differences.

KEY TO THE GENUS *Australdonta*

1. Palatal barriers absent....................2
   Palatal barriers present....................4
2. Many threadlike parietal traces....................3
   One threadlike parietal trace. *Australdonta ectopia,* new species
3. Parietal traces 4-14 (usually 7-11); Tubuai. *Australdonta radiella radiella* (Pfeiffer, 1846)
   Parietal traces 17; Rurutu. *Australdonta radiella rurutuensis* (Garrett, 1879)
4. Mean diameter of adults above 4.30 mm....................5
   Mean diameter of adults under 4.00 mm....................7
5. Parietal barriers 3 or more; D/U ratio about 5.25....................6
   Parietal barriers 2; D/U ratio about 2.75. *Australdonta pharcata,* new species
6. Periphery at aperture weakly rostrate (fig. 133e): Tubuai. *Australdonta tubuaiana,* new species
   Periphery at aperture obtusely angled (fig. 133b); Raivavae. *Australdonta raivavaeana,* new species
7. D/U ratio usually much less than 4.00....................8
   D/U ratio usually much more than 4.00....................9
8. Periphery weakly angled; ribs fine (fig. 127d); spire and apex almost flat....................*Australdonta pseudplanulata,* new species
   Periphery of body whorl strongly rostrate; ribs very coarse (fig. 127b); apex flat, spire elevated. *Australdonta magnasulcata,* new species
9. Body whorl with strongly angled periphery (fig. 129b, e)....................10
   Body whorl with weakly angled or rounded periphery (figs. 128b, e)....................11
10. Less than 80 widely spaced ribs on body whorl. *Australdonta yoshii,* new species
    More than 100 rather crowded ribs on body whorl. *Australdonta tapina,* new species
11. Mean H/D ratio about 0.450; mean D/U ratio about 4.63. *Australdonta rimatarana,* new species
    Mean H/D ratio about 0.540; mean D/U ratio about 6.50. *Australdonta degagei* (Garrett, 1879)

Australdonta pseudplanulata, new species. Figure 127d-f.

Diagnosis. — Shell very small, diameter 2.55-2.88 mm. (mean 2.74 mm.), with 4⅜-4⅞ rather tightly coiled whorls. Apex and spire flat or barely elevated, last whorl descending more rapidly, H/D ratio 0.413-0.430 (mean 0.420). Umbilicus broadly V-shaped, slightly and regularly decoiling, contained 3.35-3.85 (mean 3.56) times in the diameter. Apical sculpture typical, microsculpture typical, secondary spiral grooves very fine. Postnuclear whorls with narrow, prominent, crowded, slightly protractively sinuated radial ribs, 80-120 on the body whorl, whose interstices are 1½-3 times their width. Sutures deep, whorls strongly rounded above, slightly flattened laterally above very weakly angled periphery, lower palatal wall evenly rounded to sharply rounded umbilical margin. Color light yellow horn without darker markings. Aperture subcircular, slightly flattened laterally above very weakly angled periphery, inclined less than 10° from shell axis. Parietal barriers 3, rarely (12.5 per cent) 4, large, extending slightly over one-quarter whorl: upper high and bladelike, posterior third to half slightly expanded and serrated above, with very sharp anterior descension; 2nd with posterior quarter to third same as in 1st, anterior half threadlike; 3rd with posterior portion reduced in height, anterior half a weaker threadlike ridge; 4th, when present, a threadlike ridge, equal in length to 3rd parietal, moderately thickened and elevated posteriorly. Columellar barrier usually absent, rarely a deeply recessed crescentic ridge present in juveniles. Palatal barriers 3 (25 per cent) to 4 (75 per cent), prominent, extending more than one-eighth whorl: lower basal in position, slightly recessed, a long curved lamellar ridge with top edge of posterior portion flat; 2nd longer, higher, with more gradual anterior descension; 3rd higher, longer, with very gradual anterior descension, less deeply recessed; 4th, when present, a supraperipheral, V-shaped or a raised lamellar ridge, distinctly more deeply recessed and shorter than 3rd.

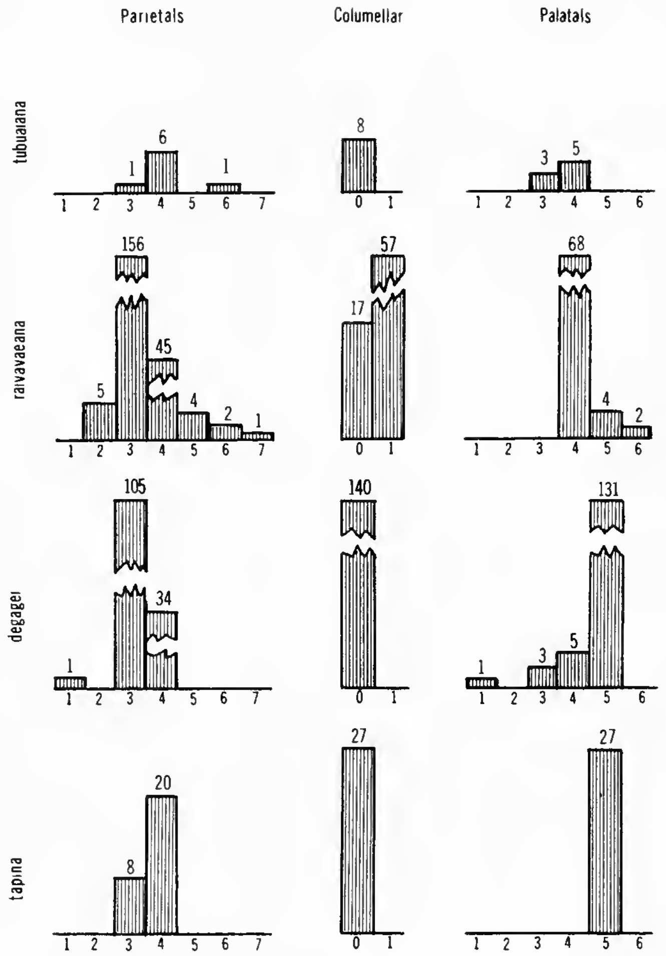

FIG. 126. Frequency distribution of apertural barriers in *Australdonta degagei, A. raivavaeana, A. tapina,* and *A. tubuaiana.*

The small size, very deep sutures, fine microsculpture, and very weakly angled periphery combine with the wide umbilicus to separate *Australdonta pseudplanulata* from other members of the genus. Both *A. degagei* and *A. rimatarana* are larger, have narrower umbilici, more elevated spire and distinct color flammulations.

Description. — Shell very small, with 4⅞ rather tightly coiled whorls. Apex slightly depressed, spire flat, last part of body whorl descending quite rapidly, H/D ratio 0.414. Apical whorls 1⅜, sculpture partly eroded, in spots widely separated radial ribs with finer microradials and microspirals clearly visible. Postnuclear whorls with narrow, prominent, crowded, slightly protractively sinuated radial ribs, 118 on the body whorl, whose interstices are 1½-3 times their width. Microsculpture very fine, of crowded radial riblets,

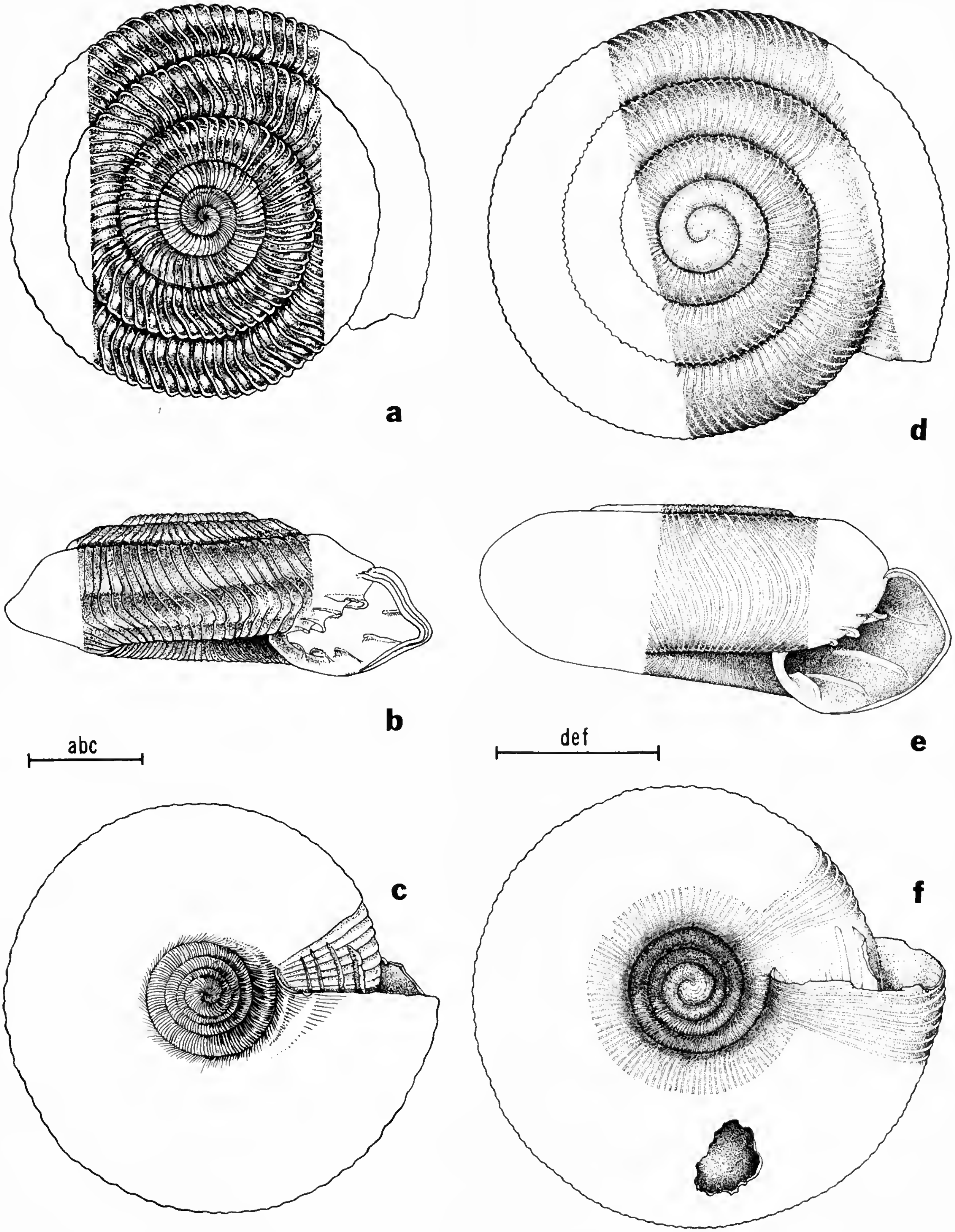

Fig. 127. **a-c**, *Australdonta magnasulcata,* new species. Station 760, Mato Naa, Rurutu, Austral Islands. Holotype. BPBM 148291; **d-f**, *Australdonta pseudplanulata,* new species. Station 754, Mato Naa, Rurutu, Austral Islands. Holotype BPBM 148204. Scale lines equal 1 mm. Microsculpture omitted in all figures. (*a-c*, SG; *d-f*, MM).

barely visible spiral microriblets, and weak, irregularly spaced spiral grooves. Sutures deep, whorls strongly rounded above, flattened laterally above weakly angled periphery. Lower palatal wall evenly rounded to baso-columellar margin, umbilical wall very strongly rounded. Color light yellow horn, without any darker markings. Umbilicus widely open, broadly U-shaped, regularly decoiling, contained 3.35 times in the diameter. Aperture subcircular, flattened laterally above periphery, inclined about 10° from shell axis. Parietal barriers 3, large, extending slightly more than one-quarter whorl: upper a high lamellar blade, posterior third slightly expanded and serrated above, anterior part broken; 2nd with posterior quarter elevated to same height as 1st, expanded above, anterior half threadlike; 3rd parietal with posterior third very reduced in height, anterior half a very faint threadlike trace. No columellar barrier. Palatal barriers 4, large, extending about one-eighth whorl: lower basal in position, a high lamellar ridge, slightly recessed, with gradual anterior descension; 2nd longer, very slightly higher, with more gradual anterior descension; 3rd a higher, longer bladelike lamella, less deeply recessed, with very gradual anterior descension; 4th supraperipheral, a rather short, low lamellar ridge, deeply recessed within aperture. Height of holotype 1.19 mm., diameter 2.86 mm.

Holotype. — Austral Islands: Rurutu Island, Station 754, near cliff of Mato Naa at 200 ft. elevation under ironwood trash. Collected by C. M. Cooke, Jr., on August 25, 1934. BPBM 148204.

Range. — Rurutu Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rurutu: vicinity of Mato Naa (Stations 754, 760) at 5-200 ft. elevation (9 specimens, BPBM 148204, BPBM 148289); north of Avera (Station 805), 50-100 ft. inland at 5-30 ft. elevation (3 specimens, BPBM 148840); north of Hauti (Station 786) at 40-75 ft. elevation (3 specimens, BPBM 148630).

Remarks. — Of the six nearly adult shells, four had the normal complement of 4 palatals, while the two adult shells from near Hauti had only 3 palatals, with the lower one absent. One juvenile from Station 760 had 4 parietals and 5 palatals, although the rest of the set had the normal complement of 3 parietals and 4 palatals.

Australdonta pseudplanulata is by far the smallest species of the genus and appears to be the most generalized in structure. Only under very high magnification is the spiral microsculpture visible. Whether this is a secondary result of rib crowding or representative of a primitive sculptural state is unknown. The relatively deep recession of the palatal barriers, deep sutures, and nearly flat spire are quite different from the situation observed in the other *Australdonta* with typical barriers.

At first glance this species seems to be an analog of the Raivavae Island *Minidonta planulata,* hence its specific name *pseudplanulata.*

Australdonta rimatarana, new species. Figure 128d-f.

Diagnosis. — Shell much smaller than average, diameter 2.90-3.22 mm. (mean 3.08 mm.), with 4⅞ - 5⅜ rather tightly coiled whorls. Apex and spire slightly elevated, lower whorls descending distinctly more rapidly, H/D ratio 0.410-0.479 (mean 0.445). Umbilicus relatively open, broadly U-shaped, last whorl decoiling more rapidly, contained 4.00-5.87 times (mean 4.63) in the diameter. Apical and microsculpture typical, secondary spiral grooving prominent. Postnuclear whorls with thin, prominent, protractively sinuated radial ribs, 104-127 (mean 115.7) on the body whorl, whose interstices are 3-4 times their width. Sutures deeply impressed, whorls strongly rounded above, curving down to very slightly angled periphery, lower palatal margin evenly rounded, slightly compressed. Umbilical margin strongly rounded. Aperture ovate, periphery weakly angled, inclined about 15° from shell axis. Parietal barriers 3, prominent, extending posteriorly about three-sixteenths of a whorl: upper with posterior third serrated above, descending slightly, then rapidly at end of barrier; 2nd parietal with equally high posterior third, anterior half a high, threadlike ridge; 3rd palatal reduced in height with slightly longer threadlike portion. Columellar barrier absent. Palatal barriers 5, rather small, extending about one-eighth whorl: lower a short recessed ridge with gradual anterior descension; 2nd, 3rd, and 4th higher, longer, with gradual anterior descension, more deeply recessed, upper edge flat; 5th a V-shaped or weakly lamellar, deeply recessed ridge, slightly shorter than 4th.

The much smaller palatals, shorter parietals, less crowded sculpture, and only faintly angled periphery easily separate *A. rimatarana* from the larger *A. tapina. A. degagei* is similar in size and form, but has a much narrower umbilicus, higher spire and longer barriers.

Description. — Shell rather small with 5 normally coiled whorls. Apex and early spire flat, lower whorls descending progressively more rapidly, H/D ratio 0.462. Apical whorls with fine, widely spaced radial ribs, a microsculpture of coequal radials and spirals barely visible under 96× magnification. Radials becoming more crowded near end of apex. Postnuclear whorls with prominent, rounded, protractively sinuated radial ribs, 127 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, three to eight between each pair of major ribs, extremely fine microspirals, and irregularly spaced, prominent spiral grooves. Sutures deep, whorls strongly rounded, then curving down to very weakly angled periphery, evenly rounded lower palatal wall, and strongly rounded umbilical margin. No supra- or subperipheral sulci. Color light yellow horn, with rather broad, irregular, reddish flammulations that fade out on shell base. Umbilicus broadly U-shaped, last whorl decoiling more rapidly, contained 4.46 times in the diameter. Aperture ovate, periphery very weakly angled, inclined about 15° from shell axis. Parietal barriers 3, extending about three sixteenths of a whorl: upper high and lamellate with posterior half slightly expanded and minutely serrated above, then angling gradually to sharp anterior descension; 2nd parietal with threadlike anterior third, posterior third as in upper tooth; 3rd parietal with proportionately longer threadlike portion and lamellate posterior reduced in height. No columellar barrier. Palatal barriers 5, prominent, extending about one-eighth whorl: lower baso-columellar in position, short, lower than 2nd, rather deeply recessed, with rather sharp anterior descension; 2nd and 3rd high, deeply thickened and weakly serrated on top, longer than 1st, with more gradual anterior descension, a little more deeply recessed, thin lamellar blades; 4th reduced in height from 3rd, much more gradual anterior descension, weakly expanded and serrated above; 5th supraperipheral, deeply recessed, a low, long lamellar ridge. Height of holotype 1.38 mm., diameter 3.22 mm.

Holotype. — Austral Islands: Rimatara, Station 837, 400 yd. northeast of Anapoto, at 35 ft. elevation. Collected by Yoshio Kondo and Donald Anderson on September 5, 1934. BPBM 149363.

Range. — Anapoto, Rimatara Island, Austral Islands.

Paratypes. — Same as list of material.

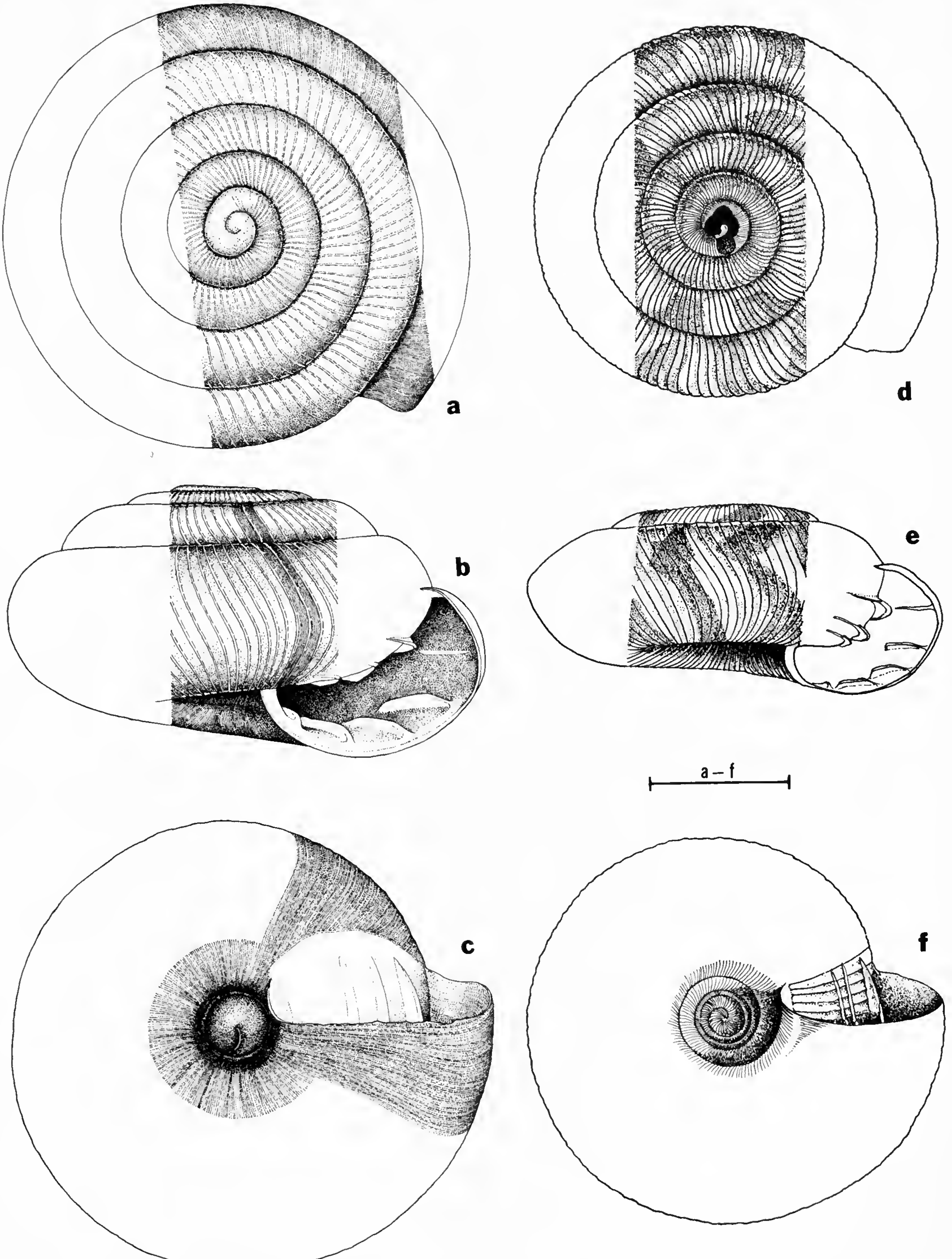

FIG. 128. **a-c**, *Australdonta degagei* (Garrett). Rurutu, Austral Islands. Lectotype. BPBM 1002; **d-f**, *Australdonta rimatarana*, new species. Station 837, Anapoto, Rimatara, Austral Islands. Holotype. BPBM 149363. Microsculpture omitted from all figures except for microradials in *b*. Scale lines equal 1 mm. (*a-c*, MM; *d-f*, SG).

Material. — Rimatara: vicinity of Anapoto (Stations 829, 837) at 20-50 ft. elevation (12 specimens, BPBM 149363-4, BPBM 149096).

Remarks. — While there is considerable overlap in basic measurements between *A. rimatarana* and *A. degagei*, the pattern of growth is noticeably different. When the H/D and D/U ratios are plotted (fig. 130), there is clear and obvious separation. Plotting of the height and diameter (fig. 131) shows the relatively more depressed shape of *A. rimatarana.* The greater angulation of the periphery and generally wider umbilicus of the latter will separate most individuals, but the similarities are many. Only a few specimens from the one area of Rimatara were obtained.

Australdonta degagei (Garrett, 1879). Figures 125d-f; 128a-c.

Pitys De Gagei Garrett, 1879, Proc. Acad. Nat. Sci., Philadelphia, **1879**, p. 18 — Rurutu, Austral Islands (Charles De Gage!).
Helix (Endodonta) De Gagei (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 65.
Endodonta (Thaumatodon) degagei (Garrett), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Diagnosis. — Shell larger than average, diameter 2.86-3.52 mm. (mean 3.23 mm.), with 5⅛ - 6¼ rather tightly coiled whorls. Apex flat or slightly elevated, later whorls descending progressively more rapidly, H/D ratio 0.467-0.644 (mean 0.540). Umbilicus quite narrow, U-shaped, only slightly decoiling, contained 4.86-8.50 times (mean 6.55) in the diameter. Apical and microsculpture typical, spiral grooving prominent. Postnuclear whorls with low, narrow, protractively sinuated radial ribs, 83-140 (mean 110.3) on the body whorl, whose interstices are 4-6 times their width, usually becoming very crowded and indistinct on last part of body whorl. Sutures prominently impressed, whorls slightly compressed and evenly rounded laterally above and below obtusely angled periphery. Umbilical margin strongly and evenly rounded. Aperture ovate, slightly compressed laterally above and below barely angled periphery, inclined about 15° from shell axis. Parietal wall usually with 3 (75.0 per cent) or 4 (24.3 per cent), rarely 1 or 5 barriers, extending less than one-quarter whorl: upper high, bladelike, weakly serrated above posteriorly, with long and gradual anterior descension; 2nd equally high for posterior third, serrated above, then descending to a threadlike ridge for anterior half; 3rd markedly reduced in height for posterior elevated portion, anterior two-thirds threadlike, occasionally absent; 4th and 5th parietals, when present, deeply recessed threadlike traces along posterior half of other parietals. No columellar barrier. Palatal wall usually with 5 (93.6 per cent), rarely 4 (3.5 per cent), very rarely only 1 or 3 barriers, extending about one-eighth whorl: 1st at baso-columellar margin, rounded, a V-shaped ridge only slightly recessed; 2nd, 3rd, and 4th, higher, progressively longer, more deeply recessed and with more gradual anterior descension, 4th slightly lower; 5th, when present, a recessed V-shaped or threadlike ridge above periphery, relatively short.

The smaller size, only slightly angled periphery, and usually 5 palatal barriers effectively separate *Australdonta degagei* from *A. tubuaiana* and *A. raivavaeana*. *A. tapina* is larger (mean diameter 3.51 mm.), more depressed (mean H/D ratio 0.461), and sharply angulated with a protruded periphery and distinct sub- and supraperipheral sulci. *A. yoshii* has much more widely spaced ribbing, and a sharply angulated, weakly protruded periphery. *A. rimatarana* is the most closely related species, but has shorter, higher barriers, a more depressed form (mean H/D ratio 0.445), wider umbilicus (mean D/U ratio 4.63), and fewer whorls (4⅞ - 5⅜).

Description. — Shell of average size with slightly less than 5¾ normally coiled whorls. Apex and early spire flat, later whorls descending progressively more rapidly, H/D ratio 0.570. Apical whorls 1½, sculpture of fine radial ribs interspersed with much finer radial riblets visible in suture. Postnuclear whorls with prominent, rounded, somewhat protractively sinuated radial ribs, whose interstices are 3-4 times their width, becoming highly irregular on last half of body whorl. Microsculpture of very fine crowded radial riblets crossed by much finer and more crowded spiral riblets, with a secondary sculpture of irregularly spaced, prominent spiral grooves developed. Sutures moderately impressed, whorls slightly flattened laterally below periphery and on basal margin. Periphery of body whorl very weakly angulated. Color light yellow horn with light, somewhat irregular, reddish flammulations. Umbilicus quite narrow, U-shaped, very slightly decoiling, contained 7.14 times in the diameter. Aperture subovate with evenly rounded margins, inclined about 20° from shell axis. Parietal barriers 3, extending posteriorly one-quarter whorl: upper parietal a high bladelike ridge, serrated above on posterior half, with gradual anterior descension; 2nd parietal equal in height and serrated posteriorly, but anterior half low and threadlike; 3rd parietal reduced in prominence posteriorly, anterior two-thirds low and threadlike. Columellar region without barrier, but with a moderately heavy callus. Palatal barriers 5, low, bladelike, extending about one-eighth whorl: lower palatal at baso-columellar margin, rounded above, V-shaped, reaching almost to lip edge; 2nd palatal higher, bladelike, very slightly recessed from edge, sharper anterior descension; 3rd and 4th palatals similar to 2nd, slightly higher, thinner, more deeply recessed, with more gradual anterior descension; upper palatal supraperipheral, a low, threadlike, relatively deeply recessed ridge. Height of lectotype 2.01 mm., diameter 3.52 mm.

Lectotype. — Austral Islands: Rurutu. Collected by Charles de Gage. BPBM 1002, ex Andrew Garrett.

Range. — Rurutu and Rimatara, Austral Islands and Mauke, Cook Islands.

Paratypes. — BPBM 1002.

Material. — Austral Islands: Rimatara (25 specimens, BPBM 53479); Southwest of Amaru, 20-200 yd. inland (Station 839) at less than 25 ft. altitude under stones, coconut husks, and dead leaves (1,552 specimens, BPBM 149163-74X, BPBM 149216).

Rurutu (7 specimens, BPBM 1002): Mato Arei, southeast of Moerai (Stations 769, 773, 774, 775) at 5-150 ft. elevation under stones (165 specimens,. BPBM 148420-1, BPBM 148425, BPBM 148478-9, BPBM 148502-9, BPBM 148540, BPBM 148557); Mato Naa, bluff north of Moerai (Stations 748, 753, 754, 760, 792) at 5-200 ft. elevation (84 specimens, BPBM 148128, BPBM 148174, BPBM 148203, ex BPBM 148289, BPBM 148686); north of Avera (Stations 804, 805) at 5-30 ft. elevation (23 specimens, BPBM 142215, BPBM 148839); north side of bluff north of Hauti (Station 786) at 40-75 ft. elevation on dead leaves (1 specimen, ex BPBM 148630); north center of Moerai village (Station 757) at 30 ft. elevation (2 specimens, BPBM 148249).

Cook Islands: Mauke, 300-500 yd. inland from Taunganui at 40-55 ft. elevation (5 specimens, BPBM 95161, BPBM 95214, BPBM 95273).

TABLE XCI. - LOCAL VARIATION IN AUSTRALDONTA

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
pseudplanulata BPBM 148630, BPBM 148840, BPBM 148204, BPBM 148289	5	1.15±0.032 (1.06-1.23)	2.74±0.062 (2.55-2.88)	0.420±0.0036 (0.413-0.430)	4 5/8 (4 1/2-4 7/8)	3.56±0.112 (3.35-3.85)
rimatarana BPBM 149363, BPBM 149364, BPBM 149096	5	1.37±0.063 (1.19-1.49)	3.08±0.055 (2.91-3.25)	0.445±0.0155 (0.410-0.479)	5 1/8- 4 7/8-5 3/8)	4.63±0.322 (4.00-5.87)
degagei Sta. 839[1] BPBM 149163-4	22	1.89±0.022 (1.72-2.22)	3.38±0.020 (3.21-3.54)	0.559±0.0058 (0.529-0.644)	5 7/8- (5 1/2-6 1/8)	6.35±0.166 (5.16-8.50)
Sta. 839[2] BPBM 149164, -71	38	1.67±0.017 (1.46-1.92)	3.15±0.021 (2.88-3.41)	0.532±0.0044 (0.484-0.607)	5 1/2+ (5 1/8-6)	6.68±0.120 (4.95-8.45)
BPBM 1002 Paratypes	7	1.74±0.066 (1.52-1.99)	3.20±0.077 (2.95-3.51)	0.541±0.0110 (0.505-0.583)	5 3/8+ (5 1/8-5 7/8)	6.73±0.367 (5.53-8.10)
Sta. 774[3] BPBM 148502-3	11	1.53±0.024 (1.39-1.66)	2.89±0.028 (2.75-3.08)	0.529±0.0112 (0.471-0.595)	5 3/8 (5 1/8-5 5/8)	5.45±0.193 (4.57-6.39)
Mauke[3] BPBM 95161, -214, -273	4	1.49±0.063 (1.39-1.66)	2.91±0.098 (2.75-3.18)	0.508±0.0046 (0.500-0.521)	5 1/4 (5-5 5/8)	6.07±0.190 (5.60-6.40)
tapina Sta. 760 BPBM 148290	5	1.58±0.064 (1.46-1.79)	3.71±0.070 (3.44-3.84)	0.425±0.0143 (0.383-0.466)	5 1/2+ (5 1/8-6)	5.40±0.340 (4.34-6.45)
BPBM 148823, BPBM 148836-8, BPBM 148867, BPBM 149045-6	21	1.56±0.019 (1.39-1.72)	3.46±0.032 (3.21-3.68)	0.452±0.0049 (0.417-0.500)	5 3/8- (5-5 5/8)	5.29±0.079 (4.82-6.00)
yoshii BPBM 148130	10	1.62±0.036 (1.36-1.72)	3.30±0.075 (2.91-3.61)	0.490±0.0066 (0.463-0.531)	5 1/4+ (5-5 1/2)	6.11±0.180 (5.20-7.39)
radiella radiella Cuming material SMF 165740-1, FMNH 46510 FMNH 46604, BPBM 106236, BPBM 167415	11	2.11±0.053 (1.84-2.43)	4.10±0.079 (3.85-4.61)	0.514±0.0053 (0.475-0.535)	5 1/4+ (5-5 5/8)	5.01±0.172 (4.07-5.90)
Sta. 699 BPBM 147706	5	2.15±0.082 (1.92-2.32)	4.07±0.111 (3.74-4.37)	0.529±0.0103 (0.508-0.565)	5 1/2 (5 1/4-5 7/8)	4.48±0.224 (3.90-5.29)
raivavaeana Sta. 674 BPBM 147515-16, -25, -29a	53	2.14±0.029 (1.82-2.68)	4.50±0.036 (4.11-5.17)	0.476±0.0039 (0.420-0.540)	6- (5 1/4-6 1/2)	5.44±0.056 (4.27-6.50)
Sta. 577 BPBM 146567-8	9	2.19±0.044 (2.02-2.35)	4.49±0.056 (4.24-4.74)	0.488±0.0070 (0.449-0.515)	6 1/8+ (6-6 1/2)	4.53±0.073 (4.27-4.79)
tubuaiana BPBM 147677, -705	8	2.02±0.085 (1.72-2.45)	4.62±0.134 (4.17-5.10)	0.437±0.0081 (0.410-0.480)	5 1/2+ (5 1/8-6)	5.21±0.159 (4.70-6.17)

1. Gerontic 2. Adults 3. Subadult

Remarks. – Not only is *Australdonta degagei* one of very few endodontid species reported from more than one island, it is the only species known from two archipelagoes. The Mauke, Cook Islands specimens were slightly subadult, but compare well in size and proportions with subadult Rurutu specimens (table XCI), except in respect to the D/U ratio. With 13 df, "*t*" = 4.2680, confirming the visual impression that their umbilici are slightly narrower. Since the Rurutu subadult shells had much wider umbilici than the types or Rimatara examples, this is not a significant difference.

Individuals of *A. degagei* were exceedingly abundant at the one station on Rimatara, and taken sparsely at one locality on Mauke. On Rurutu they were found at 13 of 17 stations from which endodontids were collected. While no early collections from Rimatara or Mauke exist, I consider it probable that the isolated colonies on these islands represent recent human introductions rather than natural occurrences.

I do not know why this species should have been subject to accidental human transport, but suspect that its ecology will prove to be unusual.

Barrier variation was less extensive than in most other large *Australdonta* (fig. 126). One freak gerontic individual had only 1 parietal and 1 palatal. One specimen of 140 examined had a fifth parietal trace, and three specimens had only 3 palatals. Otherwise, there was simple variation between 4 (3.5 per cent) and 5 (93.6 per cent) palatals, and 3 (75.0 per cent) or 4 (24.3 per cent) parietals.

The availability of the large sample from Rimatara, 1,552 specimens, allowed making a number of comparisons within the sample. Gerontic individuals with greatly reduced sculpture on the last half of the body whorl and the barriers reduced in height mostly had been segregated as BPBM 149163. A few additional gerontic individuals were found in BPBM 149164 and measured with them. Specimens from BPBM 149164 and BPBM 149171 were measured separately (table XCI). They were adult in form, but lacked the exaggerated barrier reduction plus sculpture crowding, and also had less pronounced descension of the body whorl near the aperture. The difference in whorl count is obvious, and with 58 df, "*t*" = 6.9754 for height, "*t*" = 7.3726 for diameter, "*t*" = 3.7333 for H/D ratio, and "*t*" = 1.6322 for D/U ratio. The difference in D/U ratio is not significant, but the height, diameter, and H/D ratio differences are highly significant. The meaning of these differences is simple. Once "adult" size, as measured by full genital development, is reached and the start of the gerontic shell growth syndrome commences, size increase continues for about three-eighths of a whorl. There is sharper descension of the body whorl, which increases the height by an average of 13.2 per cent, while the diameter is increasing only 7.3 per cent. The mean H/D ratio is raised 5.1 per cent by these growth changes. At the same time, the apparently insignificant change in the D/U ratio may result from the usual slight constriction in size of the apertural opening during gerontic growth. Rib formation becomes highly irregular and crowded, so that rib counts in nearly all gerontic individuals become impossible.

The type set (BPBM 1002) contained adult and gerontic material, thus being generally intermediate between the two series from Station 839 on Rimatara. In contrast, the measured specimens from Station 774 on Rurutu were distinctly subadult. Measurement of these specimens was needed for comparison with the subadult specimens collected by P.H. Buck on Mauke, Cook Islands in 1929 (BPBM 95167, BPBM 95214, BPBM 95273). They were essentially identical in height and diameter, insignificantly different in regard to H/D ratio ("*t*" = 1.0974 with 13 df) and D/U ratio ("*t*" = 1.8768) despite the apparently large difference in D/U ratio.

The large size differences between the Rurutu types collected by Garrett (BPBM 1002) and the subadults taken by the Mangarevan Expedition ("*t*"=3.4591-4.3992 for height, diameter, and D/U ratio with 16 df) are simply a factor of age and not systematically meaningful. Since proportionately few gerontic individuals were contained in the type set, differences in the H/D ratios were insignificant ("*t*"=0.7253). When the rapid whorl descension of gerontic growth occurs, the H/D ratio is significantly shifted within a population, but there is no significant change between subadult and adult examples of *A. degagei* in regard to H/D ratio.

The type specimen has a slightly more rounded periphery than most other gerontic individuals. Allowance for this should be made in comparing specimens with the type figures.

Description of soft parts. — Foot and tail slender, rather short, in preserved material a little less than one-half shell diameter, sharply truncated anteriorly, very slightly tapering posteriorly. Sole and pedal grooves typical. No caudal horn or middorsal groove. Slime network as in *A. raivavaeana.* Head projecting in front of foot. Ommatophores short, eyespots inconspicuous. Gonopore in normal position.

Body color pale yellow-white, without darker markings.

Mantle collar and glandular extension as in *A. raivavaeana.* Pneumostome and mantle lobes typical. Anus opening just within mantle collar at a slight angle, weak groove continuing through pneumostome.

Pallial region extending nearly three-quarters of a whorl, about 3.6 mm. long. Lung roof with narrow bands of white granules flanking principal pulmonary vein. Kidney about 1.5 mm. long, a short rectal lobe adjacent to hindgut, surface weakly dented by loop of intestine. Ureter typical, opening just above termination of rectal kidney arm. Heart short, slightly angled from hindgut, about one-half length of kidney. Principal pulmonary vein simple, fading out just short of weak glandular extensions of mantle collar. Hindgut typical.

Ovotestis of palmately clavate alveoli strung along a single tube, imbedded in digestive gland above stomach apex. Hermaphroditic duct (GD, fig. 125f) slender at first, greatly expanded where paralleling stomach, narrowing just before entering carrefour (X). Albumen gland (GG) typical, poorly preserved. Talon (GT) with expanded head and long slender shaft, merging with hermaphroditic duct to form an unclearly differentiated carrefour. Prostate (DG) of two to three rows of large acini opening into a narrow tube that is appressed to uterus, but not attached to it in any way. Uterus (UT) of two sections, lower shorter and much expanded.

Vas deferens (VD) a slender tube, slightly thicker than shaft of spermatheca, entering penis well below attachment of penial retractor muscle (fig. 125d). Penial retractor (PR) arising from columellar retractor and inserting on fleshy extension of penis head. Penis (P) about 1.3-1.5 mm. long, slightly expanded above, tapering to junction with vagina. Internally (fig. 125e) with typically modified two-pilaster pattern. After penis pore, both pilasters greatly enlarged, one or both splitting, forming a pocket, then tapering down to atrium. Atrium (Y) rather short, narrow.

Free oviduct (UV) with enlarged head, tapering to a tube several times diameter of vas deferens. Spermatheca (S) with enlarged head lying above pallial cavity, between albumen gland and kidney, inserting into vagina just above its union with atrium. Vagina (V) very short.

Free muscle system and digestive system as in *Australdonta raivavaeana.*

(Based on BPBM 148502, BPBM 149163-4, BPBM 95214, dissected adults 2.8-3.4 mm., with 5-5½ whorls.)

Fragmentary soft parts from one of the Mauke collections showed no differences from the genitalia of the Rimatara populations. Penial pilaster pattern matched, and since preservation was better than in the

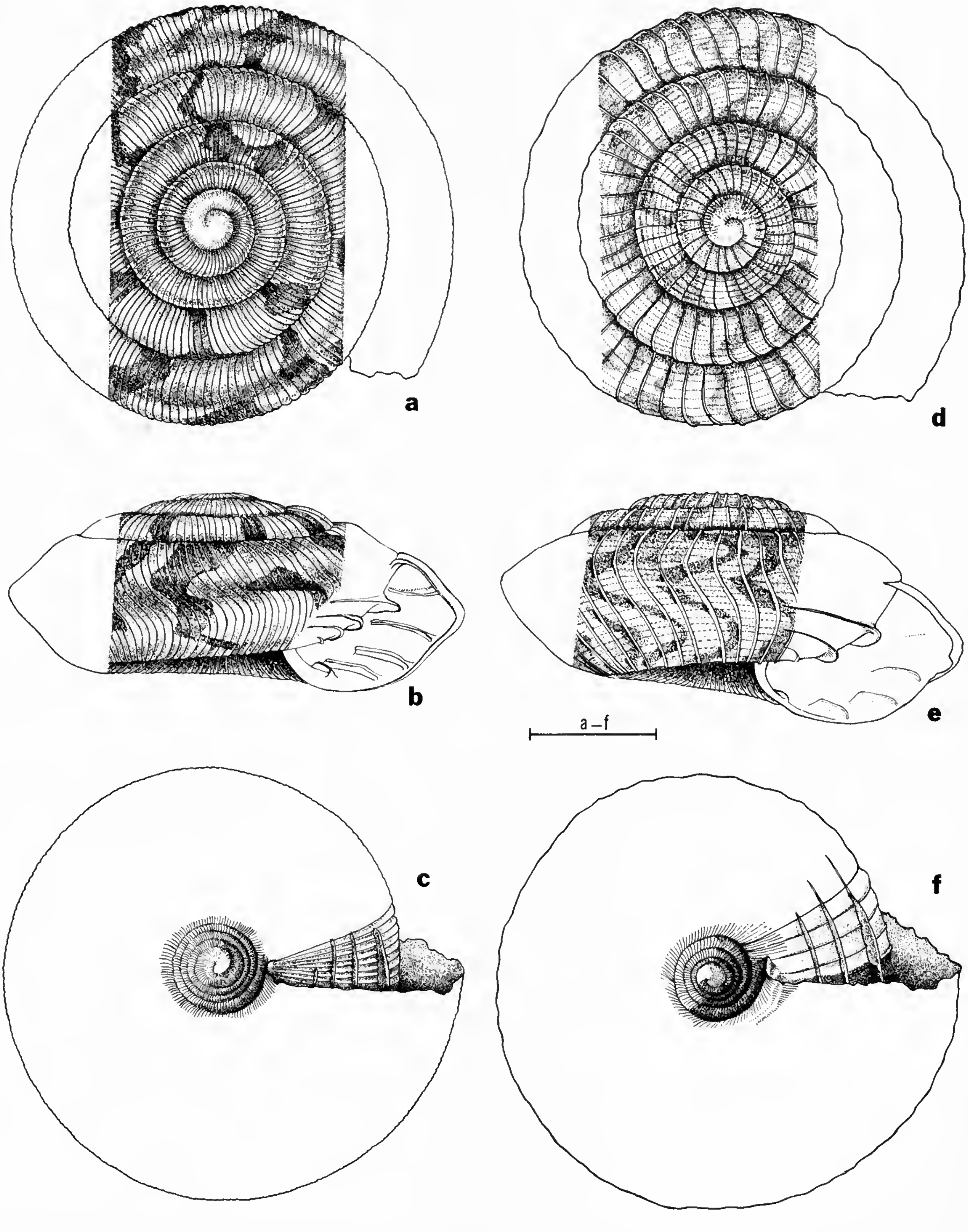

FIG. 129. **a-c**, *Australdonta tapina,* new species. Station 805, Avera, Rurutu, Austral Islands. Holotype. BPBM 148838; **d-f**, *Australdonta yoshii,* new species. Station 748, Mato Naa, Rurutu, Austral Islands. Holotype. BPBM 148130. Scale lines equal 1 mm. Microsculpture omitted except for indication of spiral grooves in *d* and *e*. (SG).

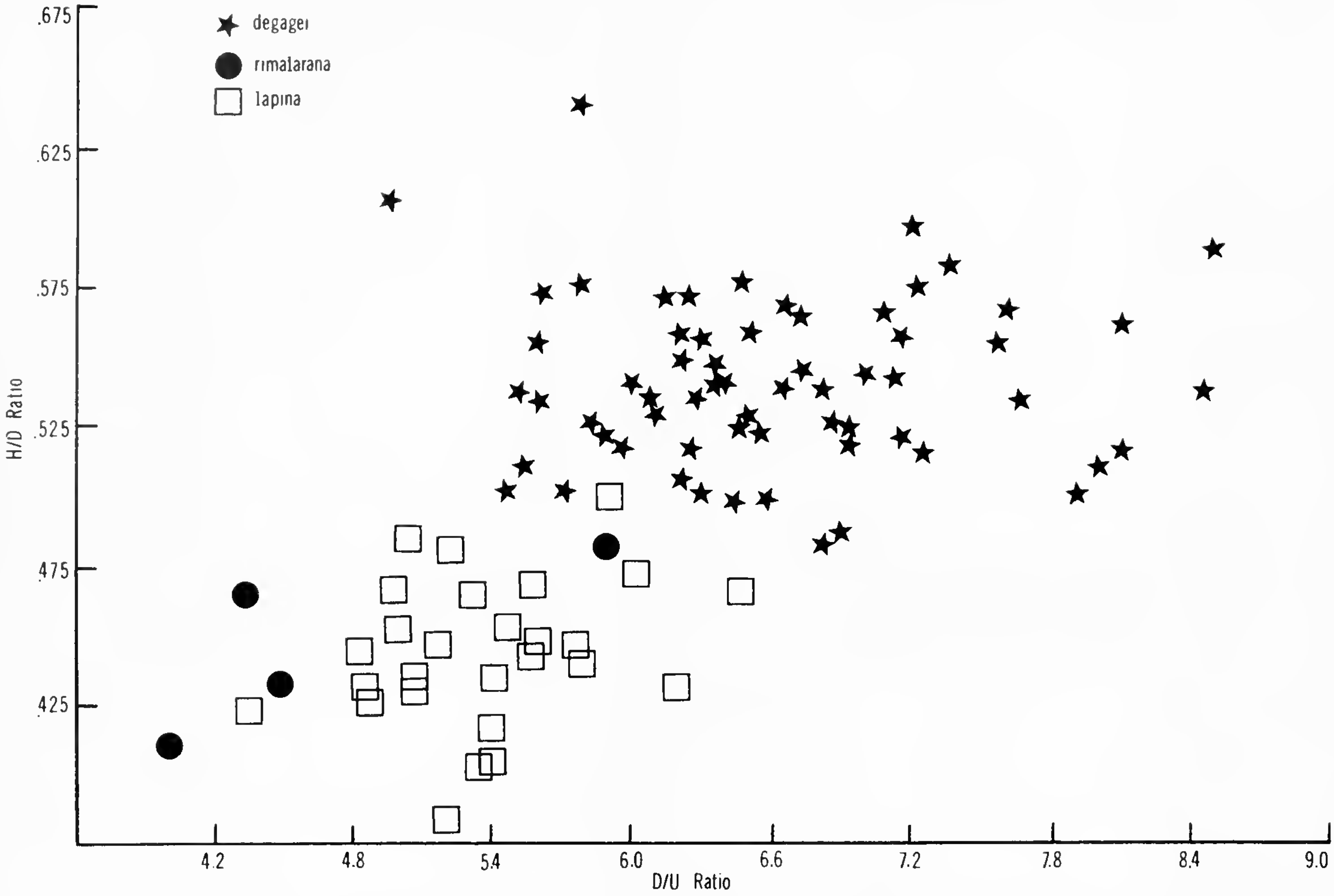

FIG. 130. Scatter diagram plotting H/D ratio and D/U ratio for *Australdonta degagei, A. rimatarana,* and *A. tapina.*

Rimatara examples, this dissection was figured (fig. 125e).

Australdonta tapina, new species. Figure 129a-c.

Diagnosis. — Shell of slightly less than average size, diameter 3.19-3.81 mm. (mean 3.51 mm.), with 5-6 rather loosely coiled whorls. Apex and spire slightly to moderately elevated, lower whorls descending a trifle more rapidly, H/D ratio 0.383-0.500 (mean 0.445). Umbilicus narrow, U-shaped, slightly decoiling, the last whorl a little more rapidly, contained 4.34-6.45 times (mean 5.35) in the diameter. Apical and microsculpture typical, spiral grooving prominent. Postnuclear whorls with narrow, prominent, crowded, strongly protractively sinuated radial ribs, 117-156 (mean 131.8) on the body whorl, whose interstices are 2-3 times their width. Sutures relatively shallow, whorls flattened above weak to moderate supraperipheral sulcus, periphery obtusely angulated, usually with noticeable subperipheral sulcus, lower palatal wall compressed and gently rounded, umbilical margin very strongly rounded. Aperture compressedly ovate, flattened laterally above slightly protruded periphery, gradually rounded below, inclined about 20° from shell axis. Parietal barriers 3 (28.6 per cent) or 4 (71.4 per cent), prominent, extending posteriorly one-quarter whorl: upper high, bladelike, serrated above on posterior half, rather sharp anterior descension after gradual slope; 2nd with posterior third equal in height to 1st, anterior third a high threadlike ridge; 3rd with posterior portion shorter and reduced in height, threadlike portion longer and lower; 4th, when present, a threadlike trace half the length of 3rd parietal, lying along posterior half or at most weakly elevated posteriorly and two-thirds length of 3rd parietal. No columellar barrier. Palatal barriers 5, prominent, extending about three-sixteenths of a whorl: lower a high ridge with moderately sharp anterior descension, lower than 2nd or 3rd; next two palatals higher, longer, slightly more deeply recessed, with more gradual anterior descension; 4th palatal a long, low flat-topped ridge with very gradual anterior descension; 5th palatal a deeply recessed, long, weak to prominent lamellar ridge.

The much more crowded ribs, larger and longer barriers, and more sharply angulated periphery easily separate *A. tapina* from *A. yoshii.* The smaller *A. rimatarana* has much smaller barriers and a less angulated periphery.

Description. — Shell of average size with 5½ rather loosely coiled whorls. Apex flat, postnuclear whorls descending slightly, H/D ratio 0.417. Apical whorls 1⅜, sculpture partly eroded, traces of fine radial ribs, two or three microradials in between, and a very fine microspiral reticulation visible in the sutures. Postnuclear whorls with narrow, prominent, strongly protractively sinuated radial ribs, 129 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, six to eight between each pair of major ribs, barely visible spiral riblets, and rather widely and irregularly spaced spiral grooves. Microsculpture finer than in most other species of *Australdonta.* Sutures rather shallow, whorls flatly rounded to weak supraperipheral sulcus, periphery nearly right angled, a weak subperipheral sulcus, then evenly rounded lower palatal wall to very strongly rounded umbilical margin. Color light yellow-white with widely spaced, irregularly shaped, reddish markings that fade out below periphery. Umbilicus narrow, U-shaped, last whorl decoiling a little more rapidly, contained 5.40 times in the diameter. Aperture compressedly ovate, somewhat flattened above and below slightly rostrate periphery, inclined about 20° from shell axis. Parietal barriers 4, extending about one-quarter whorl: upper

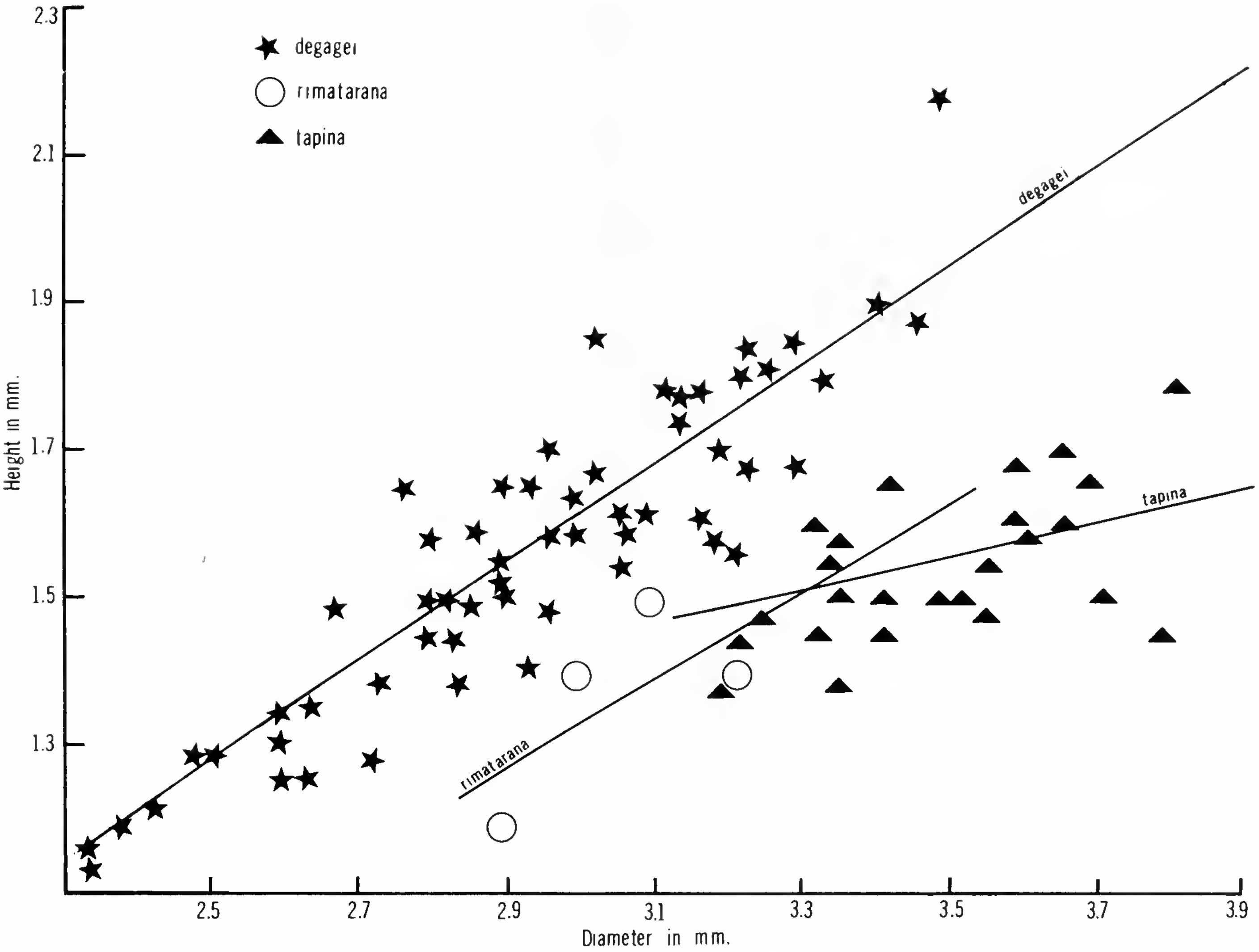

FIG. 131. Scatter diagram and regression lines for height and diameter in *Australdonta degagei, A. rimatarana,* and *A. tapina.*

high, bladelike, posterior half minutely serrated on top, gradually sloping to anterior margin; 2nd only slightly reduced in height for posterior elevated third, anterior third a high threadlike ridge; 3rd with posterior portion reduced in height and length, threadlike portion lower and longer; 4th parietal a threadlike ridge, elevated slightly posteriorly, only two-thirds length of 3rd parietal. No columellar barrier. Palatal barriers 5, extending three-sixteenths of a whorl, quite prominent: lower a slightly recessed ridge with fairly sharp anterior descension, lower than 2nd barrier; 2nd and 3rd higher, a little more deeply recessed, with much more gradual anterior descension; 4th equal in height to 1st with very gradual anterior descension; 5th palatal supraperipheral, a high ridge slightly lower than 4th palatal, deeply recessed. Height of holotype 1.48 mm., diameter 3.56 mm.

Holotype. — Austral Islands: Rurutu, Station 805, hillside north of Avera, 50-100 ft. inland, at 5-30 ft. elevation. Collected on a Makatea cliff by Yoshio Kondo and Donald Anderson on August 31, 1934. BPBM 148838.

Range. — Lowlands of Rurutu, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rurutu: Vicinity of Avera (Stations 804, 805, 806, 822) at 2-30 ft. (69 specimens, BPBM 148823, BPBM 148836-8, BPBM 148867, BPBM 149045-6); north of cave at Mato Arapia (Station 819) at 50 ft. elevation (17 specimens, BPBM 149011); bluff at Mato Naa (Station 760) at 5-15 ft. elevation (19 specimens, BPBM 148290); cliff at Mato Arei (Stations 769, 775) at 5-150 ft. elevation (7 specimens, BPBM 148426, BPBM 148558).

Remarks. — Despite many similarities, *Australdonta tapina* and *A. rimatarana* appear to be well-characterized and distinct species. The latter has an obtusely rounded periphery, deeply impressed sutures, strong spiral grooving, shorter and smaller apertural barriers that extend more than one-eighth whorl and more widely spaced ribbing. In contrast, *A. tapina* has an acutely angulated periphery, shallow sutures, weaker spiral grooving, long lamellar apertural barriers that extend nearly one-quarter whorl, and very crowded ribbing. They have very similar patterns of growth and measurements (figs. 130, 131) with identification of the species depending on the more qualitative differences outlined above. The very fine microsculpture of *A. tapina* probably is a consequence of the excessive rib crowding. In all other *Australdonta,* the microsculpture is much more prominent.

Of 28 nearly adult specimens 20 have 4 parietals and eight have only 3. As in *A. raivavaeana,* the proportion of specimens with 3 parietals suggests that possibly a simple Mendelian ratio is involved (fig. 126). In the case of *A. tapina,* however, the recessive could be responsible for the absence of the 4th parietal, which is exactly opposite the situation observed in *A. raivavaeana.* All specimens of *A. tapina* had 5 palatal barriers.

Australdonta yoshii, new species. Figure 129d-f.

Diagnosis. — Shell smaller than average, diameter 2.90-3.55 mm. (mean 3.30 mm.), with 5 - 5½ relatively loosely coiled whorls. Apex flat, postnuclear whorls descending progressively more rapidly, H/D ratio 0.463-0.531 (mean 0.490). Umbilicus narrow, U-shaped, slightly decoiling, last whorl a little more rapidly, contained 5.20-7.39 times (mean 6.11) in the diameter. Apical and microsculpture typical, spiral grooving prominent. Postnuclear whorls with low but prominent, narrow, very widely spaced, protractively sinuated radial ribs, 54-72 (mean 65.9) on the body whorl, whose interstices are 4-6 times their width. Sutures shallow, whorls flatly rounded above weak supraperipheral sulcus, periphery nearly right angled, very slight subperipheral sulcus, compressed lower palatal wall and strongly rounded umbilical margin. Aperture subovate, flattened laterally above strongly angled periphery, lower margins compressed, inclined about 15° from shell axis. Parietal barriers 3, occasionally 4 (9.1 per cent), extending posteriorly slightly more than three-sixteenths of a whorl, reduced in height: upper an elevated lamella, serrated above on posterior half, with gradual anterior descension; 2nd reduced in height, posterior half elevated, anterior third threadlike; 3rd parietal threadlike for entire length, slightly broadened, but not elevated posteriorly or with weakly lamellar elevated posterior half; 4th parietal, when present, a threadlike trace below 3rd parietal. Columellar barrier absent. Palatal barriers 5, short, low, extending less than one-eighth whorl: lower a threadlike or crescentic recessed ridge at baso-columellar margin; 2nd and 3rd elongated, raised lamellar blades with gradual anterior descension; 4th reduced in height, more deeply recessed, U-shaped, or a low lamellar ridge; 5th supraperipheral, a deeply recessed threadlike to V-shaped ridge.

The very widely spaced sculpture, reduced barrier size, and smaller diameter easily separate *Australdonta yoshii* from *A. tapina.* The latter has much finer sculpture (mean ribs 131.8), larger barriers, and is a little larger (mean diameter 3.51 mm.). The other species of similar size, *A. rimatarana* and *A. degagei,* are much less sharply angulated and have finer sculpture.

Description. — Shell of average size, with 5½ relatively loosely coiled whorls. Apex flat, whorls of spire descending progressively more rapidly, H/D ratio 0.477. Embryonic sculpture partly eroded, traces of radial ribbing visible in suture. Lower whorls with quite low and narrow, widely spaced, protractively sinuated radial ribs, 54 on the body whorl, whose interstices are 5-6 times their width. Microsculpture of exceedingly fine and numerous radial riblets, even finer and more crowded spiral riblets, plus rather prominent, irregularly spaced spiral grooves. Sutures quite shallow, whorls flatly rounded to weak supraperipheral sulcus. Periphery nearly right angled, followed by a weak subperipheral sulcus, lower palatal wall laterally compressed, evenly rounded to strongly rounded umbilical margin. Color light yellow-white, with prominent somewhat irregular, zigzagged, reddish flammulations, becoming narrower and more sharply angled on base of shell, merging near or in umbilicus. Umbilicus narrow, U-shaped, last whorl decoiling slightly more rapidly, contained 6.06 times in the diameter. Aperture subovate, slightly flattened above weakly rostrate periphery, inclined about 15° from shell axis. Parietal barriers 3, small, extending slightly less than one-quarter whorl; upper a high lamellar ridge, weakly expanded and serrated on posterior half, with gradual descension until anterior edge; 2nd less than half height of 1st on posterior third, anterior half threadlike; 3rd threadlike for entire length, weakly expanded and elevated posteriorly. No columellar barrier. Palatal barriers 5, very low, extending less than one-eighth whorl: lower columellar-basal in position, a short, moderately recessed lamellar ridge; 2nd and 3rd raised lamellar ridges, much higher than 1st, with very gradual anterior descension, moderately recessed, relatively long, with flat upper edge; 4th a long, low, V-shaped ridge, quite deeply recessed; 5th a barely visible threadlike trace, supraperipheral, about same length as 4th. Height of holotype 1.71 mm., diameter 3.59 mm.

Holotype. — Austral Islands: Rurutu, Station 748, foot of cliff, Mato Naa at 250 ft. elevation. Collected by C.M. Cooke, Jr., and Yoshio Kondo on August 25, 1934. BPBM 148130.

Range. — Known only from the type collection.

Paratypes. — Same as list of material.

Material. — Rurutu: foot of cliff, Mato Naa (Station 748) at 250 ft. elevation (115 specimens, BPBM 148130).

Remarks. — Only the one set of this very beautiful and well-characterized species was found. In general appearance and apertural barriers it is an obvious derivation of the *A. tapina* and *A. rimatarana* series, but differs strikingly by its very widely spaced sculpture, sharply angled periphery, and reduced size of the apertural barriers. The type is unusual in having the barriers smaller than in most other individuals and possessing the smallest number of ribs observed on an adult specimen. It was selected as holotype because of its excellent preservation. Only 10 individuals were clearly adult, the remainder being either partly broken shells or obvious juveniles. Barrier variation was minimal; one of the cleaned specimens had a 4th parietal.

Great pleasure is taken in dedicating this species to Dr. Yoshio Kondo of the Bernice P. Bishop Museum, without whose friendly aid and assistance this study never would have been started, much less completed.

Australdonta magnasulcata, new species. Figure 127a-c.

Diagnosis. — Shell of average size, diameter 3.76 mm., with 5⅜ rather loosely coiled whorls. Apex flat, whorls of spire descending progressively more rapidly, H/D ratio 0.377. Umbilicus broadly open, V-shaped, regularly decoiling, contained 3.36 times in the diameter. Apical and microsculpture typical. Postnuclear whorls with thick, very prominent, crowded, protractively sinuated radial ribs, 95 on the body whorl, whose interstices are about equal to their width. Sutures impressed, whorls sharply rounded down to prominent supraperipheral sulcus. Periphery protruded into corded keel, subperipheral sulcus prominent, lower palatal wall evenly rounded to very sharply turned umbilical margin. Aperture ovate, with rostrate periphery, inclined about 20° from shell axis. Parietal barriers 3 or 4, large, extending more than one-quarter whorl: upper a high lamellar ridge, posterior two-thirds minutely serrated above, with sharp anterior descension; 2nd with posterior half equally high, anterior third threadlike; 3rd with posterior half distinctly lower, anterior third threadlike; 4th, when present, a threadlike ridge only weakly elevated posteriorly. Columellar barrier absent. Palatal barriers 5, deeply recessed, large, extending more than one-eighth whorl: lower baso-columellar in position, a low lamellar ridge with gradual anterior descension; 2nd, 3rd, and 4th much higher, longer, more deeply recessed with very gradual anterior descension, posterior third with flat upper margin; 5th a high, V-shaped, supraperipheral, deeply recessed ridge, shorter and much lower than 4th palatal.

The rostrate periphery and very heavy ribbing of *Australdonta magnasulcata* immediately separate it from the other species of the genus. The very low spire and widely open umbilicus are almost as distinctive. The ribbing is very similar to that found in *Libera fratercula* from the Cook Islands and some of the *Gambiodonta* from Mangareva, but the microsculpture of irregular spiral grooves combine with the number and form of the apertural barriers to place *magnasulcata* in *Australdonta*.

Description. – Shell a little larger than average, with 5⅜ rather loosely coiled whorls. Apex flat, postnuclear whorls descending slightly and progressively more rapidly, H/D ratio 0.377. Apical whorls 1⅜, sculpture partly eroded, traces of fine radial and much finer microradial riblets remaining in suture. Postnuclear whorls with high, rounded, crowded, protractively sinuated radial ribs, 93 on the body whorl, whose interstices are about equal to their width. Ribs narrowing, but remaining distinct within umbilicus. Microsculpture of very fine and crowded radial riblets, usually worn off on top on major ribs, much finer and more crowded spiral riblets, and irregularly spaced, rather prominent spiral grooves. Sutures impressed, whorls sharply rounded down to deep supraperipheral sulcus, periphery protruded into cordlike beak, subperipheral sulcus weaker than supraperipheral, lower palatal wall flatly and evenly rounded to very sharply turned umbilical wall. Color light yellow horn with faint, irregular, rather widely spaced, reddish flammulations that fade out on base of shell. Umbilicus broadly open, V-shaped, regularly decoiling, contained 3.36 times in the diameter. Aperture ovate, with rostrate periphery, inclined about 20° from shell axis. Parietal barriers 4, extending one-quarter whorl, large in size: upper a high lamellar ridge, upper edge irregularly chipped, with gradual anterior descension; 2nd with posterior three-fourths broken off, anterior edge threadlike; 3rd with posterior half elevated to about two-thirds height of 1st parietal, anterior third threadlike; 4th parietal a threadlike ridge, very low anteriorly, slightly elevated and thickened posteriorly. No columellar barrier. Palatal barriers 5, relatively large, extending more than one-eighth whorl, badly broken off above: lower a deeply recessed lamellar ridge with very gradual anterior descension, relatively low; 2nd much higher posteriorly, longer, anterior three-fourths broken off; 3rd equal in length to 2nd, almost entire length broken off above; 4th a distinctly lower lamellar ridge, deeply recessed, with very gradual anterior descension; 5th supraperipheral, V-shaped, almost as high as 4th palatal, very deeply recessed within aperture. Height of holotype 1.41 mm., diameter 3.76 mm.

Holotype. – Austral Islands: Rurutu, Station 760, bluff at Mato Naa, 5-15 ft. elevation, about 20-30 yd. inland. Collected by Yoshio Kondo and C. M. Cooke, Jr., on August 26, 1934. BPBM 148291.

Range. – Rurutu Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Rurutu: bluff at Mato Naa (Station 760) about 20-30 yd. inland at 5-15 ft. elevation (4 specimens, BPBM 148131, BPBM 148291); mouth of cave at Mato Arapia (Station 819) at 50 ft. elevation (1 specimen, BPBM 149010).

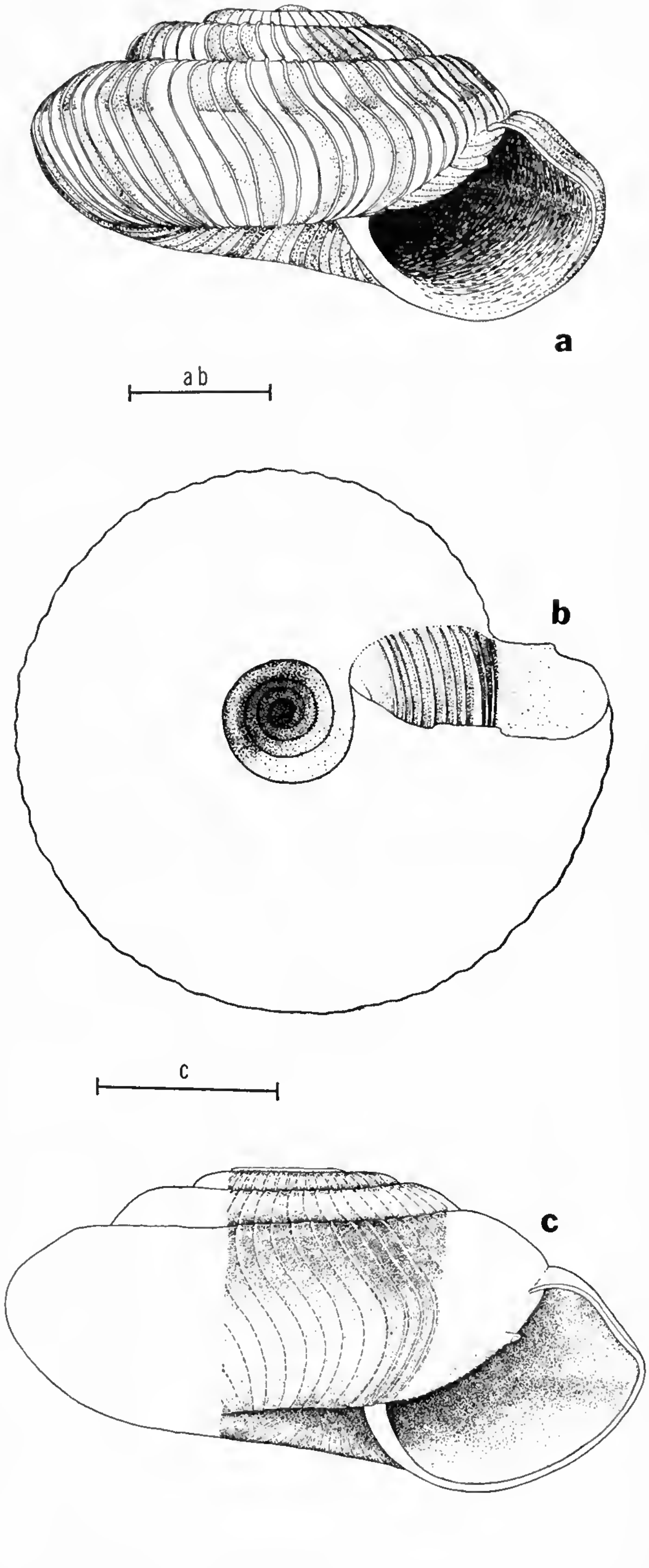

FIG. 132. **a-b**, *Australdonta radiella radiella* (Pfeiffer). Tubuai, Austral Islands. BPBM 106236; **c**, *Australdonta radiella rurutuensis* (Garrett). Rurutu, Austral Islands. Lectotype. BPBM 944. Scale lines equal 1 mm. Microsculpture omitted in all figures. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Remarks. — The flattened shape, strongly keeled periphery, and heavy ribbing recall many of the Gambier and Cook Island forms rather than the Austral Island endodontids. Only one adult and four juveniles of this evidently very rare species were obtained. The coarsening of the ribbing and markedly rostrate periphery represent the extreme shell development found in *Australdonta*. While *A. yoshii* and *A. tapina* have slightly rostrate peripheries, the development in *A. magnasulcata* is much greater. All individuals were dead when collected.

Australdonta radiella radiella (Pfeiffer, 1846). Figure 132a-b.

Helix radiella Pfeiffer, 1846, Proc. Zool. Soc. London, **1845**, p. 125 — Rapa Island (error); Pfeiffer, 1848, Monog. helic. viv., **1**, p. 100; Pfeiffer, 1852, Syst. Conchyl. Cab., I, **12**, (2), pp. 132-133, pl. 89, figs. 12-15 (plate issued in 1850); Pfeiffer, 1852, Conchol. Icon., *Helix*, pl. 112, fig. 643; Pfeiffer, 1853, Monog. Helic. viv., **3**, p. 96; Pfeiffer, 1859, *Ibid.*, **4**, p. 90; Pfeiffer, 1876, *Ibid.*, **7**, p. 162.

?*Helix pardalina* Deshayes, 1850, Hist. nat. moll. terr. fluv., **1**, pp. 88-89, pl. 83, figs. 3-4 — Ochetaroa (= Rurutu?); Pfeiffer, 1853, Monog. helic. viv., **2**, p. 96 — listed as a synonym of *radiella* Pfeiffer, 1846.

Helicella undulata "Ferussac" Pfeiffer, 1853, Monog. helic. viv., **2**, p. 96 — nude name taken from museum specimens.

Helix (*Punctum*) *radiella* Pfeiffer, Tryon, 1887, Man. Conchol., (2), **3**, p. 38, pl. 8, fig. 18 (copied from Conchol. Icon.).

Endodonta (*Thaumatodon*) *radiella* (Pfeiffer), Pilsbry, 1893, Man. Conchol., (2), **9**, pp. 26-27.

Diagnosis. — Shell large, diameter 3.59-4.61 mm. (mean 4.04 mm.), with 5⅛-5⅞ normally coiled whorls. Apex flat, whorls of spire descending progressively more rapidly, H/D ratio 0.468-0.565 (mean 0.517). Umbilicus moderately open, U-shaped, slightly decoiling, contained 3.90-5.90 times (mean 4.93) in the diameter. Apical and microsculpture typical. Postnuclear whorls with rather sharply defined, sinuately protractive radial ribs, 67-92 (mean 78.1) on the body whorl, whose interstices are 3-6 times their width. Sutures prominent, whorls evenly rounded below suture to somewhat flattened upper palatal wall, obtusely rounded periphery, evenly rounded but slightly compressed lower palatal wall and more strongly rounded basal and umbilical margins. A barely noticeable to prominent, broad and shallow supraperipheral sulcus present. Aperture subovate, slightly to strongly compressed above periphery, inclined about 15° from shell axis. Parietal wall with 4-14 (usually 7-11) threadlike barriers, extending posteriorly one-quarter whorl, with one on the upper third of the wall being a much more prominent threadlike ridge. No columellar or palatal barriers.

The absence of any palatal or columellar barriers immediately separates *Australdonta radiella radiella* from most *Australdonta*. *A. radiella rurutuensis* differs only in having 17 parietals and may not be separable when more material is available, while *A. ectopia* has a single parietal thread and a widely open umbilicus. All other species have 2-5 large parietals and prominent palatals.

Description. — Shell large, with 5½ normally coiled whorls. Apex slightly elevated, lower whorls descending more rapidly, H/D ratio 0.514. Apical whorls 1⅜, sculpture partially eroded in holotype, paratypes with sculpture of narrow but prominent radial ribs, whose interstices are 3-5 times their width at beginning, becoming more crowded lower down with one secondary riblet between each major pair for first 1¼ whorls, two secondary radial riblets on later portion. Microspiral sculpture of fine, relatively widely spaced ribs. Postnuclear whorls with narrow, rounded, protractively sinuated, moderately widely spaced radial ribs, 74 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine but relatively prominent radial ribs, crossed by much finer and more crowded spiral riblets with a secondary sculpture of impressed spiral lines most clearly seen on portions of body whorl and in umbilicus. Sutures deep, whorls flatly rounded above, flattened laterally below obtusely rounded periphery, basal and umbilical margins evenly rounded. Color faint yellowish-white with narrow zigzag reddish brown flammulations, continuing onto base of shell. Body whorl with slight supraperipheral sulcus. Umbilicus narrowly U-shaped, slightly but regularly decoiling, contained 4.60 times in the diameter. Aperture subquadrangular, strongly flattened laterally above and slightly less so below periphery, inclined about 15° from the shell axis. Lip edge broken. Parietal wall with 8 fine, regularly spaced, threadlike barriers, extending for almost one-quarter whorl; upper most prominent and nearly twice as high as remaining. Height of lectotype 2.34 mm., diameter 4.54 mm.

Lectotype. — Austral Islands: "Opara" (in error). Collected by Hugh Cuming. BMNH 1962701/1.

Range. — Tubuai, Austral Islands.

Paratypes. — "Opara" or "Opana" (=Rapa, error) (10 specimens, BMNH 1962701/2-5, BPBM 106236 ex Webb, BPBM 167415 ex Fulton, Grateloup, Pfeiffer, SMF 165740 ex Knobbe, SMF 165741 ex Pfeiffer).

Material. — Austral Islands: Tubuai, trail south of Murivai (Station 699) at 6-8 ft. elevation in sandy soil (136 specimens, BPBM 147706); 100-200 yd. west of Mataura at about 100 yd. inland (Station 696) under *Barringtonia* trees (55 specimens, BPBM 147638, BPBM 147660, BPBM 147968); south of Hoopua about 200-300 yd. inland (Station 703) at 5 ft. elevation (81 specimens, BPBM 147724-5); fossils taken from walls at Taahuaia (Stations 702, 704) (11 specimens, BPBM 147719, BPBM 147741); 75 ft. inland at Teuo (Station 707) at 3 ft. elevation (6 specimens, BPBM 147760). Rapa (error) (2 specimens, FMNH 46510 ex Fulton, FMNH 46604 ex Gude, Stevens).

Remarks. — Originally described as coming from Rapa, *Helix radiella* is moderately common in older collections. The Mangarevan Expedition found it on Tubuai in subfossil deposits, but obtained no material from Rapa. Undoubtedly, this is one of the many locality confusions present in the Cuming collection. According to St. John (1940, pp. 87-88), Hugh Cuming collected on Tubuai May 5, 1828 and this may be taken as the time when the type and paratype specimens were obtained. Probably all specimens in old collections labelled "Opara" or "Opana" are type lot specimens. I have listed as paratypes only those individuals that could be traced as coming from the Cuming or Pfeiffer collections.

All of the Mangarevan material was collected from subfossil deposits and the apertures were clogged with dirt. Thirty individuals were cleaned in order to check the parietal barriers. The extremes were 4 and 14, with considerable clustering. Ten individuals had 11 barriers, 5 had 8, and 4 had 10. Twenty-three of the 30 had 8-12, only 2 had more than 12 and 5 had 4-7. No difference was noted between Cuming and Mangarevan materials in respect to barrier count.

Comparatively few specimens were clearly adult. Of the 291 Mangarevan Expedition shells, only eight were adult and measured. The rest were subadult or so encrusted that no attempt at cleaning or measuring was made. Comparison of these shells with the Cuming material, 11 examples, showed minor differences except in regard to rib count (table XC). With 21df[1], "*t*" = 2.830 for the rib counts, reaching the 5 per cent probability level that the recent shells have more ribs than those collected by Cuming. The differences in size and shape were small enough that no question of difference arose and "*t*" was not calculated. Shells from Station 699 had relatively wide umbilici (table XCI), and the few adults from Stations 702 and 707 much narrower. Too few specimens are involved for meaningful statistical analysis.

Of the other names listed in the synonymy, *Helix undulata* is a nude name taken from museum specimens while *Helix pardalina* may refer to the Rurutu subspecies. No specimens of *pardalina* could be located, but I have chosen to consider it a synonym of *A. r. radiella*. The reference of the island name, Ocheteroa, is obscure. Either Tubuai or Rurutu could be intended.

Australdonta radiella rurutuensis (Garrett, 1879). Figure 132c.

Patula rurutuensis Garrett, 1879, Proc. Acad. Nat. Sci., Philadelphia, **1879**, p. 18 – Rurutu, Austral Islands (Charles De Gage!).

Helix (Endodonta) rurutuensis (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 61.

Endodonta (*Thaumatodon*) *rurutuensis* (Garrett), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Diagnosis. – The only significant difference from *Australdonta radiella radiella* lies in having 17 distinguishable parietals. Shape and sculpture fall within the limits of variation observed for the nominate race. The diameter (3.52 mm.) is less than that of nearly all adult *A. radiella radiella*, but the shell is clearly subadult and this difference has no significance.

Description. – Shell subadult, smaller than average of nominate race, with slightly less than 5⅛ normally coiled whorls. Apex flat, lower whorls of spire descending progressively more rapidly, H/D ratio 0.506. Apical whorls 1⅜, sculpture eroded by fungus except for traces of radial ribs in suture. Postnuclear whorls with prominent, V-shaped, protractively sinuated radial ribs, 73 on the body whorl, whose interstices are 3-6 times their width. Microsculpture of fine and crowded radial ribs, crossed by very much finer and more crowded spiral riblets. A secondary sculpture of vague, irregularly spaced, shallow spiral grooves that are more prominent on shell base. Sutures moderately impressed, evenly rounded below suture, whorls slightly flattened above and below obtusely rounded periphery, basal and umbilical margins evenly rounded. Color light yellow horn with prominent, rather wide, zigzag, reddish flammulations, becoming narrow and strongly protractive on shell base. Umbilicus moderately open, U-shaped, slowly and evenly decoiling, contained 4.86 times in the diameter. Aperture subquadrangular, flattened laterally above and below obtusely rounded periphery, inclined about 15° from shell axis. Parietal wall with 17 low, threadlike ridges, extending posteriorly beyond line of vision, 3rd from top a low, rounded ridge nearly twice the height of the others. Columellar and palatal walls without barriers. Height of lectotype 1.81 mm., diameter 3.52 mm.

Lectotype. – Austral Islands: Rurutu. Collected by Andrew Garrett. BPBM 944.

Range. – Rurutu, Austral Islands.

Material. – The lectotype was the only specimen located.

Remarks. – The original description mentions only a single parietal, but without use of a microscope, the very low and inconspicuous parietal threads easily could be overlooked. In other respects, the type description and lectotype agree.

Despite rather extensive collections made on Rurutu during the Mangarevan Expedition, no additional material of this species was found. The possibility exists that *rurutuensis* was based on an atypical specimen of *A. radiella* from Tubuai. In view of Garrett's extreme care concerning locality data, I am retaining it as a distinct taxon. If additional collections of subfossil material on Tubuai extend the parietal lamellar variational range in *A. radiella radiella* to include 17 barriers, then *A. r. radiella* and *A. r. rurutuensis* should be synonymized.

Australdonta raivavaeana, new species. Figures 125a-c, g; 133a-c.

Diagnosis. – Shell very large, diameter 4.08-5.13 mm. (mean 4.50 mm.), with 5¼-6½ normally coiled whorls. Apex and early spire flat, rarely slightly depressed, whorls of lower spire descending progressively more rapidly, H/D ratio 0.420-0.540 (mean 0.479). Umbilicus narrowly U-shaped, slightly and regularly decoiling, contained 4.00-5.50 times (mean 5.27) in the diameter. Apical and microsculpture typical, spiral grooves prominent. Postnuclear whorls with narrow, relatively high, protractively sinuated radial ribs, 81-148 (mean 109.4) on the body whorl, whose interstices are 2-5 times their width. Sutures prominent, whorls flattened laterally above weak to almost absent supraperipheral sulcus, periphery right to obtusely angled with rounded margin, lower palatal wall evenly and gently rounded although laterally compressed. Umbilical and basal margins strongly rounded. Aperture subovate, flattened laterally above periphery, inclined about 15° from shell axis. Parietal wall usually with 3 (74.6 per cent) or 4 (22.1 per cent) barriers extending posteriorly about three-sixteenths of a whorl, rarely (3.3 per cent) with one to three accessory traces present: upper a high bladelike ridge with gradual anterior descension on last sixth; 2nd with high posterior quarter, gradual descension to about midpoint, then threadlike anterior section; 3rd same as 2nd, only a little reduced in height; 4th (when present) usually a threadlike trace (occasionally with posterior eighth weakly elevated), located below and proportionately closer to 3rd parietal. Columellar wall without (23 per cent) or with a very short, threadlike ridge (77 per cent) extending less than one-eighth whorl. Palatal wall with 4 short barriers, occasionally (8.1 per cent) 1 or 2 extra present: lower a high ridge, flattened above, with fairly sharp anterior descension, extending a short distance back; 2nd and 3rd equal in height, longer, with more gradual anterior descension; upper supraperipheral, a weak V-shaped or bladelike ridge slightly shorter than 3rd barrier. Accessory traces variously distributed between lower three barriers.

A. tubuaiana from Tubuai is nearly identical in size and umbilical width, but has a much more sharply angled periphery with slight subperipheral sulcus, larger and more prominent barriers, and a lower spire (H/D ratio 0.410-0.480). The only other *Australdonta*

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[1] Rib counts could be made on a few individuals whose broken outer lip prevented measurement of the diameter, and one measured example had the sculpture obscured by fungal growth, hence $N_1 = 13$ and $N_2 = 10$ in this calculation.

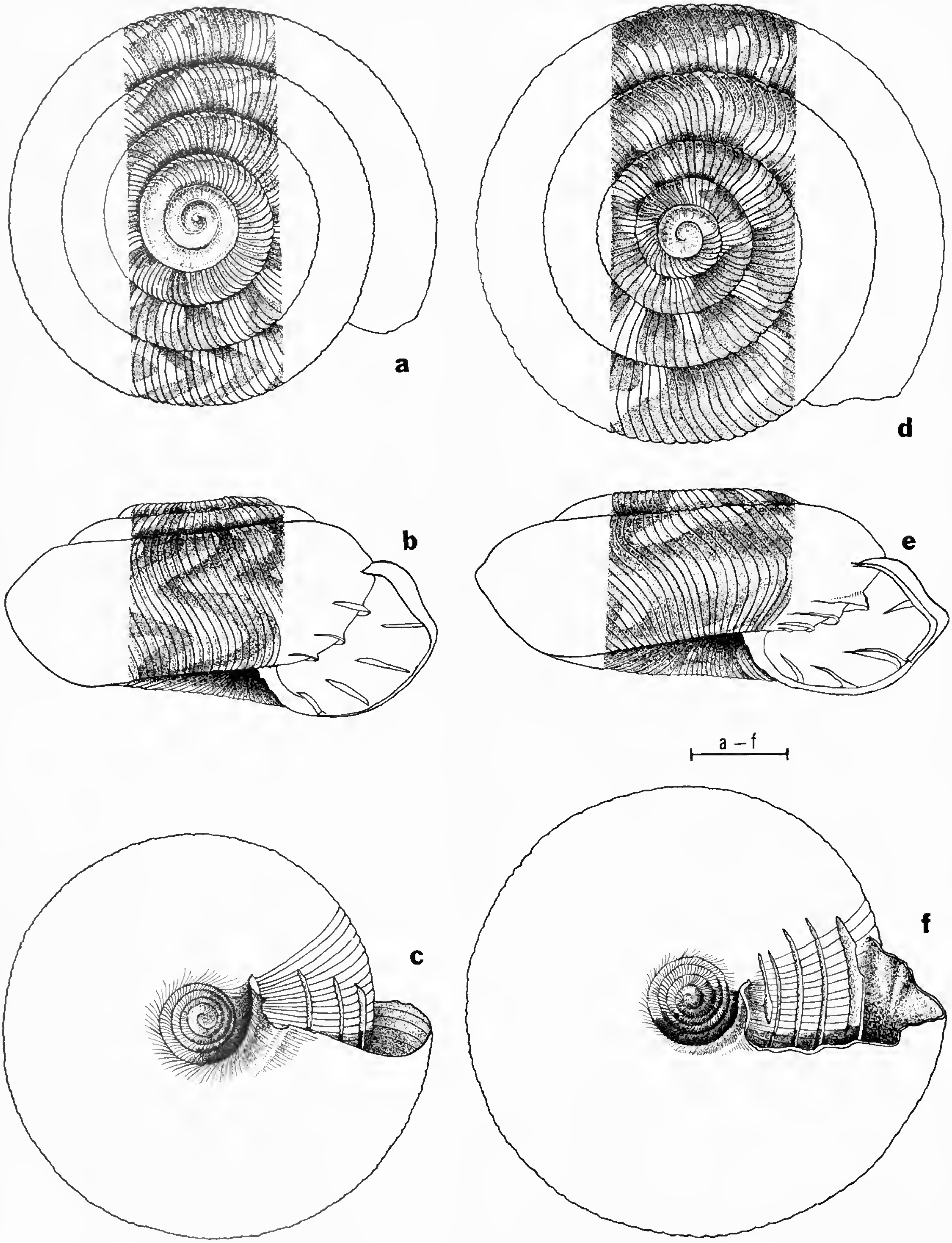

FIG. 133. **a-c**, *Australdonta raivavaeana*, new species. Station 674, Mt. Turivao, Raivavae, Austral Islands. Holotype. BPBM 147529; **d-f**, *Australdonta tubuaiana*, new species. Station 698, Murivai, Tubuai, Austral Islands. Holotype. BPBM 147705. Scale lines equal 1 mm. Microsculpture omitted in all figures. (SG).

of similar size, *A. radiella*, lacks any palatal barriers. All other species are much smaller.

Description. – Shell large, with slightly more than 6 normally coiled whorls. Apex and early spire flat, later whorls descending progressively more rapidly, H/D ratio 0.447. Apex and upper spire with sculpture eroded. Lower whorls with narrow, prominent, moderately crowded, protractively sinuated radial ribs, 123 on the body whorl, whose interstices are 3-6 times their width. Microsculpture of fine radial riblets, usually eight to twelve between major rib pairs and barely visible microspiral riblets. Secondary microsculpture of irregularly spaced spiral grooves more clearly visible than the very faint and crowded microspiral ribbing. Sutures prominent, whorls flattened laterally above weak supraperipheral sulcus, periphery obtusely angulated, lower palatal wall gently and evenly rounded to strongly rounded basal margin. Color light yellow horn with prominent, regularly spaced, zigzag, red flammulations, narrow at periphery, widening and tending to merge in umbilicus. Umbilicus narrow, U-shaped, slightly and regularly decoiling, contained 4.79 times in the diameter. Aperture subovate, slightly flattened laterally above periphery, inclined about 15° from shell axis. Parietal barriers 3, extending about three-sixteenths of a whorl posteriorly: upper high and bladelike with sharp anterior descension, upper edge slightly expanded and minutely serrated on posterior half; 2nd parietal identical for posterior quarter, gradually descending with anterior half threadlike; 3rd parietal much lower, less than posterior one-quarter elevated and serrated, anterior two-thirds low and threadlike. Columellar barrier absent. Palatal barriers 4, short, moderately recessed: lower high and bladelike, with rather sharp anterior descension; 2nd and 3rd equal in height, longer, progressively more recessed and with more gradual anterior descension; 4th supraperipheral, a deeply recessed, low, threadlike ridge, slightly shorter than 3rd barrier. Height of holotype 1.98 mm., diameter 4.40 mm.

Holotype. – Austral Islands: Raivavae Island, Station 674, south cliff of Mt. Turivao at 650 ft. elevation. Collected under clumps of *Hymenolepis* by Donald Anderson and Elwood Zimmerman on August 13, 1934. BPBM 147529.

Range. – Raivavae Island, Austral Islands.

Paratypes. – Same as list of material.

Material. – Raivavae Island: south cliff of Mt. Turivao (Station 674) at 650 ft. elevation (731 specimens, BPBM 147515-29); Ahuoivi Pt. (Station 622) at 5 ft. elevation under dead leaves (3 specimens, BPBM 142174, BPBM 147097); Anatonu (Stations 633, 636, 652) at 50-150 ft. elevation (89 specimens, BPBM 147165, BPBM 147195, BPBM 147383, BPBM 147386); pass between Mt. Hiro and Araua (Station 646) at 1,000+ ft. on ground under orange trees (1 specimen, BPBM 147266); pass between Mt. Turivao and Mt. Muatapu (Station 662) at 550 ft. elevation on dead pandanus leaves (1 specimen, BPBM 147449); south cliff of Mt. Taraia (Stations 551, 577, 589) at 850-900 ft. elevation (57 specimens, BPBM 146566-8, BPBM 146225, BPBM 146587-9).

Remarks. – *Australdonta raivavaeana* was quite common in the native vegetation on Mt. Turivao and was taken in lesser numbers alive on Mt. Taraia at 850 ft. elevation. A few scattered individuals were collected dead or as fossils in lowland localities. Many of the specimens from Mt. Taraia had the supraperipheral sulcus quite strongly developed, but most individuals approached the more typical condition found in the type population. In addition, the mean umbilical width of the Taraia examples was significantly wider (table XCI) than the Turivao examples, with 60 df, "*t*" = 6.4721 for D/U ratio, but only 1.2243 for H/D and 0.0426 for D. These could be considered different subspecies in view of the two differences cited above, but I prefer not to add another name to the literature when the differences are so minor.

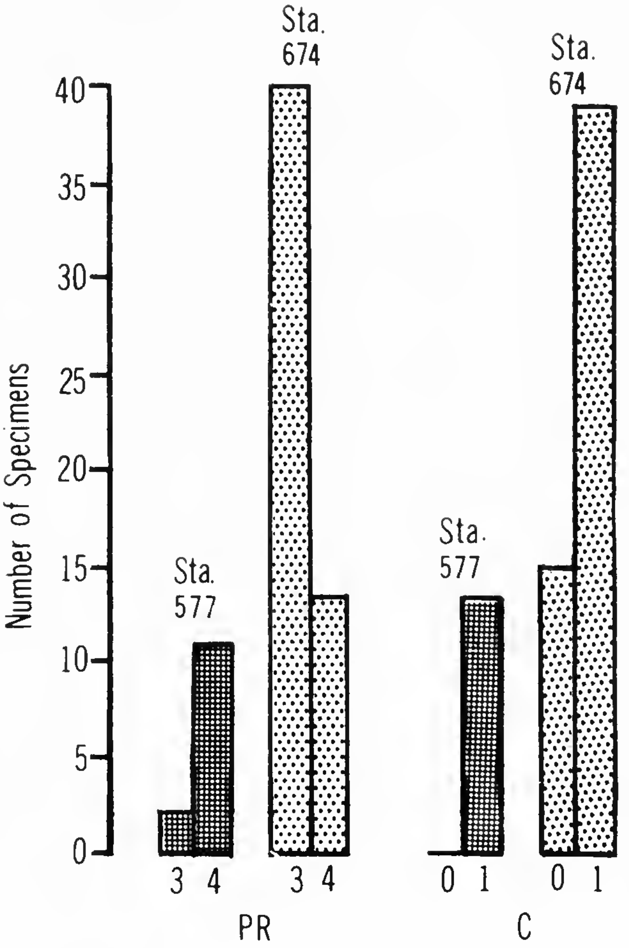

FIG. 134. Parietal and columellar lamellae frequency variations in two populations of *Australdonta raivavaeana*.

Comparatively few individuals, 66 of 882, were adult. Time did not permit complete analysis of barrier or rib variation within the material, but some data were compiled. Rib counts on 24 adult examples were bimodal, three gerontic individuals having 139, 148, and 149 ribs, while the rest had 81-123 ribs on the body whorl.

Barrier variation was somewhat correlated with age, the very young individuals having only 3 parietals and four ananeanic shells having 2 parietals. Barrier variation is summarized in Figure 134. The ratio of "0" to "1" columellar barriers is close to simple Mendelian ratio. The ratio of "3" to "4" parietals would probably be closer if the number of "3" 's was not heavily weighed by counts of juvenile individuals. Correlations of barrier numbers are shown in Figure

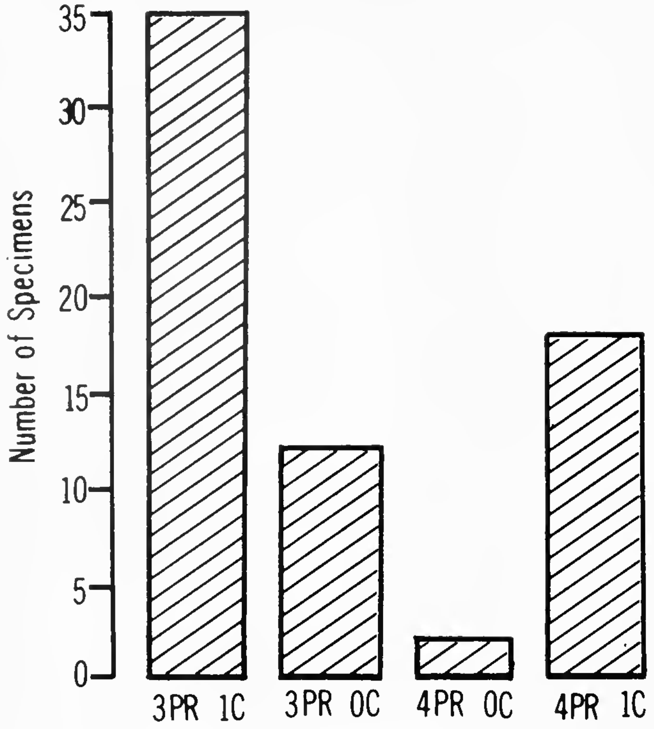

FIG. 135. Correlation of parietal and columellar lamellae in *Australdonta raivavaeana.*

135. With 3 parietals the ratio of "0" to "1" columellar is the same as in the total sample, but a disproportionate number of shells with 4 parietals have a columellar barrier. Analysis within populations showed considerable differences (fig. 134). While the total numbers approach the pattern of a Mendelian dominant for the presence of a columellar and only 3 parietals, the actual genetic picture is probably much more complex. If still extant, the populations on Mt. Turivao and Mt. Taraia would warrant quantitative sampling and attempts at cross breeding in view of the barrier ratio variations.

Description of soft parts. — Foot long, slender, bluntly truncated anteriorly, length slightly less than shell diameter. Tail bluntly rounded posteriorly, only slightly tapering. Sole undivided. Pedal grooves uniting over tail, suprapedal much weaker than pedal. No caudal horn or middorsal groove present. Slime network most conspicuous near visceral hump and on sides of tail. Head protruding markedly in front of foot edge. Ommatophores typical, eyespots relatively small. Gonopore located in normal position.

Body darkened by preservative. No distinct markings.

Mantle collar not swollen, pneumostomal opening flanked by two small lappets, a weak nodular anterior left mantle lappet and a larger, elongated right mantle flap. Latter on elongated ridge, much larger than left lappet. A modest glandular extension reaches onto lung roof. Anus (A) opening at slight angle just inside pneumostome, a weak groove continued through mantle collar.

Pallial region (fig. 125c) extending two-thirds of a whorl apically, about 5.9 mm. long. Lung roof with moderate to heavy accumulation of white granules over mantle collar, flanking principal pulmonary vein, then following sides of kidney and ureter for a short distance. A few granules along hindgut. Kidney (K) 2.3-2.6 mm. long, 2.2 times length of heart, rectal lobe abutting on hindgut, kidney base extending above loop of intestine. Ureter (KD) a narrow tube arising from anterior end of kidney, opening next to hindgut, just above anterior end of rectal kidney arm. Heart (H) lying at slight angle to hindgut, slender. Principal pulmonary vein (HV) unbranched, fading out just before mantle collar. Hindgut (HG) arising about 2.5 mm. above apex of pallial cavity, only reaching parietal-palatal margin 1.2 mm. above pallial cavity head, passing forward normally to anus.

Ovotestis (G, fig. 125a) as in *Endodonta fricki,* imbedded in digestive gland above apex of stomach, stopping far short of apex. Ovotestis of palmately clavate alveoli, lower portion of alveoli iridescent, upper branches in some examples with partly developed eggs. Hermaphroditic duct (GD) with early portion convoluted and rather slender, becoming thick and straight while running along stomach, narrowing abruptly near end of albumen gland, passing into carrefour (X) after a curving turn. Albumen gland (GG) typical, extending from apex of pallial cavity to base of stomach, poorly preserved in dissected material. Talon (GT) with slightly expanded head and long, slender shaft. Carrefour (X) not clearly delineated in dissected specimens. Prostate (DG) rather long, two to three rows of large acini opening into a narrow tube closely appressed to, but morphologically separate from, uterus. Uterus (UT) very thin walled (hidden by prostate in Figure 125a), differentiated into narrower upper and expanded basal section.

Vas deferens (VD) a slender tube, passing to penioviducal angle, then narrowing, running free along penis to insert laterally just below head of penis. Penis pore opening just below point where pilasters merge (fig. 125b). Penial retractor (PR) arising off columellar muscle just above union with tail fan, fusing into a fleshy extension of penis head. Penis (P) about 3.3 mm. long, upper portion swollen after slender neck above vas deferens insertion, tapering down to junction with free oviduct. Internally with two narrow pilasters uniting at apex, grossly expanded with a secondary union just above penis pore, smooth or complexly folded on surface, variously tapering down, merging into wall, splitting, or reappearing in basal portion (fig. 125b). Atrium (Y) narrow, rather long.

Free oviduct (UV) with enlarged head, tapering to a tube only twice diameter of vas deferens. Spermatheca (S) with enlarged head lying apicad of pallial cavity, between albumen gland and kidney apex, slender shaft passing down prostate-uterus and joining free oviduct just above union of vagina and penis. Vagina (V) very short, scarcely differentiated from atrium.

Free muscle system simple. Right ommatophoral retractor passing through penioviducal angle, uniting with right rhinophoral retractor over half way to union with tail fan. Tentacular retractors unite laterally with tail fan well below point where buccal retractor merges.

Buccal mass high, elongated, with distinct posterior protrusion of the generative sac. Buccal retractors inserting in U-shaped fan on base of mass, about one-quarter of distance from posterior end. Esophagus arising just past midpoint, extending to about 2 mm. above pallial cavity. Stomach extending a full whorl, taking less than one-quarter whorl to reach parietal-palatal margin. Intestine coiling of normal pattern, occupying less than one-quarter whorl above pallial cavity apex.

Digestive glands and salivary glands typical, latter uniting above esophagus.

Jaw (fig. 125g) of rectangular, slightly overlapping plates, about 12 per half row, that are weakly striate longitudinally.

Radula with formula 7-6-1-6-7. Central with median cusp extending well in front of basal plate edge, two small ectocones. Laterals with large mesocone, prominent ectocone, elongately rectangular basal plate, no entocone. First marginal with shortened basal plate, entocone developed on side of mesocone. Remaining marginals involve rapid shift to having entocone and mesocone subequal in size, ectocone (after 2nd marginal) split in two or three cusps (often four on last), basal plates much broader than long.

(Based on BPBM 147515, dissected whole specimen 4.67 mm. in diameter with 6¼ whorls.)

Australdonta tubuaiana, new species. Figure 133d-f.

Diagnosis. — Shell large, diameter 4.17-5.07 mm. (mean 4.62 mm.), with 5⅛-6 rather loosely coiled whorls. Apex and early spire flat, later whorls descending progressively more rapidly, H/D ratio 0.410-0.480 (mean 0.437). Umbilicus narrow, U-shaped, regularly and slightly decoiling, contained 4.70-6.17 times (mean 5.21) in the diameter. Apical and microsculpture typical. Postnuclear whorls with low, rounded, protractively sinuated radial ribs, 95-118 (mean 108) on the body whorl, whose interstices are 1½-3 times their width. Sutures shallow, whorls flattened laterally above nearly right-angled periphery, gently rounded on lower palatal margin. Weak supra- and subperipheral sulci present. Aperture typical. Parietal barriers usually 4, rarely 3 or 6, extending posteriorly about one-quarter whorl: upper high and bladelike, serrated above on posterior two-thirds with rather sharp anterior descension; 2nd and 3rd much lower, only slightly elevated posteriorly, anterior two-thirds threadlike, 3rd lower than 2nd; 4th barrier a low, threadlike ridge slightly widened, but not elevated, posteriorly. No columellar barrier. Palatal barriers 3 or 4, elongated, extending slightly more than one-eighth whorl: lower reduced in height, a little recessed, with gradual anterior descension; 2nd and 3rd coequal, higher than 1st, progressively a little more recessed, with very gradual anterior descension; 4th palatal, when present, a threadlike or weakly V-shaped, recessed, supraperipheral ridge.

The large size, very weakly rostrate periphery and depressed shape are diagnostic of *A. tubuaiana. Australdonta raivavaeana* is a more elevated (mean H/D ratio 0.479) shell with less angulated periphery, narrower major radial ribs, no subperipheral sulcus, and shorter, higher apertural barriers. *A. radiella* differs most conspicuously in lacking any palatals, while the other *Australdonta* are all much smaller.

Description. — Shell large, with 5⅞ rather loosely coiled whorls. Apex and early spire flat, lower whorls descending progressively more rapidly, H/D ratio 0.439. Apical whorls 1⅜, sculpture eroded. Postnuclear whorls with prominent, rounded, rather wide, protractively sinuated radial ribs, 98 on the body whorl, whose interstices are less than twice their width. Microsculpture of five to nine radial riblets between each major rib pair, a microspiral ribbing barely visible under 96× magnification and a secondary microspiral sculpture of irregularly spaced spiral grooves. Sutures impressed, whorls flattened laterally above weak supraperipheral sulcus, periphery right angled with a weak subperipheral sulcus, evenly and gently rounded lower palatal margin, umbilical margin strongly rounded. Color light yellow-white with broad reddish flames that coalesce on base of shell. Umbilicus narrow, U-shaped, slightly and regularly decoiling, contained 6.17 times in the diameter. Aperture compressedly ovate, periphery weakly rostrate, inclined about 20° from shell axis. Parietal barriers 4, extending posteriorly about one-quarter whorl, a partial accessory trace below 4th: upper parietal high and bladelike, serrated above posteriorly, with gradual anterior descension; 2nd and 3rd much lower, elevated posteriorly, with anterior half threadlike; 4th parietal a threadlike ridge, weakly broadened posteriorly. Columellar barrier absent. Palatals 4, elongated low barriers extending about one-eighth whorl: 1st and 2nd palatals broken off above and lip edge fragmented; 3rd a high ridge with gradual anterior descension, moderately recessed from lip edge; 4th a recessed, V-shaped ridge, supraperipheral, much lower than 3rd palatal. Height of holotype 2.47 mm., diameter 4.87 mm.

Holotype. — Austral Islands: Tubuai Island, Station 698, south of Murivai at 6-8 ft. elevation. Collected dead in sandy soil along trail by Yoshio Kondo and Donald Anderson on August 16, 1934. BPBM 147705.

Range. — Tubuai Island, Austral Islands.

Paratypes. — BPBM 147705, BPBM 147677-8.

Material. — All 17 specimens came from the type locality.

Remarks. — While undoubtedly closely related to *A. raivavaeana,* the differences in peripheral angulation, H/D ratio, length and height of apertural barriers, and major rib width readily distinguish the two species. As can be seen in Figure 136, *A. tubuaiana* and *A. raivavaeana* have slightly different growth patterns, although there is considerable overlap.

Since only eight specimens were adult, data on variation are scanty. Barrier variation is presented in Figure 126, but the numbers are too small for any meaningful analysis.

Australdonta pharcata, new species. Figure 137 a-c.

Diagnosis. — Shell very large, adult diameter about 4.60 mm., probably with 5½ tightly coiled whorls. Apex barely elevated, spire flatly coiled, last whorl descending rapidly, H/D ratio about 0.430. Umbilicus broadly V-shaped, regularly decoiling, contained 2.50-2.97 times (mean 2.74) in the diameter. Postnuclear sculpture of narrow, crowded, strongly protractively sinuated radial ribs, probably about 200-250 ribs on the body whorl, whose interstices are about equal to their width. Microsculpture occasionally visible as extremely fine microreticulation, with a secondary sculpture of prominent, rounded spiral cords (?) that are equal in size to the major radial ribs. Sutures deep, whorls strongly rounded above and on basal margin, flattened laterally above and below right-angled periphery, with evenly rounded basal margin. Aperture subovate, strongly flattened laterally above and below protruded periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper a very high and slender, bladelike lamella, very weakly expanded above on posterior visible third, with gradual anterior descension until shortly before termination; 2nd less than one-third height of upper, anterior visible half an elevated threadlike trace, extending anteriorly opposite end of upper parietal. Columellar wall without barrier. Palatal wall with 3 moderately recessed barriers, extending posteriorly almost one-quarter whorl: lower basal in position, narrow and elevated, with gradual anterior descension; 2nd on middle of lower palatal wall, slightly reduced in height and more deeply recessed, a V-shaped lamellar ridge with very gradual anterior descension; 3rd supraperipheral, very deeply recessed, a fine, raised threadlike trace.

The reduction in number and elongation of both parietal and palatal barriers, comparatively widely open umbilicus, reduced radial ribbing, and very strong secondary spiral sculpture characterize *Australdonta pharcata.* The most similar species is the even more depressed and widely umbilicated *A. ectopia* from Raivavae, which has lost its palatal barriers and retains only a single parietal trace. All other *Australdonta* have much narrower umbilici, more barriers, higher spires, and more prominent ribbing.

Description. — Shell slightly smaller than average, with 4½ normally coiled whorls. Apex slightly protruding, spire flatly coiled, body whorl descending rather rapidly, H/D ratio 0.430. Apical whorls 1⅜, typical sculpture remaining in sutures. Postnuclear sculpture of low, rounded, crowded, protractively sinuated radial ribs, whose interstices are about equal to their width. Body whorl too worn for accurate rib count. Microsculpture occasionally visible as extremely fine microreticulation, with a secondary sculpture of spiral cords (?) that are almost equal to the major radial ribs in size. Sutures deep, whorls strongly rounded above, flattened laterally down to right-

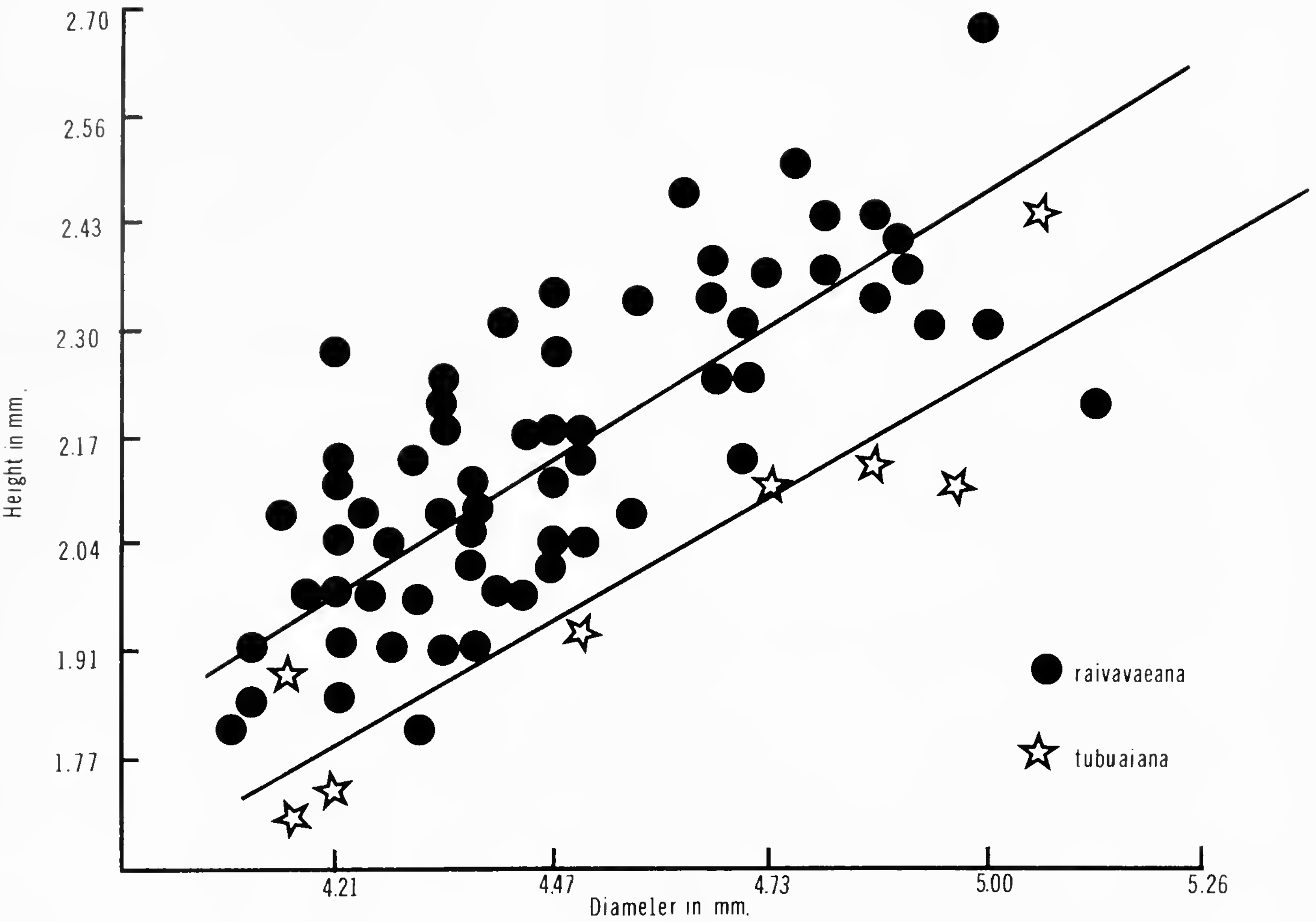

FIG. 136. Scatter diagram plotting height and diameter for *Australdonta raivavaeana* and *A. tubuaiana*.

angled periphery, lower palatal margin flattened, basal and columellar margins progressively more strongly rounded. Ground color leached from shell, traces of irregularly spaced, narrow to broad, reddish flammulations remaining above periphery. Umbilicus broadly V-shaped, regularly and evenly decoiling, contained 2.97 times in the diameter. Aperture subovate, flattened laterally above and below right-angled periphery, inclined about 20° from shell axis. Parietal wall with 2 barriers, extending posteriorly to line of vision: upper very high and slender, posterior third markedly elevated, with gradual anterior descension until just before termination; 2nd a raised threadlike ridge, slightly more elevated on posterior visible third, terminating opposite end of upper parietal. Columellar wall without barrier. Palatal barriers 3, deeply recessed, extending posteriorly almost one-quarter whorl: lower basal in position, a low lamellar blade with gradual anterior descension; 2nd more deeply recessed, slightly reduced in height, a V-shaped lamellar blade with very gradual anterior descension; 3rd slightly supraperipheral, a threadlike ridge, deeply recessed. Height of holotype 1.51 mm., diameter 3.52 mm.

Holotype. – Austral Islands: Tubuai, Station 703, 200-300 yd. inland, south of Hoopua, at 5 ft. elevation in sandy soil. Collected by Yoshio Kondo and Donald Anderson on August 18, 1934. BPBM 147726.

Range. – Tubuai, Austral Islands.

Paratype. – BPBM 147726.

Material. – Tubuai: south of Hoopua (Station 703), 200-300 yd. inland at 5 ft. elevation (2 specimens, BPBM 147726).

Remarks. – The obviously subadult holotype has patches of the microsculpture preserved. Whether this sculpture should be interpreted as an intensification of the spiral grooving seen in other *Australdonta,* or actually is very large spiral cording, is uncertain. While I have described it as the latter, only better preserved material will enable deciding this problem. The specific name *pharcata* refers to the wrinkled appearance of the shell sculpture.

Although the palatal barriers resemble those of other *Australdonta* in shape, they are much longer and the normal 2nd palatal is absent. Similarly, the parietals in *A. pharcata* seem to occupy the position of the normal 2nd and 3rd parietals, with the upper and lower lost, those remaining being greatly elongated.

As in *A. ectopia,* the ribbing is greatly reduced in prominence and very crowded. Unfortunately, the shell surface was too worn for accurate rib counts to be made. In degree of depression and umbilical width, *A. pharcata* is intermediate between *A. ectopia* and the more typical *Australdonta.*

Australdonta ectopia, new species. Figure 137d-f.

Diagnosis. – Shell very large, diameter 4.38-4.77 mm. (mean 4.57 mm.), with 5⅛ tightly coiled whorls. Apex and early spire flat or

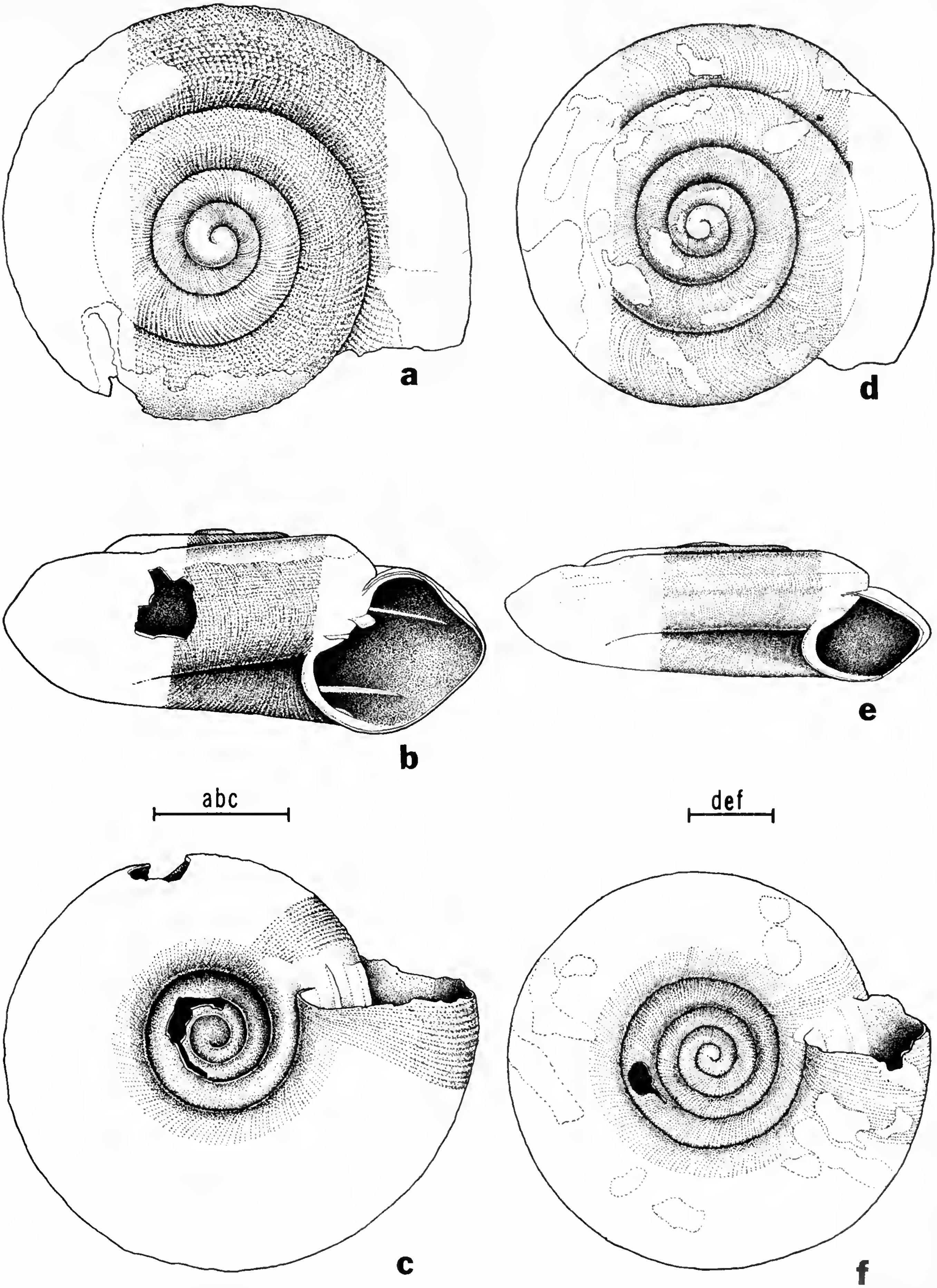

FIG. 137. **a-c**, *Australdonta pharcata*, new species. Station 703, Hoopua, Tubuai, Austral Islands. Holotype. BPBM 147726; **d-f**, *Australdonta ectopia*, new species. Station 652, Anatonu Village, Raivavae, Austral Islands. Holotype. BPBM 147389. Scale lines equal 1 mm. (MM).

barely elevated, lower spire descending slightly, last quarter to third of body whorl descending moderately, H/D ratio 0.331-0.383 (mean 0.357). Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.25-2.27 times (mean 2.26) in the diameter. Postnuclear sculpture of low, rounded, rather inconspicuous, strongly protractively sinuated radial ribs, whose interstices are about 2-3 times their width, probably about 200 on body whorl, but all specimens too worn to obtain an accurate count. Microsculpture not clearly discernable because of worn surface, except for slight traces of secondary spiral grooving on an occasional part of shell surface. Sutures deep, whorls strongly rounded above, flattened laterally above and below acutely angled periphery, basal margin evenly rounded to somewhat shouldered umbilical margin. Subperipheral sulcus relatively distinct, supraperipheral sulcus very weak or absent. Aperture subquadrangular, flattened laterally above periphery, with flatly rounded lower palatal and basal margin, inclined about 30° from shell axis. Parietal wall with single, supramedial, threadlike trace, extending posteriorly three-sixteenths of a whorl. Columellar and palatal walls without barriers.

The very wide umbilicus, extremely depressed shape, single parietal thread, and acutely angulated periphery at once separate *Australdonta ectopia* from the other species of *Australdonta*. While *A. radiella* has lost its columellar and palatal barriers, that species has many threadlike traces on the parietal wall. Extralimital species, such as *Nesodiscus fabrefactus* and some of the Hawaiian *Cookeconcha* agree in having only a single parietal remaining, but these species show numerous differences in size, shape and ribbing.

Description. — Shell very large, with slightly less than 5⅜ tightly coiled whorls. Apex and early spire very slightly sunken beneath level of antepenultimate whorl, penultimate whorl descending slowly, last third of body whorl descending moderately rapidly, H/D ratio 0.331. Embryonic whorls slightly less than 1½, sculpture near terminal part of widely spaced, low, strongly angled radial ribs, apex worn. Postnuclear whorls worn, with occasional patches of low, rounded, strongly protractively sinuated radial ribs visible. Probably about 200 ribs present on body whorl. Microsculpture occasionally detectible through weak spiral grooves, but no trace of primary sculpture remaining. Sutures deep, whorls strongly rounded above, flattened laterally down to acutely angled periphery, basal and lower palatal margin gently rounded, umbilical margin strongly rounded. Subperipheral sulcus prominent, weak supraperipheral sulcus visible on lower spire but disappearing on most of body whorl. All traces of color leached from shell. Umbilicus widely open, cup shaped, regularly decoiling, contained 2.27 times in the diameter. Aperture subquadrangular, flattened laterally above acutely angled periphery, inclined about 30° from shell axis. Parietal wall worn, a short, deeply recessed trace of the threadlike parietal visible. Columellar and palatal walls without barriers. Height of holotype 1.58 mm., diameter 4.77 mm.

Holotype. — Austral Islands: Raivavae Island, Station 652, hillside one-quarter mile east of Anatonu village at 50-150 ft. elevation. Collected by Yoshio Kondo and Donald Anderson on August 11, 1934. BPBM 147389.

Range. — Raivavae, Austral Islands.

Paratypes. — Same as list of material.

Material. — Raivavae: one-quarter mile east of Anatonu village (Station 652) at 50-150 ft. elevation (5 specimens, BPBM 147389).

Remarks. — The holotype is unusual in having nearly all of the parietal barrier worn away, but it is clearly visible in the three fragmentary examples and the other complete adult. Only the larger *Nesodiscus* have gone further in reduction of the barriers. The traces of spiral grooving and the presence of *Australdonta pharcata,* which is intermediate in spire height and umbilical width, permit this species to be classified as an *Australdonta*. Adequate material may show sufficient differences to warrant placing *A. ectopia* in a separate genus. It is the Raivavae equivalent of *Nesodiscus* in structure, but obviously derived from *Australdonta* because of its sculpture and shape.

A. pharcata is quite similar in shape and size, but differs by its 2 parietals, 3 palatals, higher spire, narrower umbilicus, and coarser ribbing.

Associated with *A. ectopia* were *A. raivavaeana* (68 specimens), *Minidonta anatonuana* (29 specimens), and four specimens each of *M. micraconica*, *M. sulcata*, and *M. planulata*, making this the single most productive station on the island.

Genus **Taipidon,** new genus

Medium- to large-sized Endodontidae, with typical apical sculpture. Secondary spiral cording absent only in *varidentata*, *woapoensis*, and *octolamellata;* weak in *anceyana* and *fragila;* strongly developed in other species. Major radial ribbing closely spaced in *petricola*, *fragila*, and *varidentata*, widely spaced only in *anceyana*. Apex and spire usually slightly to moderately elevated, depressed in *fragila*, greatly elevated in *semimarsupialis*. Body whorl slightly to moderately descending, evenly rounded or laterally compressed, only in *anceyana* with compression above and below periphery. Whorls generally 5⅛-6, rarely reduced in number (*fragila*) or greatly increased (*semimarsupialis*). Umbilicus moderately open, generally V-shaped and relatively wide (*woapoensis*, *octolamellata*, *marquesana*, and *anceyana*) or U-shaped and somewhat narrower (remaining species), except modified to form a secondary brood pouch in *semimarsupialis*. Parietal barriers variable in number: 4 in *petricola;* 3 in *woapoensis*, *octolamellata*, and *marquesana;* 2 in the remaining species; generally without accessory traces, such present normally only in *centadentata*. Columellar barrier absent or reduced in *semimarsupialis*, *woapoensis*, and *marquesana*, split into many traces in *centadentata*. Palatals highly variable in length, form and position; accessory traces present in *petricola*, all palatals split and reduced in length in *centadentata*. Penis with a submedian pustulose glandular zone and two pilasters of varying size and relative prominence, in some species split into elongated beads. Penial retractor inserting on a fleshy extension of the penis head in all species examined except for *petricola*, arising from diaphragm (*centadentata*, *semimarsupialis*) or columellar retractor (*petricola*), unknown in other species. Genital and pallial anatomy otherwise typical of Endodontidae. Jaw of separate, rectangular plates (*varidentata*, *fragila*) or more elongated plates with partial fusion (*centadentata*, *semimarsupialis*), unknown in other species. Radular teeth typical of family, number per row moderately increased in *semimarsupialis*, greatly increased in *centadentata*.

Type species. — *Pithys analogica* Pease, 1870.

The generic name *Taipidon* is derived from Taipi Valley on Nukuhiva, the setting for Herman Melville's novel "Typee" (a book that first kindled my interest in the Pacific), combined with "don" for tooth, referring to the apertural barriers. Unfortunately, none of the conchologically more generalized species were available for dissection. The anatomy of the type species, *Pithys analogica* Pease, 1870, has not been studied.

Less material was available from the Marquesas than from any other major island group, including Hawaii. Five species, including all of the more generalized, are known only from the collections of Andrew Garrett prior to the 1880's. All the remaining material was collected by members of the Bishop Museum "Pacific Entomological Survey" team, which was active in the Marquesas between 1929 and 1932 (Adamson, 1936, pp. 3-6). Although the collector of each specimen is not recorded in the Bishop Museum catalogue, comparing dates of collection with the field itinerary established that while Adamson explored niches suitable for endodontids, the other entomologists focused on different microhabitats. They collected essentially no endodontids. Thus the apparent absence of *Taipidon* from Uahuku, Fatuuku, Tahuata, Mohotani, and Fatuhiva probably expresses only the absence of collecting effort. The species described here undoubtedly represent only part of the fauna that was still extant in the early 1930's, since collections were made by non-malacologists. An estimate by Cooke (1929) that less than half of the Marquesan shells have been collected probably is conservative.

The similarities of *Taipidon* are with *Mautodontha* (*Garrettoconcha*) primarily, but a few features are shared with *Anceyodonta,* while an anatomical advance is present otherwise only in *Planudonta,* which is an obvious derivative of *Taipidon.* Generic recognition is based upon the consistent development of a pustulose glandular zone in the penis, the patterns of alteration in the penial pilasters, frequent development of a fleshy extension to the penis head, tendency towards having only 2 parietals, and different combination of conchological characters than those found in *Mautodontha* or *Anceyodonta.* The genera are at the same stage of morphological complexity and share certain trends, but represent series that are different in average pattern and with morphologic gaps between them.

The rather narrow, regularly decoiling, either U- or V-shaped umbilicus of *Taipidon* with somewhat corresponding low or moderately elevated spire agrees with the pattern of *Mautodontha* (*Garrettoconcha*) and *Mautodontha, s.s.,* respectively. Similarly, the 4 parietals of *T. petricola,* with some size reduction in the 2nd and 3rd, find their near duplication in *M. consobrina, M. saintjohni,* and *M. maupiensis. T. petricola* agrees with the tendencies in *Anceyodonta* in its possession of accessory apertural traces and the presence of secondary spiral cording. *Mautodontha* tends toward very fine and crowded ribbing with secondary spiral cording appearing only in the Austral Island *M. ceuthma. Anceyodonta* has a very narrow umbilicus, sometimes rapidly decoiling on the last whorl, has a strong tendency toward development of sulci and tends to have a very elevated shell. Unfortunately, only fragmentary anatomical material of *Mautodontha* was available, so that the extent of anatomical variation remains unknown. The two equal-sized, low and rounded penial pilasters, lack of a pustulose zone in the penis, and absence of a fleshy extension to the penis head contrast with the structures in *Taipidon,* where the pilasters are highly unequal, there is a distinct pustulose zone in the penis, and there is a fleshy extension to the penis head in all but *T. petricola.*

Except for *T. petricola,* which is by far the smallest *Taipidon* (table XCII), the species show a strong trend toward the presence of only 2 parietals and lack accessory traces (except the obvious secondary specialization of *T. centadentata*). This differs from both *Anceyodonta* and *Mautodontha,* although the latter shows a strong trend toward loss of the palatal and parietal barriers (*M. consimilis,* etc.). At first, *T. petricola* would seem more similar to *Mautodontha* because of its parietal barriers, accessory traces, relatively high spire, and lack of a fleshy extension to the penis head. The strong secondary spiral cording, pustulose zone within the penis, and very unequal penial pilasters clearly relate it to the remaining *Taipidon.* Its presence on Eiao and Hatutu, the northwestern outliers of the Marquesas, is of uncertain importance. Its small size and 4 parietal barriers would seem generalized, but this is the smallest species in which the penial retractor originates from the columellar muscle. Since in both the relatively large *T. centadentata* and *T. semimarsupialis* the penial retractor originates from the diaphragm, this is particularly unusual. No other aspect of the anatomy shows size reduction associated characters, such as were found in *Rhysoconcha* (pp. 255-256), but more detailed study of *T. petricola* is needed.

Patterns of variation in *Taipidon* are relatively simple, but of uncertain systematic importance. With the frustratingly limited material available, it seems best to retain this as a single genus, but somewhat more broadly defined than the Rapan genera, for example. Together with *T. petricola,* the species described by Garrett and Pease, *T. woapoensis, T. octolamellata, T. marquesana, T. anceyana,* and *T. analogica,* form a reasonably unitary series. They are geographically separated, with only *T. anceyana* and *T. octolamellata* described from the same island (Hivaoa). No exact locality is known for *T. analogica.* The species show minor variations in a few characters and differ in their combinations, except for *T. petricola,* which is significantly smaller, has 4 parietals and much more crowded ribbing (probably essentially a function of smaller size). The other species will have either 3 (*woapoensis, octolamellata, marquesana*) or 2 (*anceyana, analogica*) parietals; a relatively wide and V-shaped (*woapoensis, anceyana, marquesana*) or narrower and U-shaped (*octolamellata, analogica*) umbilicus; strong (*analogica*), weak (*octolamellata,*

TABLE XCII. - RANGE OF VARIATION IN TAIPIDON

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
woapoensis (Garrett)	8	85.0(69-92)	1.98(1.79-2.20)	4.33(4.01-4.77)	0.451(0.435-0.476)	5 3/4+(5 5/8-6 1/8)	2.98(2.76-3.20)	2-3	0-1	3-4
octolamellata (Garrett)	1	70	2.17	4.47	0.486	5 1/4	3.58	3	1	4
marquesana (Garrett)	12	65.0(52-80)	1.81(1.62-2.04)	3.91(3.64-4.34)	0.463(0.420-0.527)	5 1/2+(5 1/8-6)	3.00(2.67-3.22)	2-3	0-1	4
anceyana (Garrett)	3	61.3(51-73)	2.24(2.09-2.32)	4.96(4.50-5.33)	0.453(0.435-0.463)	5 3/4-(5 3/8-6)	2.89(2.78-2.96)	2	1	4
analogica (Pease)	4	86.3(80-95)	2.62(2.28-3.48)	4.36(3.97-5.26)	0.597(0.556-0.660)	6 3/8-(6-7 1/4)	3.94(3.65-4.14)	2	1+0-3	4
scmimarsupialis	3	90.3(85-97)	3.12(2.78-3.41)	4.23(4.07-4.34)	0.738(0.683-0.787)	7 1/4+(6 7/8-7 1/2)	5.25(4.92-5.46)	2	0	4
centadentata	56	98.9(83-137)	2.73(2.45-3.11)	4.73(4.30-5.56)	0.577(0.539-0.633)	6(5 1/2-6 3/8)	4.24(3.82-4.77)	2+15-20	MANY	MANY
p. petricola	19	117.3(108-124)	1.66(1.42-1.82)	2.88(2.65-3.15)	0.575(0.512-0.614)	5 3/8-(5-5 5/8)	4.79(4.40-5.31)	4+1	1	4+5-7
p. decora	37	102.2(95-107)	1.79(1.52-2.05)	3.02(2.75-3.51)	0.591(0.542-0.629)	5 5/8-(5 1/4-5 7/8)	5.12(4.65-6.00)	3-4+1-2	1+0-1	4+5-7
varidentata	4	147.0(115-179)	1.82(1.59-2.05)	3.68(3.48-4.01)	0.495(0.457-0.540)	5 1/8+(4 7/8-5 1/2)	3.21(2.98-3.43)	2	1-2	3-5
fragila	10	122.3(101-133)	1.81	3.36	0.539	4 3/4	4.96	1-2	1	1-2-3

anceyana), or no (*marquesana, woapoensis*) secondary spiral cording; an absent or weak (*marquesana, woapoensis*), typical (*analogica*) or prominent (*anceyana, octolamellata*) columellar lamella; with a slightly (*woapoensis, octolamellata, marquesana*), moderately (*anceyana*), to strongly (*analogica*) elevated spire, which also is present in *petricola*. Very limited material was seen and, except for *T. woapoensis*, these are lowland species that undoubtedly are extinct. Despite the differences of *T. petricola,* this is a unified series of species (table XCII).

Two pairs of species depart significantly from this basic pattern in one or more character complexes. On Hivaoa, *T. fragila* and *T. varidentata* have extremely thin and fragile shells, palatal barriers that are very short plus variable in number and positon, no spiral cording in *T. varidentata* and extremely fine secondary cording in *T. fragila,* and major radial ribbing that is much finer, but not more crowded than in the remaining *Taipidon*. Only partial soft parts were available of each species and there are no anatomical peculiarities confined to this pair.

On Nukuhiva, *T. centadentata* and *T. semimarsupialis* share an anatomical trend unique in the Endodontidae, but have differing sets of conchological specializations. Both species have the number of radular teeth significantly enlarged (13-15 laterals and 10-13 marginals in *semimarsupialis;* 22-23 laterals and 16-17 marginals in *centadentata*) compared with the normal 8-10 laterals. In *T. centadentata* the teeth are proportionately narrower than normal, but not greatly altered in shape. Whether this accompanies a change of diet or is caused by some other factor is unknown, but should be investigated. *T. centadentata* otherwise agrees well with the *analogica* series in shape and sculpture, differing only in its peculiarly altered apertural barriers. The major parietal barriers are greatly elongated and there are fifteen to twenty accessory traces. The columellar and palatal walls have many very short threadlike traces mounted on a raised callus. This is quite different from the patterns of palatal traces found elsewhere in the Endodontidae (see pp. 62-63). *T. semimarsupialis* has developed a secondary brood pouch by gradual narrowing of the opening. The high spire and greater whorl count (table XCII) of *semimarsupialis* are correlatives of brood pouch formation. The absence of radial sculpture from the umbilical walls is not surprising, considering the apparently abrupt alteration to brood pouch structure.

Without collection of additional material, particularly from the islands unexplored for endodontids, it will not be possible to assess the systematic importance of the variations outlined above. Pending the availability of further material, I prefer to list them as species groups within *Taipidon*.

No trends of variation within the genus are clear, unless the reduction in number of parietals is more than just correlated with size increase. There is an interesting pattern of variation in essentially sympatric species. On Nukuhiva, *T. centadentata* and *T. semimarsupialis* are sympatric, and on Hivaoa, *T. fragila* and *T. varidentata* were collected on the same ridge within 90 ft. elevation of each other.[1] Each of these pairs has one species with the pilaster pattern as in the typical *Taipidon,* the other with the penis shorter and the major pilaster broken up or partly modified into elongated globular knobs (figs. 138f, h; 139b, f). Such a pattern of change would act to reinforce isolation between the species, a necessity when species are sympatric. The penial differences between these pairs are much greater than between allopatric species pairs (see pp. 80-81).

Classification of the *Taipidon* species is as follows:

Group of *Taipidon analogica* — shell small to very large; usually with secondary spiral cording; umbilicus U- or V-shaped; 2-4 parietals; spire slightly to moderately elevated —

Taipidon petricola petricola, new species and subspecies

T. petricola decora, new subspecies

T. octolamellata (Garrett, 1887)

T. woapoensis (Garrett, 1887)

T. marquesana (Garrett, 1887)

T. anceyana (Garrett, 1887)

T. analogica (Pease, 1870)

Group of *Taipidon centadentata* — shell large; secondary spiral cording present; umbilicus U-shaped or modified to form a brood pouch; 2 parietals; spire moderately to strongly elevated; radular teeth increased in number —

T. semimarsupialis, new species

T. centadentata, new species

Group of *Taipidon varidentata* — shell small and very thin; ribbing very fine; umbilicus narrow, U-shaped; palatals short and clustered on lower palatal wall; spire depressed to weakly elevated —

T. varidentata, new species

T. fragila, new species

While possibly *Planudonta* could be considered a species group of *Taipidon*, the reasons for generic recognition are discussed below.

KEY TO THE GENUS *Taipidon*

1. Umbilicus not modified to form a brood pouch............................2
Umbilicus modified to form a brood pouch.
Taipidon semimarsupialis, new species

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[1] *T. fragila* was found only above 3,900 ft. elevation; *T. varidentata* only below 3,860 ft. elevation. The collections of the two species were made at different times, usually in different years or at least six months apart. Whether they are altitudinally separated or not remains to be determined. Since only one or two examples were collected each time, probably by different people, the reality of this separation requires the Scotch verdict "not proved."

2. Palatal wall with 3 or 4 typical barriers..5
Palatal wall with many traces or short barriers clustered on lower palatal wall. 3
3. Palatal barriers very short, 1-5 in number, located on lower palatal wall (figs. 145a, c)...4
Palatal barriers numerous short traces on a raised callus (fig. 144a, b)...................................*Taipidon centadentata,* new species
4. Spire flat or depressed; umbilicus contained about 5.00 times in diameter; barriers reduced in size.
Taipidon fragila, new species
Spire slightly and evenly elevated; umbilicus contained about 3.25 times in the diameter; barriers larger.
Taipidon varidentata, new species
5. Parietal barriers normally 4; mean diameter less than 3.5 mm.; accessory palatal traces present..6
Parietal barriers 2 or 3; mean diameter over 3.9 mm.; no accessory palatal traces...7
6. First palatal trace small; Hatutu Island.
Taipidon petricola petricola, new species and subspecies
First palatal trace large; Eiao Island.
Taipidon petricola decora, new subspecies
7. Columellar barrier very weak or absent...8
Columellar barrier typical to large in size......................................9
8. Shell larger, ribs more numerous; Uapou Island.
Taipidon woapoensis (Garrett, 1887)
Shell smaller, ribs fewer in number; Nukuhiva Island.
Taipidon marquesana (Garrett, 1887)
9. Spire low, mean H/D ratio less than 0.550..................................10
Spire elevated, mean H/D ratio about 0.600.
Taipidon analogica (Pease, 1870)
10. Parietal barriers 3; umbilicus U-shaped.
Taipidon octolamellata (Garrett, 1887)
Parietal barriers 2; umbilicus V-shaped.
Taipidon anceyana (Garrett, 1887)

GROUP OF *Taipidon analogica* (Pease, 1870)

Taipidon petricola petricola, new species and subspecies. Figures 138a-b; 140a-b.

Diagnosis. — Shell very small, diameter 2.65-3.15 mm. (mean 2.88 mm.), with 5-5⅝ tightly coiled whorls. Apex and spire moderately elevated, rounded above, last whorl descending a little more rapidly, H/D ratio 0.512-0.614 (mean 0.575). Umbilicus narrow, U-shaped, slightly and regularly decoiling, contained 4.40-5.31 times (mean 4.79) in the diameter. Postnuclear sculpture of narrow, crowded, lamellate, protractively sinuated radial ribs, 108-124 (mean 117.3) on the body whorl, whose interstices are 1½-2 times their width. Microsculpture of very fine radial riblets, three to six between each pair of major ribs, crossed by barely visible, extremely crowded spiral riblets, with a secondary microsculpture of prominent spiral cording over entire shell surface. Sutures deep, whorls strongly rounded above and on basal margin, with evenly rounded outer margin. Aperture ovate, with evenly rounded outer margin, inclined about 10° from shell axis. Parietal barriers 4, extending posteriorly almost one-quarter whorl, with one threadlike accessory trace; 1st parietal high and bladelike, expanded and serrated above on posterior half, with gradual anterior descension; 2nd parietal with posterior slightly reduced in height, sharply descending to threadlike anterior two-thirds that terminates slightly in front of upper parietal; 3rd parietal equal or slightly higher than 1st on expanded posterior third, with rather gradual anterior descension to threadlike anterior half; 4th parietal slightly reduced in height from 3rd, slightly shorter posteriorly, with longer anterior threadlike portion. Parietal trace inconspicuous, rather short, deeply recessed within aperture. Columellar barrier a moderately prominent ridge, twisting slightly downwards from plane of coiling, reaching across top of columellar callus. Palatal barriers 4, extending posteriorly almost three-sixteenths of a whorl, generally with six or seven accessory traces: lower on basal margin, a high thin lamella, expanded and serrated above on posterior half, somewhat sinuately twisted anteriorly, with rather sharp anterior descension, only slightly recessed within aperture; 2nd and 3rd distinctly higher and longer than 1st, progressively more deeply recessed and with more gradual anterior descension, superior expansion and serration more obvious; 4th supraperipheral, greatly reduced in height, scarcely more prominent than second and third accessory traces. Accessory traces located between columellar and 1st palatal; 1st and 2nd palatal; 2nd and 3rd palatals; 3rd and 4th palatals; with two or three above 4th palatal. Second and third palatal traces much larger than upper or lower traces.

The presence of 4 major parietals and six or seven accessory palatal traces combine to separate *Taipidon petricola petricola* from the other Marquesan taxa. A subspecies from nearby Eiao Island, *T. petricola decora,* differs in its reduced 2nd parietal, enlarged first palatal trace and weaker secondary spiral cording.

Description. — Shell of average size, with 5⅝ relatively loosely coiled whorls. Apex and spire moderately elevated, rounded above, last whorl descending more rapidly, H/D ratio 0.579. Embryonic whorls 1⅜, sculpture eroded above, visible in umbilicus as relatively widely spaced radial riblets, crossed by very fine and widely spaced spiral ribs. Remaining whorls with quite closely set, lamellate, protractively sinuated radial ribs, 124 on the body whorl, whose interstices are about twice their width. Microsculpture consisting of very fine radial riblets, extremely fine spiral riblets, and quite prominent, rather widely spaced spiral cords. Microsculpture somewhat reduced on upper shell surface. Sutures relatively deep, whorls rounded above, slightly flattened below periphery. Umbilicus narrowly U-shaped, regularly decoiling, contained 4.52 times in the diameter. Color very light yellow-brown with narrow, irregular, reddish flammulations. Aperture ovate, laterally compressed, inclined about 15° from shell axis. Parietal barriers 4, extending less than one-quarter whorl: numbers 1, 3, and 4 high lamellate blades that are rounded above with minute serrations; 2nd reduced in size to a lamellate ridge. Columellar barrier a short broad ridge, nearly reaching apertural margin. Major palatal barriers 4, slightly more than one-eighth whorl in length: lower 3 moderately high, with rounded and serrated tops; upper palatal a narrow, V-shaped ridge, not recessed within aperture. Palatal traces located between columellar and 1st palatal; 1st and 2nd palatals; 2nd and 3rd palatals; 3rd and 4th palatals and with three above the upper palatal barrier. All palatal traces low, short threadlike structures. Height of holotype 1.81 mm., diameter 3.13 mm.

Holotype. — Marquesas Islands: Hatutu Island, uplands near the middle of island on east side at 1,080 ft. elevation. Collected from a very dry hillside under dead wood on September 29, 1929 by members of the Pacific Entomological Survey. BPBM 95576.

Range. — Hatutu Island, Marquesas.

Paratypes. — Same as list of material.

Material. — Marquesas Islands: Hatutu Island, uplands near the middle of island on east side at 1,080 ft. elevation (19 specimens, BPBM 95574-6).

Remarks. — The name *petricola* was chosen to characterize the small size of the island from which this form is known. Hatutu is in the northeastern outliers of the Marquesas and only a few miles from Eiao on which a very closely related subspecies, *Taipidon petricola decora,* is found. This species shows the most similarities to *Anceyodonta* and *Mautodontha* of any Marquesan endodontid, but the genital anatomy clearly relates it to the other

TABLE XCIII. - LOCAL VARIATION IN TAIPIDON

Name	Number of Specimens	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
petricola petricola BPBM 95574-6	6		1.67±0.068 (1.42-1.82)	2.88±0.069 (2.65-3.15)	0.575±0.0147 (0.512-0.614)	5 3/8 (5-5 5/8)	4.79±0.131 (4.40-5.31)
petricola decora BPBM 95542-3, BPBM 95524, BPBM 95526, BPBM 95553-4	14		1.76±0.040 (1.52-2.05)	2.96±0.038 (2.75-3.15)	0.594±0.0083 (0.542-0.629)	5 1/4 (4 3/4-5 3/4)	5.18±0.123 (4.21-6.00)
woapoensis BPBM 3464, BPBM 8693	7		1.95±0.038 (1.79-2.09)	4.27±0.062 (4.01-4.44)	0.450±0.0057 (0.435-0.476)	5 3/4 (5 5/8-6)	2.96±0.061 (2.76-3.20)
marquesana BPBM 3437	3	56.5±4.50 (52.0-61.0)	1.81±0.127 (1.62-2.05)	3.87±0.099 (3.77-4.07)	0.466±0.0214 (0.430-0.504)	5 5/8 (5 1/2-5 3/4)	3.01±0.117 (2.78-3.17)
Zurich	9	67.8±2.64 (56.0-80.0)	1.81±0.023 (1.72-1.92)	3.92±0.071 (3.64-4.34)	0.462±0.0100 (0.420-0.527)	5 1/2+ (5 1/8-6)	3.00±0.053 (2.67-3.22)
anceyana BPBM 3118	3	64.7±6.44 (52.0-73.0)	2.24±0.077 (2.09-2.32)	4.96±0.242 (4.50-5.33)	0.453±0.0087 (0.435-0.463)	5 3/4 (5 3/8-6)	2.89±0.055 (2.78-2.96)
analogica BPBM 115307 BPBM 115291	4		2.62±0.285 (2.28-3.48)	4.36±0.302 (3.97-5.26)	0.597±0.0230 (0.556-0.660)	6 3/8- (6-7 1/4)	3.94±0.105 (3.65-4.14)
semimarsupialis BPBM 96051-2	3		3.12±0.184 (2.78-3.41)	4.23±0.080 (4.08-4.34)	0.738±0.0300 (0.683-0.787)	7 1/4+ (6 7/8-7 1/2)	5.25±0.167 (4.92-5.46)
centadentata BPBM 96053, BPBM 96096, BPBM 96100-1	25		2.73±0.044 (2.45-3.11)	4.72±0.062 (4.30-5.56)	0.577±0.0050 (0.539-0.633)	6+ (5 1/2-6 3/8)	4.24±0.050 (3.82-4.77)
varidentata BPBM 104635, BPBM 98793, -63, BPBM 94799	4		1.82±0.116 (1.59-2.05)	3.68±0.118 (3.48-4.01)	0.495±0.019 (0.457-0.540)	5 1/8 (4 7/8-5 1/2)	3.21±0.095 (2.98-3.43)

Taipidon. According to Adamson (1935, p. 32) it was collected "under bark," although the data in the catalogue at the Bishop Museum only mention that BPBM 95574 (two juveniles) were collected "on ground" and the "others under dead wood on ground." Possibly *T. petricola* lives under loose bark on gently slanting stilt roots as do some of the Samoan Charopidae (Solem, *unpublished*). If so, this would be a major change from the ground restricted habitat shown by most Endodontidae.

Differences from *T. petricola decora* are covered in the diagnosis above. The size difference (table XCIII) may be an artifact of sampling, since the measured material of *T. p. decora* contained many more gerontic individuals than the measured material of *petricola*. The barrier differences appear constant and were used to differentiate the subspecies.

Description of soft parts. — Foot partly retracted in all specimens; tail rounded behind, not tapering. Sole undivided. Pedal grooves typical, no caudal horn or middorsal groove. Head retracted completely.

Body color light yellow-white, no darker markings.

Mantle collar with thickened edges, no glandular extension onto lung roof. Pneumostome and anus typical.

Pallial region extending five-eighths whorl apically. Lung roof with fine white granulations edging principal pulmonary vein and kidney. Kidney about 1.15 mm. long, rectal arm 0.45 mm. long. Ureter typical, reflexing and opening next to hindgut, opposite end of kidney rectal arm. Heart 0.5 mm. long, not parallel to hindgut. Principal pulmonary vein relatively broad, prominent almost to mantle collar, unbranched. Hindgut typical.

Ovotestis (fig. 138a, G) typical in structure and clump orientation, extending about one-half whorl above stomach apex. Hermaphroditic duct (GD) greatly swollen medially, of normal length, narrowing and reflexing abruptly before entering carrefour. Albumen gland (GG) larger than shown in drawing, surface rather finely textured. Talon (fig. 138b, GT) very long and slender with small, expanded head. Carrefour (X) elongated and expanded, receiving hermaphroditic duct laterally (fig. 138b). Prostate (DG) short, two rows of large, bulbous acini opening into a narrow tube that becomes vas deferens. Uterus (UT) typically bipartite, expanded lower chamber extending well below end of prostate, tapering to free oviduct.

Vas deferens (VD) typical, entering penis 0.6 mm. below head and to side of main pilaster. Penial retractor (PR) arising from columellar retractor, inserting directly on head of penis. Penis (P) about 1.51 mm. long, internally with one very high, thin pilaster with a second much lower, fading out in central region to a pustulose area, reappearing basally. Atrium (Y) short, wide.

Free oviduct (UV) about equal in length to prostate, only tapering slightly. Spermatheca (S) with expanded head next to albumen gland, shaft inserting on penioviducal angle.

Free muscle and digestive systems typical.

Jaw not successfully mounted.

Radula with centrals about 7-8μ wide and 8μ long, tricuspid mesocone equal in length to basal plate, ectocones very small.

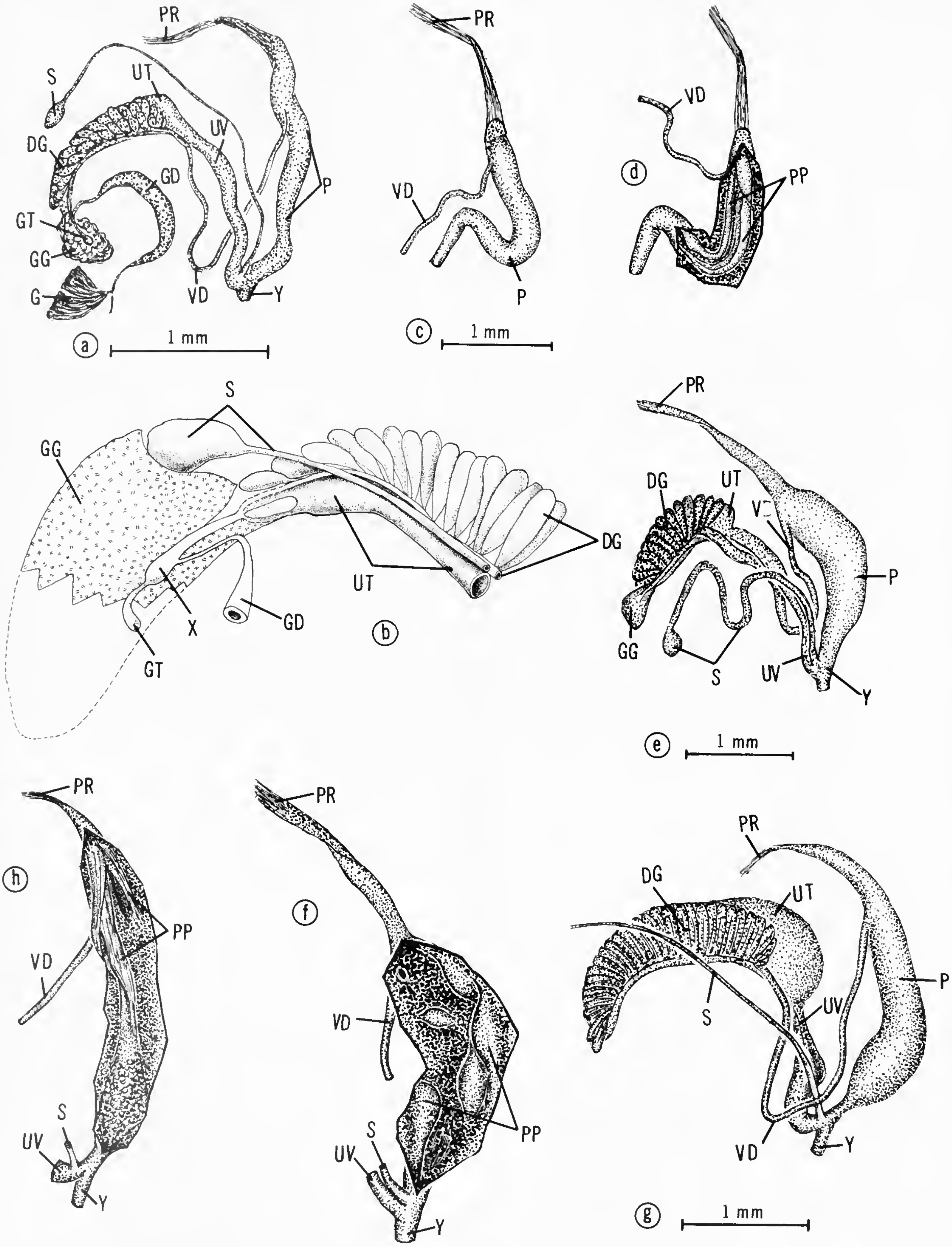

FIG. 138. Anatomy of *Taipidon:* **a-b**, *T. petricola petricola*. East side of Hatutu Id., Marquesas. BPBM 95575. *a*, genital system, *b*, details of carrefour region; **c-d**, *T. petricola decora*. Eiao Id., Marquesas. BPBM 95525, BPBM 95542. *c*, penis, *d*, interior of penis; **e-f**, *T. fragila*. Mt. Temetiu, Hivaoa, Marquesas. BPBM 115704. *e*, genitalia, *f*, interior of penis; **g-h**, *T. varidentata*. Mt. Temetiu, Hivaoa, Marquesas. BPBM 94799. *g*, genitalia, *h*, interior of penis. (See Appendix for explanation of abbreviations.)

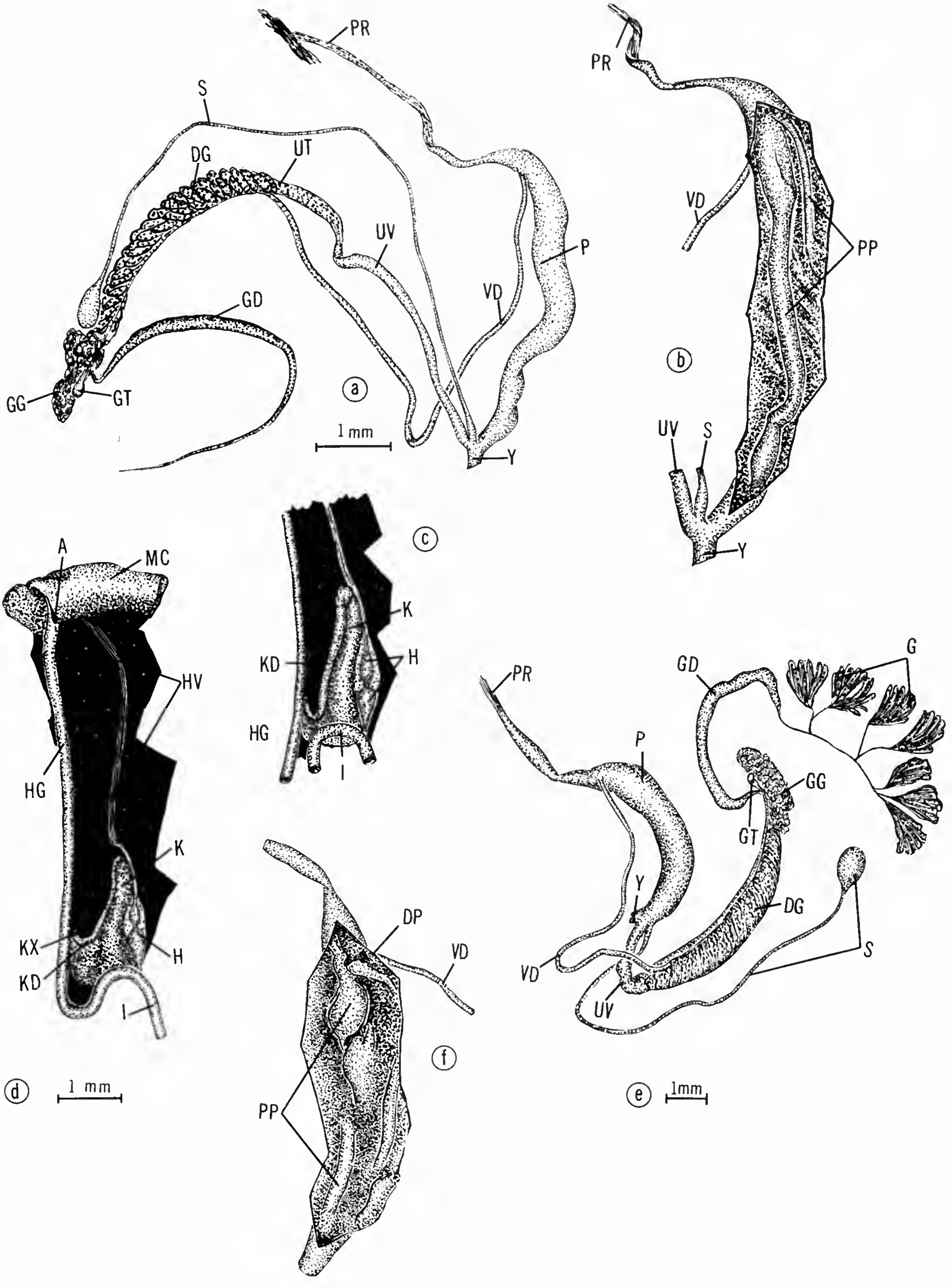

FIG. 139. Anatomy of *Taipidon*: **a-c**, *T. semimarsupialis*, Mt. Ooumu, Nukuhiva, Marquesas. BPBM 96051-2. *a*, genitalia, *b*, interior of penis, *c*, apical portion of pallial cavity; **d-f**, *T. centadentata*. Mt. Ooumu, Nukuhiva, Marquesas. BPBM 96053. BPBM 96096. *d*, pallial complex. *e*, genitalia, *f*, interior of penis. (See Appendix for explanation of abbreviations.)

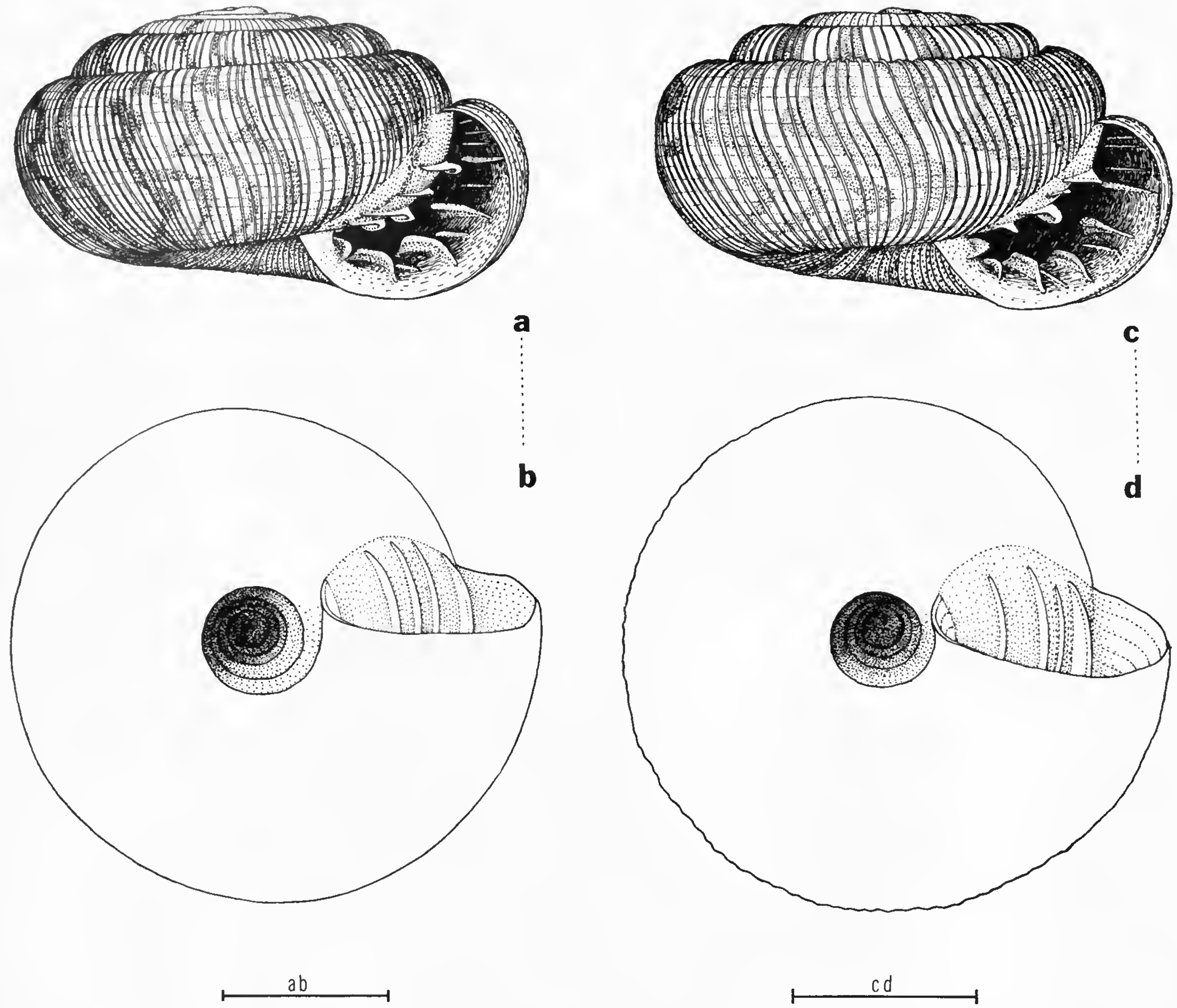

FIG. 140. **a-b**, *Taipidon petricola petricola*, new species and subspecies. Uplands of Hatutu Island, Marquesas. Holotype. BPBM 95576; **c-d**, *Taipidon petricola decora*, new subspecies. Eiao Island at 1,850 ft., Marquesas. Holotype. BPBM 95543. Scale line equals 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Laterals about 6, ectocone progressively larger, entocone appearing on 6th tooth. Transition to marginals between 6th and 9th tooth. Outer marginals missing in all mounts, those present with square plates, becoming elongately rectangular, very short cusps with split endocone much longer than mesocone or ectocone.

(Based on BPBM 95575, several whole and partly extracted examples.)

Taipidon petricola decora, new subspecies. Figures 49a-c; 138c-d; 140c-d.

Diagnosis. — Shell much smaller than average, diameter 2.75-3.51 mm. (mean 3.02 mm.), with 5¼-5⅞ normally coiled whorls. Apex and spire moderately and evenly elevated, sometimes rounded above, last whorl descending distinctly more rapidly, H/D ratio 0.542-0.629 (mean 0.591). Umbilicus narrowly open, U-shaped, regularly decoiling, contained 4.65-6.00 times (mean 5.12) in the diameter. Postnuclear whorls with narrow, prominent, crowded, protractively sinuated radial ribs, 95-107 (mean 102.2) on the body whorl, whose interstices are 1½-2 times their width. Microsculpture of fine radial riblets, three to six between each pair of major ribs, crossed by extremely fine and crowded spiral riblets, with weak secondary spiral cording usually visible on shell base. Sutures prominent, whorls strongly rounded above and on basal margin, with evenly rounded outer margin. Aperture ovate, with evenly rounded outer margin, inclined about 15° from shell axis. Parietal barriers 3 (15 per cent) or 4 (85 per cent), extending posteriorly three-sixteenths of a whorl, with one (85 per cent) or two (15 per cent) accessory traces: upper parietal high and slender, weakly expanded and serrated above on posterior five-eighths, with rather gradual anterior descension until just before termination; 2nd parietal, when not reduced to a deeply recessed threadlike trace, a very low bladelike lamella, weakly elevated and expanded on posterior third, with anterior threadlike portion that terminates opposite end of upper parietal; 3rd parietal distinctly higher than 1st, expanded and serrated above on elevated posterior third, with rather gradual descension to anterior third that is an elevated threadlike ridge; 4th parietal intermediate in height between 2nd and 1st, moderately expanded above on posterior half, with gradual anterior descension.

Accessory trace located below 4th parietal, short and very deeply recessed; often 2nd parietal reduced to a deeply recessed barely visible threadlike trace. Columellar wall with high, prominent, bladelike barrier, with relatively sharp anterior descension, twisted slightly downward midway across columellar callus. Occasionally a barely visible to weak threadlike trace lies above columellar. Major palatal barriers 4, extending posteriorly more than one-eighth whorl, with five to seven accessory traces, the lower almost equal in height to upper palatal: lower three palatals high and bladelike, flattened and expanded above posteriorly, with progressively more gradual anterior descension; 4th palatal supraperipheral, greatly reduced in height, a moderately recessed, V-shaped ridge. Accessory traces located between columellar and 1st palatal; 1st and 2nd palatals; 2nd and 3rd palatals; 3rd and 4th palatals, occasionally absent; and two or three above 4th palatal.

The great reduction of the 2nd parietal and much larger size of the lower palatal trace are the systematically important characters separating *Taipidon petricola decora* from the nominate subspecies. The great development of accessory traces at once serves to separate both races of *T. petricola* from other Marquesan species.

Description. — Shell small, with 5¼ normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.578. Apical whorls 1⅜, sculpture of fine radial riblets with faint traces of micro-radial ribbing and distinctly finer and more crowded spiral riblets. Postnuclear whorls with high, prominent, lamellar, crowded, protractively sinuated radial ribs, 107 on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by barely visible spiral riblets, with a secondary microsculpture of irregularly spaced spiral cording on shell base. Sutures impressed, whorls strongly rounded above and on basal margin, slightly compressed laterally below periphery. Color light yellow-brown, with prominent, zigzagged, reddish flammulations that narrow on shell base. Umbilicus rather narrow, U-shaped, regularly decoiling, contained 5.29 times in the diameter. Aperture elongately-ovate, slightly compressed laterally, with evenly rounded outer margin, inclined about 15° from shell axis. Parietal barriers 4, extending posteriorly about three-sixteenths of a whorl, with one very faint, deeply recessed threadlike trace below 4th parietal: form of parietals as in "*Diagnosis.*" Columellar barrier prominent and bladelike, slightly twisted downward from plane of coiling, with rather sharp descension midway across columellar lip. Palatal barriers 4, extending posteriorly more than one-eighth whorl, with six accessory traces: lower 3 high and bladelike, moderately expanded and serrated above posteriorly, with progressively more gradual anterior descension; 4th slightly supraperipheral, a more deeply recessed, prominent V-shaped ridge. Lower palatal trace, lying between columellar and 1st palatal, almost as large as 4th palatal; threadlike traces between 1st and 2nd, 2nd and 3rd, with three above 4th palatal. Height of holotype 1.71 mm., diameter 2.96 mm.

Holotype. — Marquesas: Eiao Island, uplands toward north end on east side of island at 1,850 ft. elevation. Collected on September 29, 1929, by members of the Pacific Entomological Survey. BPBM 95543.

Range. — Eiao Island, Marquesas Islands.

Paratypes. — Same as list of material.

Material. — Eiao: uplands toward north end, east side of island at 1,850 ft. elevation (25 specimens, BPBM 95542-3); same area at 1,650 ft. elevation (9 specimens, BPBM 95524-7) in coconut plantation near center of island at 1,450 ft. elevation under rotting stem of miro palm (3 specimens, BPBM 95553-4); Vaitahu Valley at 600 ft. elevation, under decaying logs (24 specimens, BMNH 1970. 98, collected May 3, 1970 by John Peake).

Remarks. — The presence of the enlarged palatal trace is constant in all individuals of *Taipidon petricola decora* and immediately separates them from specimens of the nominate form in which this barrier is a threadlike trace. The difference in size of the 3rd parietal is generally equally obvious.

Specimens from the upland areas are noticeably smaller than those from the coconut plantation (table XCIII). The former are essentially the same size as those from Hatutu, but the latter are significantly larger in respect to diameter (with 15 df, "*t*" = 4.1553), but not significantly different in H/D or D/U ratios ("*t*" = 0.9207 and 1.2471, respectively). The large size of the coconut plantation shells may reflect an accident of timing. Adamson (1936, p. 68) recorded that "... in 1927-1929 a party of Tahitians was employed to plant coconuts near the middle of the island ...." The coconut plantation specimens of *Taipidon petricola decora* were collected October 1, 1929 under a rotting *miro* palm stem. Probably they represented the gerontic remnant of the population in this very recently disturbed area. This collection does not necessarily indicate the persistance of the population under conditions of cultivation. Exactly when the plantation was planted and how much was cleared is not known to me.

Additional specimens were obtained in 1970 by John Peake during a British Museum (Natural History)-Bishop Museum expedition to the Marquesas. These specimens from Vaituhu Valley were studied in 1972 and used to prepare Figure 49 of the anatomy. The shells themselves were typical *Taipidon petricola decora* in barrier structure, and consisted of 23 juveniles and 11 adults. Size variation in adults also agreed with the variation seen in other sets. Only means and S.E.M.'s are given with shell height 1.69 ± 0.05, diameter 3.03 ± 0.06, H/D ratio 0.560 ± 0.010, D/U ratio 4.51 ± 0.09, and whorl count 5.18 ± 0.09. Because the specimens were preserved in expanded condition, rib counts were not attempted, nor could barrier variation be studied.

Dissection of the more complete Vaituhu specimens revealed (fig. 49a) typical *Taipidon* anatomy, and showed one possibly significant difference from the fragmentary material (BPBM 95525, BPBM 95542) dissected earlier (fig. 138c, d). The vas deferens (VD) inserts far lower on the penis in the Vaituhu specimen, but pilaster patterns and location of the pustulose zone are identical. The penis in the Vaituhu specimen was about 1.8 mm. long, and those studied earlier about 1.65 mm. long. In all of the specimens, the penial retractor inserted directly on the penis head, and the Vaituhu example showed that it originated from the columellar muscle, as in *T. p.*

petricola. Since the anatomy of the Vaituhu specimen showed no differences of a significant nature from other *Taipidon,* I did not prepare a formal description. The radular teeth (fig. 52) have been discussed previously.

Taipidon octolamellata (Garrett, 1887). Figure 141e-f.

Pitys octolamellata Garrett, 1887, Bull. Soc. Malacol. France, 4, p. 18 – Dominique (= Hiva Oa), Marquesas; Pilsbry, 1892, Man. Conchol., (2), **8**, p. 95.

Endodonta (Thaumatodon) octolamellata (Garrett), Pilsbry, 1893, *op. cit.,* (2), **9**, p. 26.

Description. – Shell larger than average, with 5¼ normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.486. Embryonic whorls 1⅜, sculpture of very fine and crowded radial ribbing, with indication of microradials near the end of embryonic growth, crossed by slightly finer and distinctly more crowded spiral riblets. Postnuclear whorls with high, prominent, protractively sinuated radial ribs, 70 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, eight to twelve between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification. A weak secondary spiral cording is barely visible on shell base near umbilical margin. Sutures deep, whorls strongly rounded above and on umbilical margin, slightly compressed laterally above and below evenly rounded outer margin. Color light yellow horn, with prominent, rather widely spaced, reddish flammulations above periphery, that become narrowed, less distinct, and strongly zigzagged below periphery to umbilical margin. Umbilicus U-shaped, regularly decoiling to last whorl, which decoils somewhat more rapidly, contained 3.58 times in the diameter. Aperture ovate, slightly flattened laterally above and below rounded periphery, inclined about 10° from shell axis. Parietal barriers 3, extending posteriorly about three-sixteenths of a whorl: upper a high bladelike lamella, weakly expanded and serrated above on posterior five-eighths, with rather sharp and regular anterior descension; 2nd parietal slightly reduced in height, equally expanded above on posterior half, with gradual anterior descension until just before end, which extends moderately in front of upper parietal termination; 3rd parietal an elevated threadlike ridge, equal in length to 2nd parietal, with posterior half slightly more elevated than anterior portion. Columellar barrier a high bladelike ridge, moderately expanded above, slightly twisted downward from plane of coiling, with sharp anterior descension midway across lip edge. Palatal barriers 4, extending posteriorly about one-eighth whorl: lower high and crescentic, moderately expanded above, with abrupt anterior descension almost to lip edge; 2nd and 3rd slightly reduced in height, somewhat flattened above posteriorly, with more gradual anterior descension; 4th supraperipheral, greatly reduced in height and length, moderately recessed within aperture, with gradual anterior descension. Height of lectotype 2.17 mm., diameter 4.47 mm.

Lectotype. – Marquesas Islands. Collected by Andrew Garrett. BPBM 4362.

Range. – Known only from the original collection on Hivaoa Island, Marquesas Islands.

Materials. – Marquesas (1 specimen, BPBM 4362).

Remarks. – Although Garrett (1887c, p. 18) reported that "Quelques individus ont été trouves à ile Dominique, sous du bois pourri," only the single specimen was located. No material was found by the Pacific Entomological Survey team, and *T. octolamellata* may be an extinct lowland species. Its smaller umbilicus, trace of spiral cording, and large columellar barrier suggest relationship to *T. analogica* and *T. petricola,* while its low spire and 3 parietals suggest affinities with *T. woapoensis* and *T. marquesana.*

Taipidon woapoensis (Garrett, 1887). Figure 141a-d.

Pitys woapoensis Garrett, 1887, Bull. Malacol. Soc. France, 4, p. 17 – Woapo (= Uapou) Island, Marquesas, under decaying vegetation at 2,000 ft. elevation; Pilsbry, 1892, Man. Conchol., (2), **8**, p. 95 (name only).

Endodonta (Thaumatodon) woapoensis (Garrett), Pilsbry, 1893, *op. cit.,* (2), **9**, p. 27 (name only).

Diagnosis. – Shell somewhat larger than average, diameter 4.01-4.77 mm. (mean 4.33 mm.), with 5⅝ - 6⅛ rather tightly coiled whorls. Apex and spire very slightly and evenly elevated, not rounded above, last whorl descending distinctly more rapidly, H/D ratio 0.435-0.476 (mean 0.451). Umbilicus broadly open, V-shaped, regularly decoiling, last whorl not decoiling more rapidly, contained 2.76-3.20 times (mean 2.98) in the diameter. Postnuclear sculpture of low, prominent, rounded, protractively sinuated radial ribs, 69-92 (mean 85.0) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine, radial riblets, eight to twelve between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. No secondary spiral sculpture on shell. Sutures impressed, whorls strongly rounded above and on basal margin, somewhat compressed laterally. Aperture ovate, somewhat compressed laterally, inclined about 20° from shell axis. Parietal barriers 2 (25 per cent) or 3 (75 per cent), extending posteriorly about three-sixteenths of a whorl: upper high and bladelike, weakly expanded above on posterior half, with very gradual descension over anterior half until just before termination; 2nd with posterior third slightly higher and more broadly expanded than upper, descending rather abruptly to threadlike anterior half that extends slightly beyond edge of upper parietal; 3rd, when present, equal in height to upper posteriorly or greatly reduced in height, with anterior threadlike portion weaker than in 2nd parietal. Columellar barrier absent (38 per cent) or a very deeply recessed, low, and threadlike trace lying parallel to plane of coiling (62 per cent). Palatal barriers 3 (12 per cent) or 4 (88 per cent), moderately high and lamellate, extending posteriorly more than one-eighth whorl: lower basal in position, moderately elevated, with gradual anterior descension, slightly recessed within aperture; 2nd slightly higher than 1st or equal in height, a little more deeply recessed, with more gradual anterior descension; 3rd distinctly more elongated, slightly lower, with very gradual anterior descension, more deeply recessed; 4th, when present, supraperipheral, a vague, threadlike trace that is deeply recessed and usually partly surrounded by a thickened callus.

Taipidon woapoensis is most closely related to the Nukuhiva species *T. marquesana.* They both agree in the extreme reduction or loss of the columellar barrier, by reduction of the upper palatal, and their almost identical shape and umbilical structure. *T. marquesana* is, on the average, much smaller (mean diameter 3.91), and has fewer (mean 65.0 ribs) and more widely spaced radial ribs on the body whorl. Other species of *Taipidon* are distinguished by their larger columellar barrier, or presence of marked secondary spiral cording and possession of a narrower umbilicus.

Description. – Shell relatively large, with 5⅝ planulate whorls. Apex flat, spire weakly elevated, body whorl descending more rapidly, H/D ratio 0.462. Embryonic whorls 1⅝, with very fine radial riblets crossing lower, quite widely spaced, narrow spiral ribs. Postnuclear sculpture of relatively closely spaced, narrow, quite protractively sinuated radial ribs, 91 on the body whorl, whose

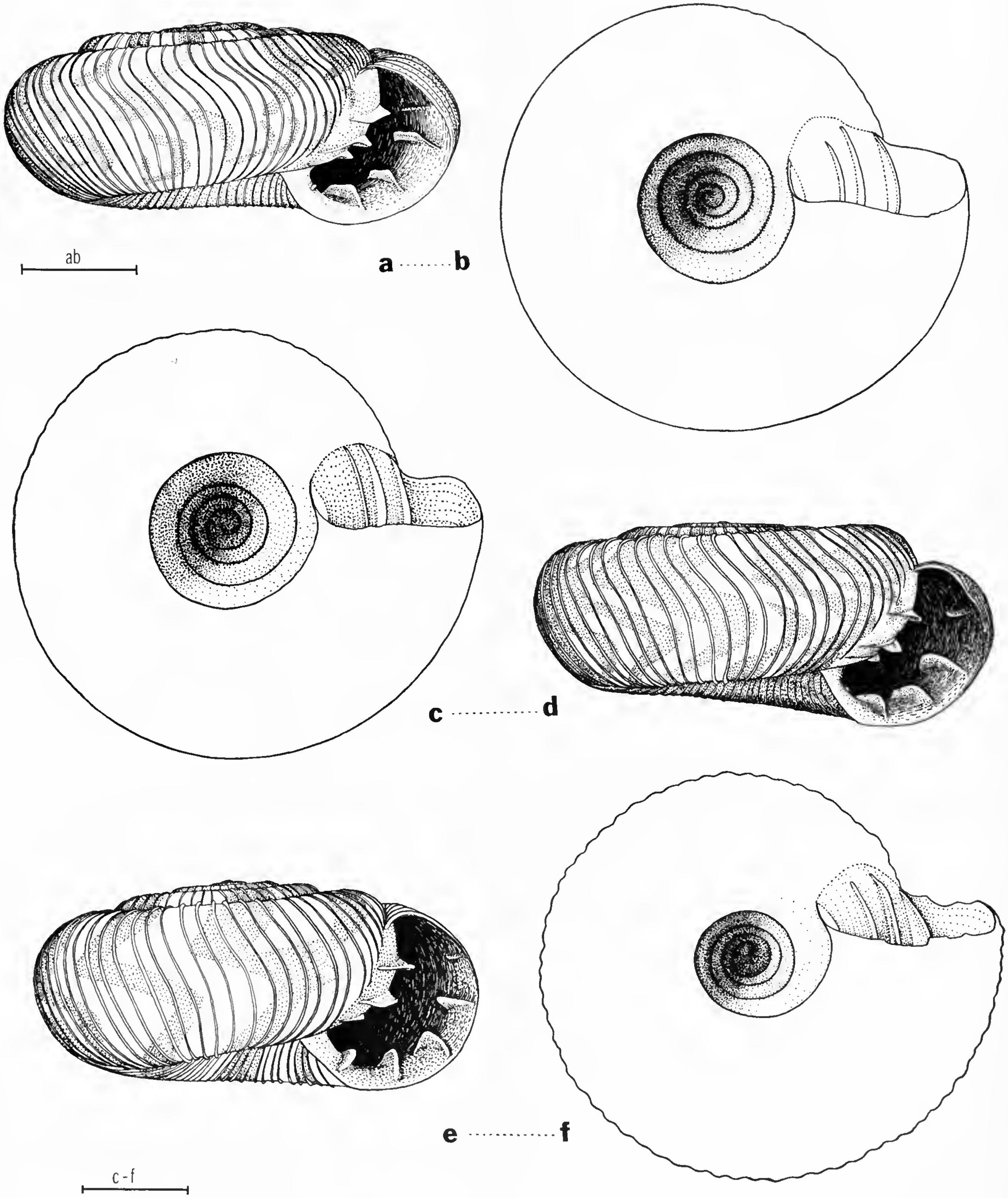

FIG. 141. **a-d**, *Taipidon woapoensis* (Garrett, 1887). *a-b*, Woapo (=Uapou) Island, Marquesas. Lectotype. BPBM 3464; *c-d*, Uapou, Marquesas. Possible paratype. BPBM 8693; **e-f**, *Taipidon octolamellata* (Garrett, 1887). Dominique (=Hivaoa) Island, Marquesas. Lectotype. BPBM 4362. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

interstices are 3-5 times their width. Microsculpture of fine radial riblets, eight to twelve between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures relatively deep, whorls strongly rounded above suture, slightly flattened laterally with gradually rounded lower margin leading to umbilical shoulder. Umbilicus broadly V-shaped, regularly decoiling, contained 3.10 times in the diameter, with obtusely shouldered margins. Color very light yellow-brown, with numerous scattered reddish flammulations present. Aperture ovate, somewhat flattened laterally, inclined more than 15° from shell axis. Parietal barriers 3, extending posteriorly three-sixteenths of a whorl: upper 2 equally high and lamellate posteriorly, 2nd with anterior half threadlike and extending beyond end of upper; lower much lower and shorter posteriorly, with long anterior threadlike portion. Columellar barrier a deeply recessed, very low, threadlike trace, lying parallel to plane of coiling. Palatal barriers 4, extending slightly more than one-eighth whorl: lower 3 bladelike, gradually descending anteriorly across the low, thin apertural callus, moderately recessed; upper a more deeply recessed threadlike trace. Height of lectotype 1.84 mm., diameter 3.98 mm.

Lectotype. — Marquesas Islands: Uapou (= Woapo Island). Collected by Andrew Garrett. BPBM 3464.

Range. — Uapou Island, Marquesas Islands.

Paratype. — BPBM 3464, BPBM 8693.

Material. — Marquesas (3 specimens, BPBM 8693, FMNH 155824, Uapou (5 specimens, BPBM 3464).

Remarks. — In one of the five syntypes from Uapou Island (BPBM 3464) both the lower parietal barrier and the upper palatal trace are missing. Two other examples have the columellar barrier absent. Otherwise, the specimens agree completely in barrier size. While the average differences from *Taipidon marquesana* are large, overlap does exist and considerable confusion can result if simple measurements are used. The ribs in *T. marquesana* are slightly higher and more sharply outlined than in *T. woapoensis.* Possibly, only subspecific differences are involved, but until new material is available, I follow Garrett in considering them to be distinct species.

Taipidon marquesana (Garrett, 1887). Figure 142c-d.

Pitys marquesana Garrett, 1887, Bull. Soc. Malacol. France, 4, pp. 18-19 — Nukuhiva, Marquesas; Pilsbry, 1892, Man. Conchol., (2), 8, p. 96.

Endodonta (Thaumatodon) marquesana (Garrett), Pilsbry, 1893, *op. cit.*, (2), 9, p. 26.

Diagnosis. — Shell slightly larger than average, diameter 3.64-4.34 (mean 3.91 mm.), with 5⅛-6 rather tightly coiled whorls. Apex and spire flat to slightly and evenly elevated, last whorl descending distinctly more rapidly, H/D ratio 0.420-0.527 (mean 0.463). Umbilicus broadly open, V-shaped, regularly decoiling, contained 2.67-3.22 times (mean 3.00) in the diameter. Postnuclear sculpture of narrow, prominent, strongly protractively sinuated radial ribs, 52-80 (mean 65.0) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine radial riblets, six to ten between each pair of major ribs, crossed by fine and exceedingly crowded spiral riblets that are visible only under 96× magnification. Sutures impressed, whorls strongly rounded above and on basal margin, slightly compressed laterally. Aperture ovate, slightly compressed laterally, inclined about 20° from shell axis. Parietal barriers 2 (25 per cent) or 3 (75 per cent), extending posteriorly about three-sixteenths of a whorl: upper parietal high and bladelike, weakly expanded above on posterior third, with gradual anterior descension until just before end; 2nd parietal distinctly higher and more strongly expanded above posteriorly, with rather sharp anterior descension to anterior threadlike half which extends slightly in front of upper parietal termination; 3rd parietal, when present, a threadlike ridge that is slightly higher and expanded on posterior half. Columellar barrier absent (50 per cent) or a weak, deeply recessed threadlike trace (50 per cent). Palatal barriers 4, extending posteriorly one-eighth whorl: lower basal in position, a high lamellar ridge, slightly recessed within aperture, with rather sharp anterior descension; 2nd and 3rd distinctly higher, longer, with more gradual anterior descension; 4th supraperipheral, a low threadlike ridge that is more deeply recessed and shorter than 3rd parietal.

The smaller size and generally fewer and more widely spaced major radial ribs are the primary characters separating *Taipidon marquesana,* found on Nukuhiva, from the very similar *T. woapoensis,* found on Uapou Island. The absence of secondary spiral cording and the greatly reduced size of the columellar barrier in *T. marquesana* separate it from the other Marquesan species.

Description. — Shell a little larger than average, with 5⅝ rather tightly coiled whorls. Embryonic whorls slightly elevated, remaining whorls of spire planulately coiled, last whorl descending distinctly more rapidly, H/D ratio 0.465. Embryonic whorls 1½, badly worn, with only traces of microradial ribbing remaining. Postnuclear whorls with widely spaced, protractively sinuated, narrow, lamellate radial ribs, 52 on the body whorl, whose interstices are 3-4 times their width. Sutures deep, whorls strongly rounded above, compressed laterally down to obtusely margined umbilicus. Umbilicus broadly V-shaped, regularly decoiling, contained 2.78 times in the diameter. Microsculpture of exceedingly fine radial riblets, eight to twelve between each pair of major ribs, crossed by barely visible spiral riblets. Color white with numerous zigzag, reddish-brown flammulations. Aperture ovate, strongly rounded above and at umbilical margin, inclined about 15° from shell axis. Parietal barriers 3, extending posteriorly three-sixteenths of a whorl: form of parietals as above in "*Diagnosis.*" Columellar barrier a low, deeply recessed thread, lying parallel to plane of coiling. Palatal barriers 4, extending posteriorly about one-eighth whorl: lower 3 moderately high, slightly recessed, with gradual anterior descension; 4th supraperipheral, a weak, deeply recessed, threadlike trace. Height of lectotype 1.74 mm., diameter 3.76 mm.

Lectotype. — Marquesas Islands: Nukuhiva. Collected by Andrew Garrett. BPBM 3437.

Range. — Nukuhiva, Marquesas Islands.

Paratypes. — BPBM 3437.

Material. — Marquesas (9 specimens, Zurich, FMNH 116986): Nukuhiva (3 specimens, BPBM 3437).

Remarks. — Reported as being taken in rotting wood from a mountain ravine, this was not found by members of the Pacific Entomological Survey who collected extensively on Nukuhiva. It may well be that *Taipidon marquesana* was a lowland species that is now extinct. The only additional specimens located were in the Mousson collection (Zurich), misidentified as *T. analogica* (Pease, 1870).

Differences from the very similar *T. woapoensis* are covered in the discussion of that species. Quite possibly they are only subspecifically separable, but without additional material I accept Garrett's judgment.

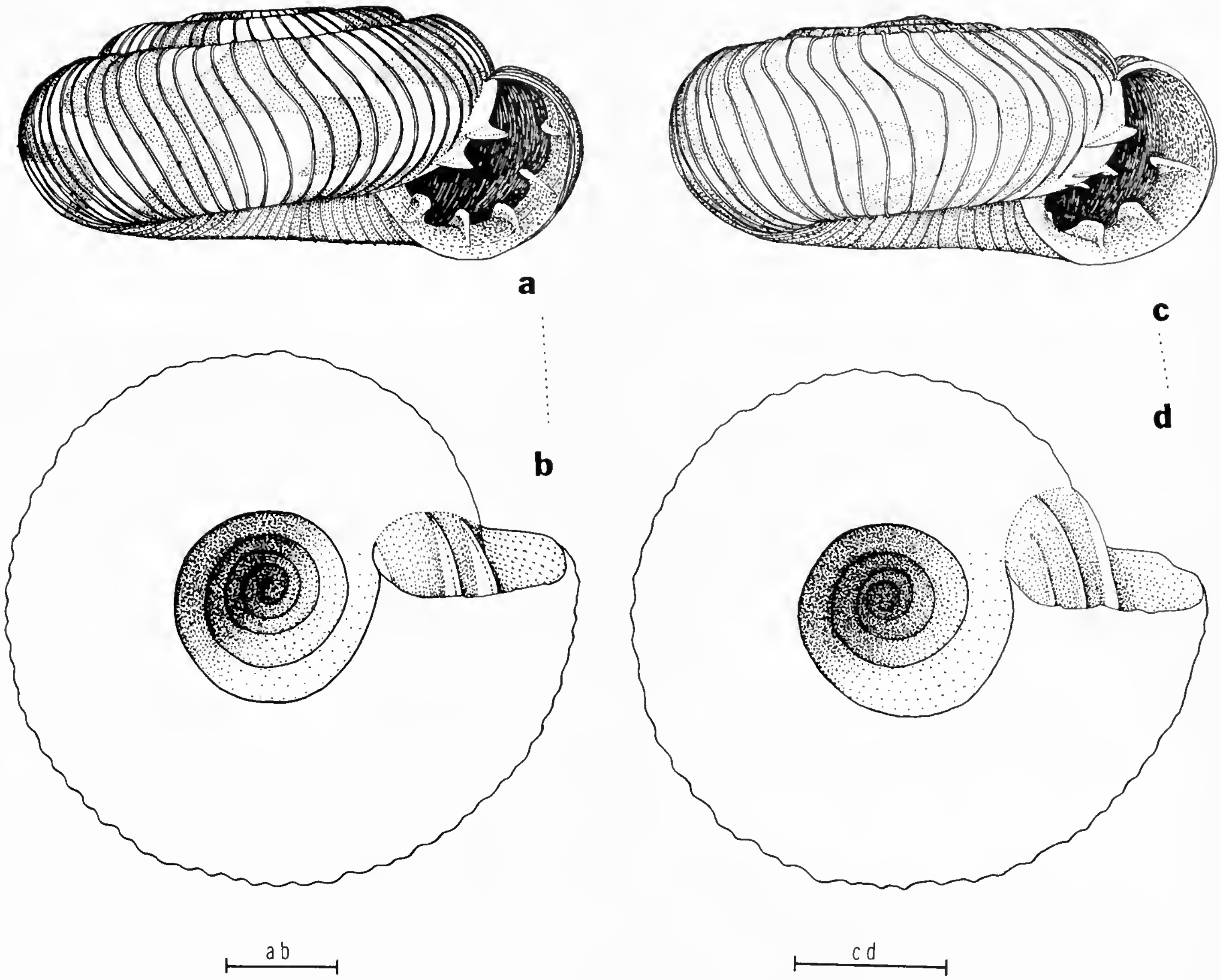

FIG. 142. **a-b,** *Taipidon anceyana* (Garrett, 1887). Dominique (=Hivaoa), Marquesas. Lectotype. BPBM 3118; **c-d,** *Taipidon marquesana* (Garrett, 1887). Nukuhiva, Marquesas. Lectotype. BPBM 3437. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of the Bernice P. Bishop Museum.

Taipidon anceyana (Garrett, 1887). Figure 142 a-b.

Pitys anceyana Garrett, 1887, Bull. Soc. Malacol. France, 4, pp. 19-20 – Dominique (= Hivaoa), Marquesas; Pilsbry, 1892, Man. Conchol., (2), 8, p. 96.

Endodonta (Thaumatodon) anceyana (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Diagnosis. – Shell very large, diameter 4.50-5.33 mm. (mean 4.96 mm.), with 5⅜-6 normally coiled whorls. Apex and early spire flat, lower whorls descending somewhat more rapidly, last whorl descending distinctly more rapidly, H/D ratio 0.435-0.463 (mean 0.453). Umbilicus widely open, broadly V-shaped, regularly decoiling, contained 2.78-2.96 times (mean 2.89) in the diameter. Postnuclear sculpture of prominent, sharply defined, protractively sinuated radial ribs, 51-73 (mean 61.3) on the body whorl, whose interstices are 3-5 times their width. Microsculpture of very fine radial riblets, eight to twelve between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification. Weak secondary spiral cording is occasionally visible on shell base. Sutures impressed, whorls strongly rounded above and on weakly shouldered basal margin, flattened and compressed laterally above and below obtusely rounded periphery. Aperture ovate, compressed laterally above and below periphery, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly less than three-sixteenths of a whorl: upper a high lamellar blade, expanded and serrated above on posterior half, with gradual anterior descension until terminal quarter of length; 2nd parietal equal in height to 1st, slightly more expanded posteriorly, with more gradual anterior descension, terminating beyond end of upper parietal. Columellar barrier a high bladelike ridge, weakly expanded above, slanting downwards from plane of coiling, abruptly descending almost to lip margin. Palatal barriers 4, extending posteriorly one-eighth whorl: lower basal in position, high and flattened above, with rather sharp anterior descension to lip edge; 2nd and 3rd equal in height to 1st, with progressively more gradual anterior descension; 4th supraperipheral, a moderately deeply recessed, V-shaped ridge, much lower than other palatals.

The very wide umbilicus and presence of a prominent columellar barrier at once separate *Taipidon anceyana*. The other Marquesan species with a prominent columellar barrier, *T. octolamellata,* differs in its narrower umbilicus, smaller size, and presence of 4 large palatals. Both *T. woapoensis* and *T. marquesana* differ in having the columellar reduced to a threadlike trace. *T. analogica* and *T. petricola* differ in their narrow umbilici and much more elevated spires.

Description. — Shell very large, with 5¾ loosely coiled whorls. Apex flat with repaired injury at end of embryonic whorls, lower whorls descending gradually, last whorl more rapidly, H/D ratio 0.460. Embryonic whorls 1½ with very closely set radial riblets crossing moderately widely spaced spiral ribs. Postnuclear whorls with widely spaced, slightly protractively sinuated, lamellar radial ribs, 69 on the body whorl, whose interstices are 3-4 times their width. Microsculpture of very fine and closely spaced radial riblets, eight to twelve between each pair of major ribs, microscopic spiral riblets, and weak spiral cording on base of shell. Sutures moderately deep, whorls strongly rounded above, somewhat flattened above and below periphery, giving an obtuse angulation to the body whorl. Umbilicus broadly V-shaped, contained 2.92 times in the diameter, with slightly shouldered margin. Color light yellow-brown with irregular, reddish flammulations. Aperture circular, slightly flattened above and below periphery of body whorl, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly about one-eighth whorl: structure as in "*Diagnosis*." Columellar barrier a high lamellate ridge, slanted downward from plane of coiling across weak umbilical callus almost to lip edge. Palatal barriers 4, extending posteriorly one-eighth whorl: lower 3 short and high; upper a moderately prominent V-shaped ridge. Height of lectotype 2.30 mm., diameter 5.00 mm.

Lectotype. — Marquesas Islands: Dominique (= Hivaoa). Collected by Andrew Garrett. BPBM 3118.

Range. — Hivaoa, Marquesas Islands.

Paratypes. — BPBM 3118.

Material. — Marquesas (3 specimens, BPBM 3118).

Remarks. — Only *Taipidon marquesana* and *T. woapoensis* approach the umbilical width of this species. The large columellar barrier and only 2 parietals separate *T. anceyana* immediately. Probably this is another lowland species that has become extinct.

Taipidon analogica (Pease, 1870). Figure 143a-d.

Pithys analogica Pease, 1870, Jour. de Conchyl., **18**, pp. 396-397 — Marquesas.

Pitys analogica Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 454; Garrett, 1887, Bull. Soc. Malacol. France, **4**, p. 14.

Helix (Pithys) analogica (Pease), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 257.

Helix (Endodonta) analogica (Pease), Tryon, 1887, Man. Conchol., (2), **3**, p. 63.

Endodonta (Thaumatodon) analogica (Pease), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Diagnosis. — Shell relatively large, diameter 3.97-5.26 mm. (mean 4.36 mm.), with 6-7¼ tightly coiled whorls. Apex and spire moderately elevated, slightly rounded above, body whorl descending distinctly more rapidly, H/D ratio 0.556-0.660 (mean 0.597). Umbilicus relatively narrow, U-shaped, last whorl decoiling slightly more rapidly, contained 3.65-4.14 times (mean 3.94) in the diameter. Postnuclear sculpture of high, prominent, strongly protractively sinuated radial ribs, 80-95 (mean 86.3) on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, six to nine between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets, with a secondary sculpture of prominent, rather widely spaced spiral cords visible over entire shell surface. Sutures impressed, whorls strongly rounded above and on basal margin, almost evenly rounded on outer margin. Aperture ovate, with evenly rounded outer margin, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly almost one-quarter whorl: upper high and bladelike, strongly thickened and serrated above on posterior three-quarters, with gradual anterior descension until just before termination; 2nd parietal equally high and expanded above on posterior three-eighths, with gradual anterior descension to point beyond termination of upper parietal. Columellar barrier a weak to moderately prominent threadlike trace or ridge, reaching almost to lip margin or deeply recessed, generally without, but occasionally with three threadlike accessory traces. Palatal barriers 4, extending posteriorly more than one-eighth whorl: lower basal in position, a high prominent lamellar ridge with sharp anterior descension, or reduced to a threadlike trace that is deeply recessed; 2nd and 3rd high and bladelike, very slightly recessed within aperture, with progressively more gradual anterior descension than normal sized 1st palatal; 4th palatal supraperipheral, moderately to strongly reduced in height, more deeply recessed, with very gradual anterior descension.

The distinctly elevated spire, presence of prominent secondary spiral cording, and relatively narrow, U-shaped umbilicus of *T. analogica* at once separate this species from the other Marquesan taxa. Of the other Marquesan species with prominent secondary spiral cording, *T. semimarsupialis* has the umbilicus modified to form a brood chamber; *T. centadentata* has the apertural barriers reduced to short traces on the palatal wall; and the much smaller *T. petricola* has a much narrower umbilicus and very crowded radial ribbing.

Description. — Shell large, with 7¼ relatively tightly coiled whorls. Spire moderately elevated, rounded above, last whorls descending sharply, H/D ratio 0.660. Embryonic whorls 1⅝, all sculpture eroded. Remaining whorls with high, thin, protractively sinuated, rather widely spaced radial ribs, 80 visible on the body whorl, whose interstices are 2 or 3 times their width. Last third of body whorl containing gerontic growth with ribbing reduced to irregular growth lines. Microsculpture mainly eroded, obvious remnants consisting of very fine radial riblets crossing narrow, closely spaced spiral cords. Sutures well marked, whorls strongly rounded above, very slightly flattened laterally. Umbilicus U-shaped, contained 3.98 times in the diameter, last whorl decoiling more rapidly, with angulately flattened margins. Color leached from shell with only faint traces of a few irregular, reddish flammulations. Aperture ovate, somewhat compressed laterally, inclined about 15° from the shell axis. Parietal wall with 2 barriers, extending posteriorly almost one-quarter whorl: upper lamellate for its entire length, descending gradually for anterior half, expanded and serrated above posteriorly; lower with anterior threadlike extension for anterior third. Columellar barriers 2, upper a deeply recessed threadlike ridge, the lower high and apically expanded, reaching almost to lip margin. Two minor accessory threads are located near the umbilical basal margin, one in position of lower palatal. Major palatal barriers 3, lower 2 high and lamellate, extending about one-eighth whorl, upper a slightly shorter, low ridge. Height of lectotype 3.50 mm., diameter 5.24 mm.

Lectotype. — Marquesas Islands. BPBM 115307 ex W. H. Pease (MCZ 17260).

Range. — Marquesas Islands (exact locality unknown).

Material. — Marquesas (4 specimens, BPBM 115307, ANSP 83209).

Remarks. — The only material known of this species is without exact locality data. No specimens were obtained by Andrew Garrett in his collecting during the 1880's or by the Bishop Museum Pacific

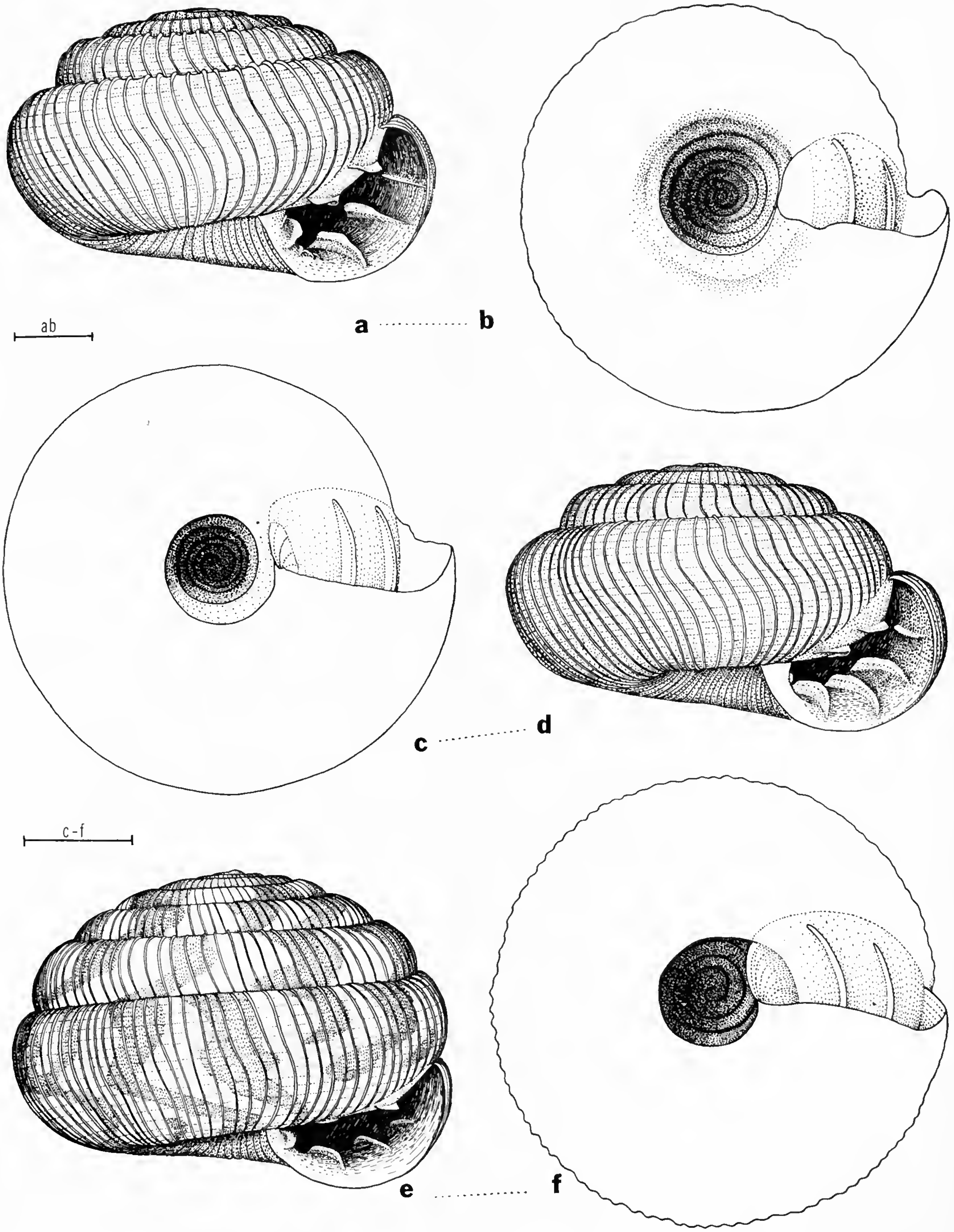

FIG. 143. **a-d**, *Taipidon analogica* (Pease, 1870). *a-b*, Marquesas. Lectotype. BPBM 115307; *c-d*, Marquesas. BPBM 115291; **e-f**, *Taipidon semimarsupialis*, new species. Mt. Ooumu, 4,050 ft., Nukuhiva, Marquesas. Holotype. BPBM 96051. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Entomological Survey in the 1920's and 1930's. Other than the types, the only specimens available are ANSP 83209 (part of this set is BPBM 115291 and BPBM 164566), received from C. D. Voy as coming from the Marquesas Islands. They (table XCIII) are smaller (diameter 3.95-4.08 mm., mean 4.04 mm.), lower (H/D ratio 0.550-0.600, mean 0.576), and have slightly different apertural barriers (fig. 143d) than the types. The former have 4 palatals, and the upper palatal is much less reduced in size than is that of the lectotype (fig. 143a). Certainly, they represent different populations, quite possibly different taxa. It is quite possible that *T. analogica* may yet be discovered at higher elevations on one of the islands.

In its reduction of the lower palatal in some specimens and strong development of spiral cording, *T. analogica* appears transitional between the more generalized *Taipidon* and *T. semimarsupialis.*

GROUP OF *Taipidon centadentata*

Taipidon semimarsupialis, new species. Figures 139a-c; 143e-f.

Diagnosis. — Shell large, diameter 4.07-4.34 mm. (mean 4.23 mm.), with 6⅞ - 7½ very tightly coiled whorls. Apex and spire dome-shaped, lower whorls descending quite rapidly, H/D ratio 0.683-0.787 (mean 0.738). Umbilicus broadly open apically, U-shaped, flat-sided, internally without sculpture, secondarily narrowed on last one and one-quarter whorls to form a brood pouch, which is contained 4.92-5.46 times (mean 5.25) in the diameter. Postnuclear sculpture of high, narrow, rather crowded, slightly protractively sinuated radial ribs, 85-97 (mean 90.3) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of rather prominent radial riblets, three to five between each pair of major ribs, crossed by spiral riblets that are barely visible under 96× magnification. Secondary microsculpture of low, rather widely spaced spiral cords that fade out near periphery. Sutures impressed, whorls almost evenly rounded on outer margin, more sharply rounded on umbilical and columellar margins. Aperture elongately ovate, with evenly rounded outer margin, inclined about 10° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper slender and bladelike, weakly expanded above on visible posterior two-thirds, with gradual anterior descension; 2nd equal in height to 1st on expanded posterior half, with rather sharp descension to an elevated threadlike ridge that extends anteriorly beyond end of upper parietal. Columellar wall smooth, without any barriers. Palatal barriers 4, extending posteriorly about one-eighth whorl, upper greatly reduced: lower at baso-columellar margin, high, slender, and bladelike, with rather sharp anterior descension to lip edge; 2nd and 3rd progressively slightly reduced in height, with more gradual anterior descension, 3rd slightly more deeply recessed within aperture; 4th palatal subperipheral, a very faint, deeply recessed, threadlike trace.

The secondary narrowing of the umbilicus to form a brood chamber in *Taipidon semimarsupialis* immediately distinguishes it from all other Marquesan species. Juvenile specimens can be recognized by the absence of radial sculpture on the umbilical whorls and the extreme elevation of the spire when compared with other *Taipidon.*

Description. — Shell large, with 7½ very tightly coiled whorls. Apex barely elevated, whorls of spire descending rapidly, producing a globosely dome-shaped shell, H/D ratio 0.744. Embryonic whorls 1⅜, sculpture of moderately widely spaced radial ribs crossed by relatively narrow spiral ribs. Remaining whorls with nearly vertical, lamellate radial ribs, 89 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of very fine radial riblets crossed by low, regular, secondary spiral cords. Secondary spiral sculpture strong on base, weaker above periphery. Sutures relatively shallow, whorls slightly shouldered above, somewhat flattened laterally. Umbilicus widely opened internally, constricted by inward growth of last 1¼ whorls to form a modified brood chamber. Remaining opening nearly circular, contained 5.38 times in the diameter. Inner walls of umbilicus without sculpture. Color light yellow-brown with prominent, zigzag reddish flammulations. Aperture compressedly ovate, nearly parallel to the shell axis, somewhat flattened basally. Parietal barriers 2, extending to line of vision: both low sharp ridges, 2nd with anterior third a raised threadlike ridge. Columellar wall without barriers. Palatal barriers 4, extending one-eighth whorl: lower 3 relatively low and bladelike, slanting gradually across weak apertural callus; upper palatal subperipheral, a deeply recessed low threadlike ridge. Height of holotype 3.16 mm., diameter 4.25 mm.

Holotype. — Marquesas Islands: Nukuhiva, ridge near summit of Mt. Ooumu, at 4,050 ft. elevation. Collected on November 12, 1929, by members of the Pacific Entomological Survey team. BPBM 96051.

Range. — Ridge near summit of Mt. Ooumu at 4,050 ft. elevation, Nukuhiva, Marquesas Islands.

Paratypes. — BPBM 96052.

Material. — Nukuhiva, ridge near summit of Mt. Ooumu at 4,050 ft. elevation (3 specimens, BPBM 96051-2).

Remarks. — Brood chamber formation in *Taipidon semimarsupialis* is quite different from the pattern seen in *Libera* or *Gambiodonta.* As in all species with brood chambers, the apical part of the umbilicus is widely open with narrowing a secondary phenomenon occurring near the aperture. About 1¼ whorls behind the aperture, the entire columellar wall curves inward, tracing a narrowing circle, until the restricted external opening is formed. There is no marked alteration of the columellar wall or baso-columellar angle. In *Gambiodonta* the narrowing occurs over a comparatively short distance and in both *Libera* and *Gambiodonta* there are considerable modifications in the columellar wall and baso-columellar angle. *Taipidon semimarsupialis* also is unusual in that the entire columellar wall has no trace of radial ribbing.

Without study of much more material, it will be impossible to determine the homologies of the apertural barriers. I have interpreted them as 4 palatals, but it is quite possible that the lower palatal represents a displaced and enlarged columellar. In this view, the ribless functioning columellar wall could be interpreted as a displaced section of the parietal wall, such as is found in *Planudonta* (fig. 146), with the original columellar wall deflected downward and outward to accomodate the demands of a dome-shaped coiling pattern and secondary narrowing of the umbilical opening. If the above structural alterations occurred, then what I have called the 1st palatal is really the columellar. While this is probably correct, the conservative course has been adopted and the barriers are referred to as palatals.

The name *semimarsupialis* emphasizes the different and seemingly incomplete pattern of brood chamber formation when compared with *Libera* or *Gambiodonta*. Despite the drastic shape and coiling changes that accompanied brood chamber formation, *T. semimarsupialis* unquestionably is closely related to *T. analogica* and *T. centadentata*.

The multiplication of radular teeth in *T. semimarsupialis* is less pronounced than in *T. centadentata*, but the presence of about 26 teeth per half row is almost 50 per cent greater than the norm for Endodontidae. Otherwise the anatomy is without unusual features, except for the diaphragm serving as origin for the penial retractor, a condition shared with *T. centadentata*.

Description of soft parts. — Based on fragmentary, extracted and torn specimens.

Body color yellow-white, no darker markings.

Mantle collar (MC) narrow, not thickened, a faint glandular extension onto lung roof into which principal pulmonary vein merges. Pneumostome and anus (A) normal.

Pallial region (fig. 139c) about 12.8 mm. long, very narrow. Lung roof clear, without granulations. Kidney (K) about 2 mm. long, tapering anteriorly, rectal arm 0.6 mm. long, posterior end broadly rounded, thin, with loop of intestine lying under it. Ureter (KD) typical, opening next to hindgut just above anterior end of rectal kidney arm. Heart (H) about 1 mm. long, not parallel to hindgut. Principal pulmonary vein (HV) typical. Hindgut (HG) extending about one-eighth whorl above apex of pallial cavity.

Ovotestis not available for study. Hermaphroditic duct (fig. 139a, GD) very long and slender apically, moderately expanded in central and anterior portion, reflexing abruptly before entering carrefour. Albumen gland (GG) elongated, narrow, with relatively large acini. Talon (GT) tapered with moderately expanded head, rather short, carrefour not clearly differentiated in available material. Prostate (DG) with two rows of rather large, short acini opening into a narrow tube. Uterus (UT) with upper glandular zone clearly differentiated, upper tubular section three-quarters length of prostate, lower quarter the typical expanded chamber with heavily glandularized walls.

Vas deferens (VD) lightly bound to peniovidueal angle, entering penis about 0.4-0.5 mm. below head, opening between pilasters. Penial retractor (PR) arising from diaphragm, inserting on head of penis without a fleshy extension. Penis (P) about 4.9-5.25 mm. long, only slightly tapering anteriorly, internally (fig. 139b) with two pilasters, one short and slender, the other high, slender and complexly folded apically, becoming low and rounded after apical third, continuing to last quarter where it becomes swollen and higher. Lower two-thirds of penis with pustulose glandular development, somewhat sculptured by transverse rugosities extending from pilaster. Atrium (Y) short and wide.

Free oviduct (UV) equal in length to prostate-uterus, very slender and not tapering. Spermatheca (S) with elongately oval head lying next to albumen gland, shaft slightly swollen basally, entering on peniovidual angle.

Free muscle system without unusual features except very elongated parts.

Jaw about 50μ wide, composed of partly fused, elongately rectangular plates about 4-5 times as long as wide, only fragments successfully mounted. Central area fused.

Radula with more than 115 rows, centrals 6-8μ wide, 8μ long, tricuspid. Laterals 13-15, with 10-13 marginals, no sharp transition. Shape of teeth differing from *T. centadentata* only in having the lateral ectocone smaller.

(Based on BPBM 96051-2, extracted and partly fragmented specimens.)

Taipidon centadentata, new species. Figures 139d-f; 144.

Diagnosis. — Shell very large, diameter 4.30-5.56 mm. (mean 4.73 mm), with 5½ - 6⅜ rather tightly coiled whorls. Apex and spire moderately and almost evenly elevated, somewhat rounded or occasionally flattened above, last whorl descending more rapidly, H/D ratio 0.539-0.633 (mean 0.577). Umbilicus relatively narrow, U-shaped, slightly and regularly decoiling, contained 3.82-4.77 times (mean 4.24) in the diameter. Postnuclear sculpture of high, prominent, crowded, protractively sinuated radial ribs, 83-137 (mean 98.9) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by barely visible, extremely crowded spiral riblets, with a secondary spiral cording that is strongest on base of shell and fades out near periphery. Sutures impressed, whorls strongly rounded above and on umbilical margin, slightly compressed laterally. Aperture ovate, slightly compressed laterally below periphery, inclined about 10° from shell axis. Major parietal barriers 2, extending posteriorly beyond line of vision, with fifteen to twenty accessory threadlike traces: upper parietal a narrow, relatively low, bladelike ridge, weakly expanded and serrated above posteriorly, with rather sharp anterior descension; 2nd slightly reduced in height, with more gradual anterior descension, terminating beyond end of upper parietal. Accessory traces located five to eight above upper parietal, four to six between two major parietals, and six to eight below 2nd parietal. Columellar and palatal walls with numerous, very short, threadlike traces located on top of a raised callus that extends less than one-eighth whorl and is moderately recessed within aperture. Juvenile specimens with one basal and one subperipheral palatal trace distinctly elevated (fig. 144a); many adults with subperipheral trace still distinctly higher than the remaining ones.

The short and numerous threadlike traces on the palatal wall immediately separate *Taipidon centadentata* from all other Marquesan species except *Planudonta intermedia*. That species, also found on Nukuhiva, has a depressed spire, very widely open umbilicus, and the threadlike traces extend well into the aperture. Differences from other Pacific Island species with reduced apertural barriers are given below under remarks.

Description. — Shell large, with 6½ normally coiled whorls. Apex and spire moderately elevated, rounded, last whorl descending a little more rapidly, H/D ratio 0.591. Embryonic whorls 1⅜, sculpture of very fine, widely spaced radial riblets crossing much finer, rather closely spaced spiral cords. Postnuclear whorls with high, lamellate, slightly protractively sinuated radial ribs, 96 on the body whorl, whose interstices are 2-4 times their width. Many radial ribs with periostracal extensions. Microsculpture of fine radial riblets and barely visible spiral riblets crossed by broadly rounded, low, closely set spiral cords that are stronger in the umbilical and basal regions than on upper portions of the whorls. Sutures relatively shallow, whorls broadly rounded above without obvious flattenings. Umbilicus narrowly U-shaped, slightly and regularly decoiling, contained 4.08 times in the diameter. Aperture ovate, inclined about 5° from shell axis. Major parietal barriers 2, extending beyond line of vision, with seventeen accessory threadlike traces: upper a low, lamellate ridge, rounded and minutely serrated above; lower a prominent threadlike ridge. Columellar and palatal walls with a relatively wide, rather deeply recessed apertural callus, on which are numerous threadlike ridges. Height of holotype 3.09 mm., diameter 5.23 mm.

Holotype. — Marquesas Islands: Nukuhiva, ridge of Mt. Ooumu at 3,900 ft. elevation. Collected on dead leaves and other debris on November 13, 1929, by members of the Pacific Entomological Survey. BPBM 96096.

Range. — Mt. Ooumu, 3,900-4,050 ft. elevation, Nukuhiva, Marquesas Islands.

Paratypes. — Same as list of material.

Material. — Nukuhiva: ridge of Mt. Ooumu at 3,900 ft. elevation (43 specimens, BPBM 96096-101); ridge near summit of Mt. Ooumu at 4,050 ft. elevation (13 specimens, BPBM 96053-6).

Remarks. — At least partial reduction of the apertural barriers to numerous threadlike ridges has also taken place in the Marquesan *Planudonta intermedia;* the Tubuaian and Rurutuan *Australdonta radiella;* the Hawaiian *Nesophila;* and in the Rapan *Opanara megomphala.* In *A. radiella* and *Nesophila* the barriers are restricted to the parietal wall, while in *O. megomphala* and *P. intermedia* they extend on all walls well past the line of vision. Thus, *Taipidon centadentata* differs from both types in having elongated threadlike barriers on the parietal wall, and very short and limited ones on the columellar and palatal walls. These should be considered parallel developments in unrelated stocks. The form and sculpture of *T. centadentata* clearly ally it to the group of *T. analogica,* despite its highly modified apertural barriers.

The name *centadentata* is appropriate not only for the many apertural barriers, but also for the large number of radular teeth. The 22-23 laterals and 16-17 marginals represent the largest count found in the Endodontidae examined to date. As mentioned above (p. 317), the penial differences between *T. semimarsupialis* and *T. centadentata* parallel the difference between the Hivaoa sympatric pair, *T. fragila* and *T. varidentata,* with one species having the pilasters partly broken into beads. Presumably this serves to bolster specific separation.

Description of soft parts. — Foot and tail narrow, quite elongated, rounded behind, not tapering. Sole undivided, pedal grooves relatively low on foot, pedal much more prominent than suprapedal, no caudal horn or middorsal groove present. Slime network prominent, irregular in shape and relatively small divisions. Head retracted in all available specimens.

Body color yellow-white, no darker markings.

Mantle collar (MC) without lobes or glandular extension into pallial cavity. Pneumostome and anus normal.

Pallial region (fig. 139d) with lung roof clear, no granulations. Kidney (K) about 2.11 mm. long, rectal arm 1.12 mm. long, base evenly rounded. Ureter (KD) typical, reflexing up rectal kidney arm and opening next to anterior tip of same, slightly removed from hindgut. Heart (H) about 1.1 mm. long, slightly angled from hindgut axis. Principal pulmonary vein (HV) narrow, extending almost to edge of mantle collar, unbranched. Hindgut (HG) typical.

Ovotestis (fig. 139e, G) with widely spaced clumps of palmately clavate alveoli, with typical orientation. Hermaphroditic duct (GD) somewhat irregularly expanded, not coiled, slightly iridescent, narrowing abruptly before reflexing into carrefour. Albumen gland (GG) narrow and elongated, extending apically past tip of talon, with rather large acini. Talon (GT) long, gradually tapering, with moderately expanded head, carrefour region structure not deter-

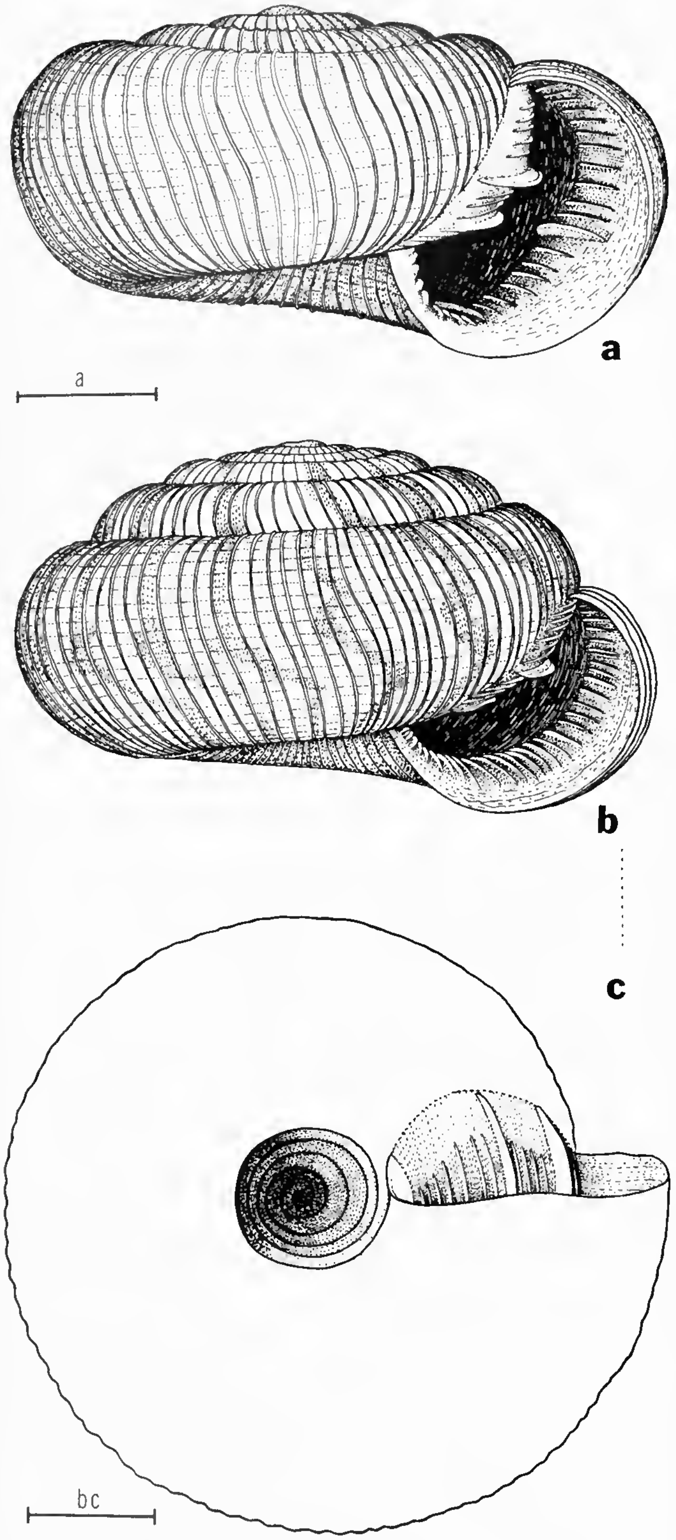

FIG. 144. **a-c**, *Taipidon centadentata,* new species. Mt. Ooumu, 3,900 ft., Nukuhiva, Marquesas. *a,* juvenile paratype. BPBM 96099; *b*-c, Holotype. BPBM 96096. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

mined. Prostate (DG) equal in length to uterus, of very slender acini, two rows, opening into very narrow duct. Uterus (UT) bipartite, expanded lower chamber not extending past base of prostate.

Vas deferens (VD) a continuation of prostatic duct, entering penis laterally between weak apical pilasters, about 0.67 mm. below penis head. Penial retractor (PR) inserting on fleshy head of penis, origin from diaphragm. Penis (P) about 4.3 mm. long, only slightly expanded just below vas deferens insertion, internally (fig. 139f) with two pilasters that are greatly reduced above vas deferens entrance, becoming partly split into elongated, globular beads in midsection, more typical basally, with a median pustulose zone in wall of penis. Atrium (Y) short.

Free oviduct (UV) short, narrow, only slightly tapering. Spermatheca (S) with oval, very large head, inserting into peniovidulcal angle.

Free muscle and digestive systems not studied.

Jaw about 50μ wide, individual plates 4-5 times as long as wide, central area fused, outer plates partly fused.

Radula with centrals about 6μ long, 4μ wide, more than 100 rows with 22-23 laterals and 16-17 marginals, the latter with square basal plates. Laterals with endocone appearing after 20th lateral, ectocone progressively larger. Outer marginals with variously split cusps. Ectocone on laterals quite prominent.

(Based on BPBM 96053, one adult 4.64 mm., in diameter, and BPBM 96096, several fragmentary adults.)

GROUP OF *Taipidon varidentata*

Taipidon varidentata, new species. Figures 138g-h; 145c-d.

Diagnosis. — Shell rather small, diameter 3.48-4.01 mm. (mean 3.68 mm.), with 4⅞ - 5½ normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending much more rapidly, H/D ratio 0.457-0.640 (mean 0.495). Umbilicus widely V-shaped, regularly decoiling, contained 2.98-3.43 times (mean 3.21) in the diameter. Postnuclear sculpture of narrow, prominent, crowded, vertically sinuated radial ribs, 115-179 (mean 147.0) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, four to six between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures deep, whorls strongly rounded above and on basal margin, with evenly rounded outer margin. Aperture nearly circular, with evenly rounded outer margin, lying almost parallel to shell axis. Parietal barriers 2, extending posteriorly less than three-sixteenths of a whorl: upper a high slender blade, weakly expanded above on posterior two-thirds, with gradual anterior descension; 2nd reduced in height, more broadly expanded above on posterior two-thirds, with gradual anterior descension to point well in front of upper termination. Columellar wall with 1 (75 per cent) or 2 (25 per cent) prominent barriers: major columellar located at baso-columellar margin, a high crescentic blade, somewhat flattened above, with abrupt anterior descension almost to lip margin; 2nd, when present, reduced in height and located above major columellar with equally abrupt anterior descension. Palatal barriers variable in number (3-6) and height, mainly high crescentic blades, sometimes flattened above, clustered along lower palatal and basal lip margins, sometimes with a minute threadlike supraperipheral trace present.

The short crescentic palatal barriers that cluster near the basal margin immediately separate *Taipidon fragila* and *T. varidentata* from the other Marquesan species. The former differs in its flat spire, much narrower umbilicus and extremely fine ribbing.

Description. — Shell of less than average size, with 5½ relatively loosely coiled whorls. Apex and upper spire slightly elevated, body whorl descending much more rapidly, H/D ratio 0.512. Apical whorls 1⅝, sculpture eroded outside, internally showing relatively widely spaced radial riblets crossed by smaller, widely spaced spiral riblets. Remaining whorls with very narrow, lamellate, closely set, vertically sinuated, radial ribs, 179 on the body whorl, whose interstices are about twice their width. Microsculpture of three to seven radial riblets between each pair of major ribs and barely visible spiral riblets. Sutures relatively deep, whorls strongly rounded above and on baso-columellar margin, evenly rounded laterally. Color light, yellowish-olive-brown with faint, irregular, reddish flammulations above periphery. Aperture nearly circular, strongly rounded above and slightly flattened on columellar margin. Parietals barriers 2, extending about one-quarter whorl: both high and lamellate for entire length, upper bladelike, lower more expanded and minutely serrated above. Columellar and palatal walls with 6 barriers: lower 5 very short, high and crescentic, reaching apertural margin; first 3 grouped at columellar and basal margin, abruptly descending anteriorly; 4th located midway up lower palatal wall, descending more gradually anteriorly; 5th slightly subperipheral in position, a more ridgelike and lower barrier; 6th a minute, supraperipheral, threadlike trace. Height of holotype 2.04 mm., diameter 3.98 mm.

Holotype. — Marquesas Islands: Hivaoa, ridge of Mt. Temetiu at 3,860 ft. elevation. Collected from dead leaves on December 27, 1930, by members of the Pacific Entomological Survey. BPBM 104635.

Range. — Hivaoa Island, Marquesas Islands.

Paratypes. — See list of material.

Material. — Hivaoa: ridge of Mt. Temetiu at 3,860 ft. elevation (1 specimen, BPBM 104635); Matauuna, north of Mt. Temetiu summit at 3,800 ft. elevation (1 specimen, BPBM); valley of Matauuna at 2,800 ft. elevation (1 specimen, BPBM 98763); crest to north of Mt. Temetiu at 2,615 ft. elevation (1 specimen, BPBM 94799).

Remarks. — Only four specimens, each from a slightly different locality, are known of *Taipidon varidentata*. Although similar in size, shape, and sculpture, they differed widely in the form of the columellar and palatal barriers. The situation in the type is described above. The remaining three examples show: 1) Matauuna at 3,800 ft. elevation: 4 barriers grouped near columellar and basal margin with 1st slightly reduced and 3rd greatly reduced in size; plus another located one-fourth way up palatal wall; 2) Matauuna Valley at 2,800 ft. elevation: 1 columellar thread parallel to the plane of coiling; 3 equal-sized barriers grouped at columellar and basal margin; 3) crest north of Mt. Temetiu at 2,615 ft. elevation: 4 barriers grouped near columellar and basal margins with 1st relatively reduced and the 3rd slightly reduced in size; one located midway up palatal wall; one subperipheral; and one small trace located above periphery.

The latter specimen is quite similar in barrier location to that of the type, but the others varied considerably. Unfortunately, only single specimens are known from each locality, and we have no data as to how characteristic the palatal barrier structures may be of any single population.

T. varidentata and *T. fragila* might be altitudinal replacements, with the former only found below

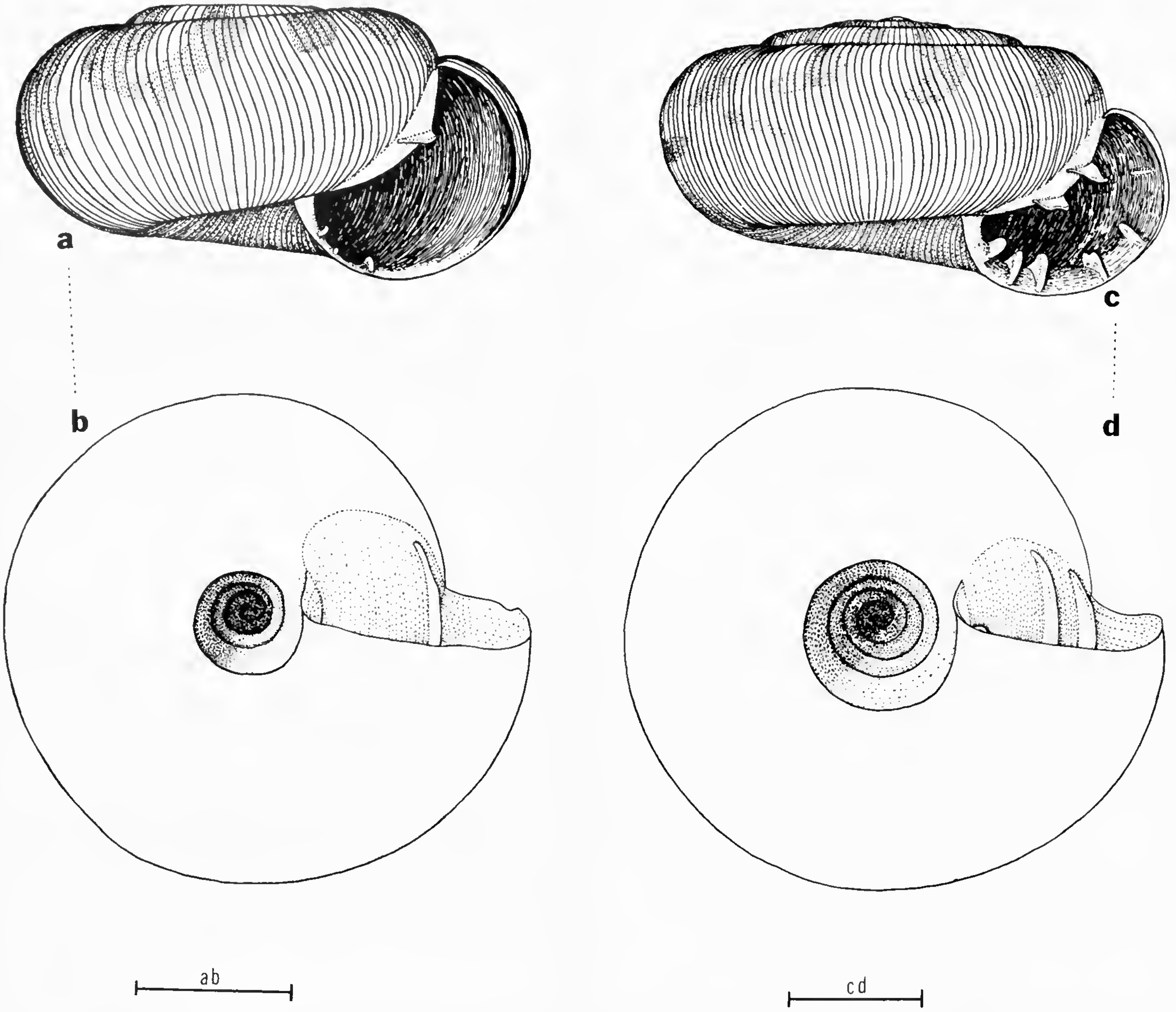

FIG. 145. **a-b**, *Taipidon fragila,* new species. Mt. Temetiu, 3,980 ft., Hivaoa, Marquesas. Holotype. BPBM 98652; **c-d**, *Taipidon varidentata,* new species. Mt. Temetiu, 3,860 ft., Hivaoa, Marquesas. Holotype. BPBM 104635. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

3,900 ft. elevation and the latter only taken above 3,900 ft. So few records are involved, that this more probably is an accident of collecting.

Description of soft parts. — A single retracted, only partly extracted animal was available and yielded data only in respect to terminal genitalia.

Prostate (fig. 138g, DG) about 2 mm. long, two rows of large acini opening into a slender tube appressed to margin of clearly bipartite uterus (UT). Latter typical in structure and internal texture. Free oviduct (UV) sharply narrowed with finer internal pustulations than in uterus. Spermatheca (S) with head not available, shaft inserting directly into peniovidiucal angle. Vas deferens (VD) entering penis about 0.4 mm. below apex.

Penis (P) about 2.5 mm. long with a slender fleshy extension to head, slender apically, gradually enlarging until just before basal area which is swollen, then constricting sharply to long atrium (Y). Internally (fig. 138h) penis with two pilasters (PP) that merge apically, one short and slender, the other very high, slender and complexly folded, becoming broadly expanded and merging into pustulose region occupying swollen portion of penis.

Jaw about 45μ wide, composed of broadly rectangular plates, about 18 in entire jaw. Length of jaw about 240μ.

Radula fragmented in mounting. Central tricuspid, mesocone much larger than ectocones and only slightly shorter than basal plate, about 8μ wide and 10μ long. Laterals 7, with progressively larger ectocone, endocone appearing only on last lateral or first marginal. Marginals about 13, basal plates becoming square, mesocone narrowing and shortening, ectocone splitting in two on outer teeth, endocone remaining slightly shorter than mesocone. About 82 rows in mounted specimen.

(Based on BPBM 94799, one extracted individual.)

Taipidon fragila, new species. Figures 138e-f; 145a-b.

Diagnosis. — Shell small, diameter about 3.36 mm., with 4¾ normally coiled whorls. Apex and early spire slightly depressed or flat, body whorl descending quite rapidly, H/D ratio 0.439. Umbilicus very narrow, U-shaped, last whorl decoiling much more rapidly, contained about 4.96 times in the diameter. Postnuclear sculpture of very fine, crowded, lamellate, protractively sinuated radial ribs, 101-133 (mean 122.3) on the body whorl, whose interstices are 3-4 times their width. Many ribs have long periostracal extensions. Microsculpture of very fine radial riblets, three to five between each pair of major ribs, with barely visible traces of extremely fine secondary spiral riblets. Sutures relatively shallow, with evenly rounded outer margin, aperture ovate, with evenly rounded outer margin, inclined about 5° from shell axis. Parietal barriers 1 (60 per cent), or 2 (40 per cent), extending slightly more than one-eighth whorl: upper a low lamellate ridge, weakly expanded and serrated above on posterior three-quarters, with gradual anterior descension; 2nd, when present, a reduced threadlike ridge, extending slightly beyond termination of upper parietal. Columellar wall with single threadlike to elevated ridgelike, very short barrier, with rather sharp anterior descension almost to lip edge. Palatal wall with one to three traces clustered on basal and lower palatal margins: traces all much less than one-eighth whorl in length, very low, variable in height, usually only one present, but variable in position.

The reduced size and number of apertural barriers, flat or depressed apex and early spire, and much narrower umbilicus immediately separate *Taipidon fragila* from the otherwise very similar *T. varidentata*. Other Marquesan species have much larger and more numerous apertural barriers, thicker shell, and much stronger radial sculpture.

Description. — Shell small, with 4¾ loosely coiled whorls. Apex distinctly depressed below whorls of spire, last whorl descending rapidly, H/D ratio 0.539. Embryonic whorls 1⅞, sculpture eroded externally, visible inside umbilicus as typical microradial and microspiral sculpture. Remaining whorls with low, rounded slightly protractively sinuated radial ribs, 133 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of relatively large, widely spaced radial riblets, three to four between each pair of major ribs, with barely visible microspirals. Sutures relatively shallow, whorls evenly rounded. Umbilicus narrowly U-shaped, contained 4.96 times in the diameter, last whorl decoiling more rapidly. Color greenish-yellow with irregular, reddish flammulations above periphery. Aperture large, circular, nearly parallel to the shell axis. Parietal wall with single, almost medial, low barrier extending slightly more than one-sixteenth of a whorl. Columellar and basal lips with two small ridgelike barriers and a very faint trace between them. Height of holotype 1.81 mm., diameter 3.36 mm.

Holotype. — Marquesas Islands: Hivaoa, ridge of Mt. Temetiu at 3,980 ft. elevation. Collected from dead leaves on December 12, 1929, by members of the Pacific Entomological Survey. BPBM 98652.

Range. — Hivaoa Island, Marquesas Islands.

Paratypes. — See list of material.

Material. — Hivaoa: ridge of Mt. Temetiu at 3,980 ft. elevation (2 specimens, BPBM 98652); same area at 4,160 ft. elevation (1 specimen, BPBM 115704); Tenatinaei, Feani Ridge at 3,905 ft. elevation in dry moss (7 specimens, BPBM 115693).

Remarks. — The type is the only adult whole specimen of this very fragile, thin-shelled species. The remaining adult specimens range from broken to smashed, including one live collected example whose shell literally collapsed of its own weight. While rib counts were made on three specimens, only one adult example could be measured.

The size and shape of the aperture, sunken apex, broad body whorl, and fine ribbing immediately characterize *Taipidon fragila* and separate it from all other Marquesan species. At first glance, it seems to be a variation of *T. varidentata* from the same localities, but the relative whorl and umbilical width, different spire shape and reduced barriers in *T. fragila* are constant.

Of greater significance is the difference in penial structure. The much shorter (1.5 mm.) penis of *T. fragila* has the major pilaster broken up into elongated lumps (fig. 138f), while in *T. varidentata* the longer (2.5 mm.) penis has the major pilaster simple in structure (fig. 138h). Exactly the same pattern of variation is seen in the Nukuhiva sympatric species, *T. semimarsupialis* and *T. centadentata* (fig. 139b, f), one having a smaller penis with pustulose pilaster, the other a larger penis with simple pilaster.

Description of soft parts. — A single extracted specimen available, partly broken.

Pallial region typical, kidney about 1.38 mm. long, rectal arm 0.79 mm., ureter and heart typical.

Ovotestis of rather tightly compacted clumps of palmately clavate acini lying transversely to columellar axis, less interspersed with digestive gland than in *Taipidon centadentata.* Hermaphroditic duct, albumen gland and talon broken off in handling, not illustrated. Talon as in *Planudonta concava* (fig. 147c). Prostate (fig. 138e, DG) short, about 1 mm. long, with large acini in one or two rows. Uterus (UT) bipartite, extending only slightly below end of prostate. Free oviduct (UV) typical both internally and externally.

Vas deferens (VD) entering penis just below apex to one side of pilaster (fig. 138f). Penial retractor origin unknown, inserting onto fleshy head of penis proper. Latter not sharply differentiated externally. Penis (P) about 1.50 mm. long, swollen apically, tapering rapidly on lower half, internally (fig. 138f) with a large pilaster occupying upper two-thirds that is partly divided into elongated lumps, with a smaller pilaster in lower portion and a reduced pustulose zone just before basal narrowing. Spermatheca (S) inserting on peniovidual angle. Atrium (Y) short.

Jaw about 50μ wide, of rectangular, slightly over-lapping plates, 11 in a half jaw, each plate about 3 times as long as wide.

Radula with about 105 rows, central about 8μ wide, 10-11μ long, tricuspid, mesocone only slightly larger than ectocones, all cusps much shorter than basal plate. Laterals about 10μ square, 7 or 8 in number, transition to marginals in one or two teeth, mainly by shortening of basal plate. Marginals 9-10, with endocone becoming larger than mesocone, both longer than basal plate, often by 3rd or 4th mesocones and ectocones weakly splitting, outer marginals with square basal plate, endocone only slightly larger, mesocone and ectocone bi- or tricuspid.

(Based on BPBM 115704, an extracted and broken individual.)

Genus **Planudonta,** new genus

Large Endodontidae with typical apical and microradial sculpture, secondary microsculpture found only in *intermedia.* Postnuclear sculpture of high, prominent, rather widely spaced (ribs/mm. 3.61-6.54), slightly to strongly protractively sinuated radial ribs, 44 -84 on the body whorl. Apex and early spire slightly (*subplanula*) to deeply (*concava*) sunken below level of penultimate whorl, last whorl descending rapidly (except in *subplanula*). Whorls more than 6 (except *matauuna*), tightly coiled. Umbilicus broadly V-shaped to cup-shaped, regularly decoiling, with upper one-quarter to one-half of each umbilical whorl having drastically altered ribbing (fig. 146a). Parietal barriers 2, short to very long, without any traces (*subplanula* and *concava*) or with a few (*matauuna*) to many (*intermedia*) accessory traces. Columellar wall without barriers; with two small barriers in *matauuna*; or with numerous traces in *intermedia*. Palatal barriers absent in *concava*; 3 in *subplanula* and *matauuna*; many traces in *intermedia*. Anatomy only partly known. Penial retractor arising from columellar muscle, inserting directly onto fleshy extension of penis head. Vas deferens entering penis well below head. Penis internally with two pilasters, variously modified, and a pustulose zone in central region. Jaw with or without partial fusion of central plates. Radular teeth typical in structure and number.

Type species. – Planudonta concava, new species.

In possessing the fleshy extension to the penis head and the well-developed pustulose glandular zone in the central portion of the elongated penis, the species of *Planudonta* clearly are related to *Taipidon.* A fleshy extension to the penis head also is developed in various Rapan taxa (*Opanara,* figs. 96, 97, and *Orangia,* fig. 121) and the Austral Island *Australdonta* (fig. 125), but is absent from other Endodontidae. Other anatomical features, so far as are known, show no unusual structure.

Unfortunately, only five specimens are known of this genus, four from Nukuhiva and a broken shell from Hivaoa. Differences are so large that description of four species is necessary. Undoubtedly, adequate collecting would have revealed additional species.

Planudonta differs from *Taipidon* in its patterns of coiling. It might be polyphyletic in origin. In giving it generic level recognition, I am influenced by the great extent of the single change and the degree to which it has altered the basic shell pattern. The growth pattern of *Planudonta* is not duplicated elsewhere in the Endodontidae. Extra-limital flat-spired species include the Hawaiian *Cookeconcha decussatulus, C. lanaiensis, C. ringens, C. hystricellus,* and *C. jugosus;* the nominate race of the Society Island *Nesodiscus obolus;* and the Palau Island *Aaadonta kinlochi.* Except for the *Nesodiscus,* which is modified for brooding the eggs in the umbilicus, all have only moderately open umbilici, with mean D/U ratios of 2.48 - 3.81 (average 3.13). Those extra-limital species with distinctly depressed apices – the Hawaiian *Cookeconcha hystrix* and *C. stellulus;* Rapa Island *Opanara depasoapicata;* Mangarevan *Anceyodonta alternata;* and Society Island *Mautodontha aoraiensis* – have D/U ratios of between 2.72 and 3.10 (average 2.91). In contrast, the species of *Planudonta* have very widely open umbilici with D/U ratios of 1.68 - 2.07 (average 1.85). *Taipidon fragila* does have the apex depressed, but is an obvious relative of *T. varidentata.*

Not only is the umbilicus very wide, but the internal sculpture is quite unusual (fig. 146a). For nearly the upper one-quarter to one-half of each whorl there is no trace of major or microradial sculpture, but only irregular growth striae. Normal growth pattern involves deposition of a smooth callus over the parietal wall, either after partial resorption of the ribbing or

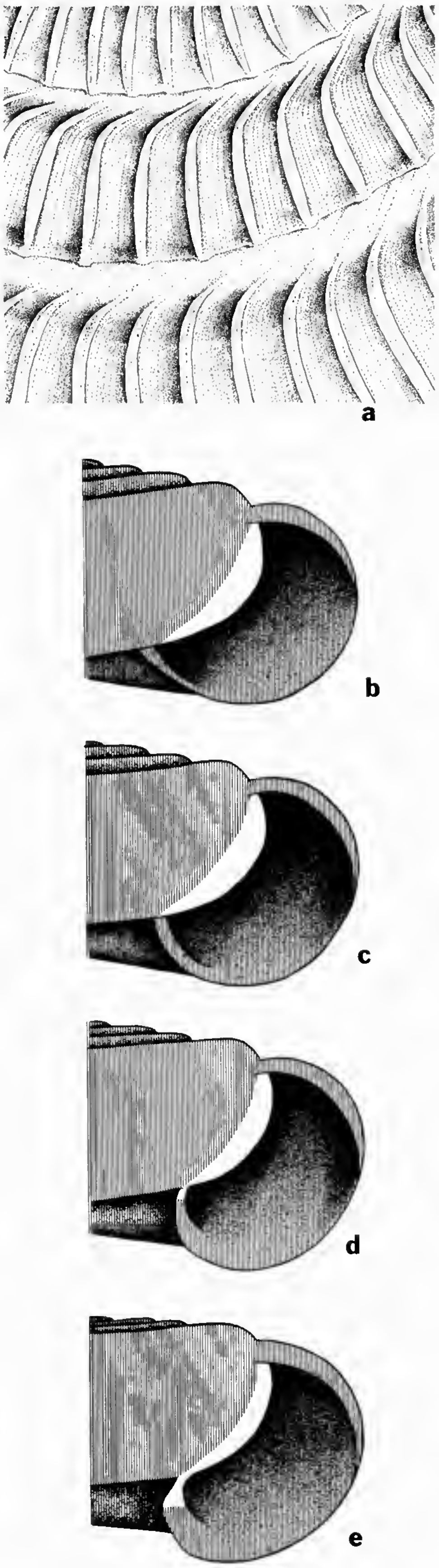

FIG. 146. Umbilical sculpture and origin in *Planudonta:* **a**, umbilical sculpture in *Planudonta concava.* Holotype. BPBM 96102; **b-e**, hypothesized intermediate stages in origin of this sculptural pattern. (MM).

covering the ribbing on the preceding whorl. A sudden change in growth pattern that involved lowering the apex and simultaneously widening and making the umbilicus shallower could move part of the parietal callus growth outward and downward below the edge of the preceding whorl (fig. 146b). This would produce the sculptural alteration found in the umbilicus of *Planudonta*. Since the ribbing in the umbilicus would have no obvious special function, there would not be selection pressure for extension of the ribbing. While *Planudonta* undoubtedly is derived from *Taipidon,* the retention of the peculiar umbilical sculpture does not have any necessary implications as to the time of origin.

The umbilical alterations and depression of the spire are linked characters caused by the major change in coiling pattern. While the probability of such a major change occurring more than once is low, it must be considered. At first glance, the changes in apertural barriers suggest multiple origins. *Planudonta concava* has lost all but the parietals, while *P. intermedia* and *P. matauuna* have accessory traces. The latter are present in *Taipidon petricola,* much as in *P. matauuna,* but the palatal traces in *T. centadentata* are very short and those in *P. intermedia* extend beyond the line of vision. Only *P. subplanula* has relatively "normal" barriers. Actually, a progression from normal barriers to traces, then reduction and elongation of all palatal and columellar barriers to traces, and finally a loss of the palatals and columellar is a logical sequence of changes. Such a change is seen in the three Nukuhiva species, *P. subplanula*, *P. intermedia*, and *P. concava,* which also show a progressive depression of the spire (almost flat to deep), concomitant increase in the ribless portion of the umbilical whorls, and decrease in umbilical depth. It is not possible to relate the fragmentary Hivaoa species, *P. matauuna*, to this series. Under these circumstances, I have no hesitation in considering these species a monophyletic series.

Other variation is comparatively minor. The ribs are quite prominent and weakly to strongly protractive. Spacing (table XCIV) is variable, the change within *P. subplanula* being larger than the differences between the species. Only *P. intermedia* shows traces of secondary spiral cording. Diameter at four and five whorls, measured from the apex to the suture, also shows more variation within *P. subplanula* than between the other species (table XCIV).

As would be expected, the genital differences between the essentially sympatric *P. intermedia* (fig. 147b) and *P. concava* (fig. 147d), both taken within 150 ft. elevation on Mt. Ooumu, are greater than the differences between *P. subplanula* (fig. 147g) and *P. intermedia.*

Except for the single shell of *P. subplanula* from the Tovii region of Nukuhiva at 200 ft. elevation, all available material was taken at above 3,400 ft. elevation. Quite probably Andrew Garrett did not collect much above 2,000 ft. (*Taipidon woapoensis*). His failure to collect this group has no significance. All records, except for the type or *P. subplanula,* indicate collection "under dead leaves." While the latter was recorded as "collected on ferns or shrubs," I am not convinced that this is an arboreal species. I suspect that the entomologist who collected this specimen picked it up from the ground and put it in a vial with the large and conspicuous *Philonesia ordinaria* taken from ferns and shrubs at the same station (see H. B. Baker, 1940, p. 153). I am very doubtful that *P. subplanula* will be found to leave the ground stratum.

TABLE XCIV. - RIB SPACING AND WHORL DIAMETER IN PLANUDONTA

Name	Ribs	Ribs/mm.	4 whorl diameter in mm.	5 whorl diameter in mm.
subplanula				
Holotype	84	5.85	1.15	1.64
BPBM 98252	44	4.00	1.41	2.01
intermedia				
Holotype	77	6.54	1.05	1.51
concava				
Holotype	69	3.79	1.25	1.84
matauuana				
Holotype	44	3.61	1.48	2.01

Although forest destruction in the Marquesas has proceeded to a great extent, it is very possible that material of *Planudonta* can still be found at high elevations in patches of native forest.

KEY TO THE GENUS *Planudonta*

1. Barriers present on palatal wall 2
Barriers absent from palatal wall; diameter more than 5.25 mm.
Planudonta concava, new species
2. Several accessory traces present on parietal wall..........................3
No accessory traces present on parietal wall.
Planudonta subplanula, new species
3. Ribbing crowded, ribs/mm. 6.50; many palatal traces extending beyond line of vision; Nukuhiva.
Planudonta intermedia, new species
Ribbing widely spaced, ribs/mm. 3.60; no accessory palatal traces; Hivaoa ....*Planudonta matauuna*, new species

Planudonta subplanula, new species. Figures 147f-g; 148.

Description. – Shell large, with 6⅜ tightly coiled whorls. Apex and spire depressed slightly below level of body whorl, last whorl descending a trifle, H/D ratio 0.346. Apical whorls slightly less than 1½, sculpture typical on most of surface, slightly worn in spots. Postnuclear whorls with high, prominent, lamellate, protractively sinuated radial ribs, 84 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, four to six between each pair of major ribs, with barely visible traces of microspiral ribbing. Sutures deep, whorls very strongly rounded above and on moderately shouldered umbilical margin, with evenly rounded outer margin. Umbilicus broadly V-shaped, regularly decoiling, contained 1.68 times in the diameter. Walls of umbilicus slightly flattened internally, ribbing sharply angled and becoming very slender just before umbilical sutures. Color light yellow horn,

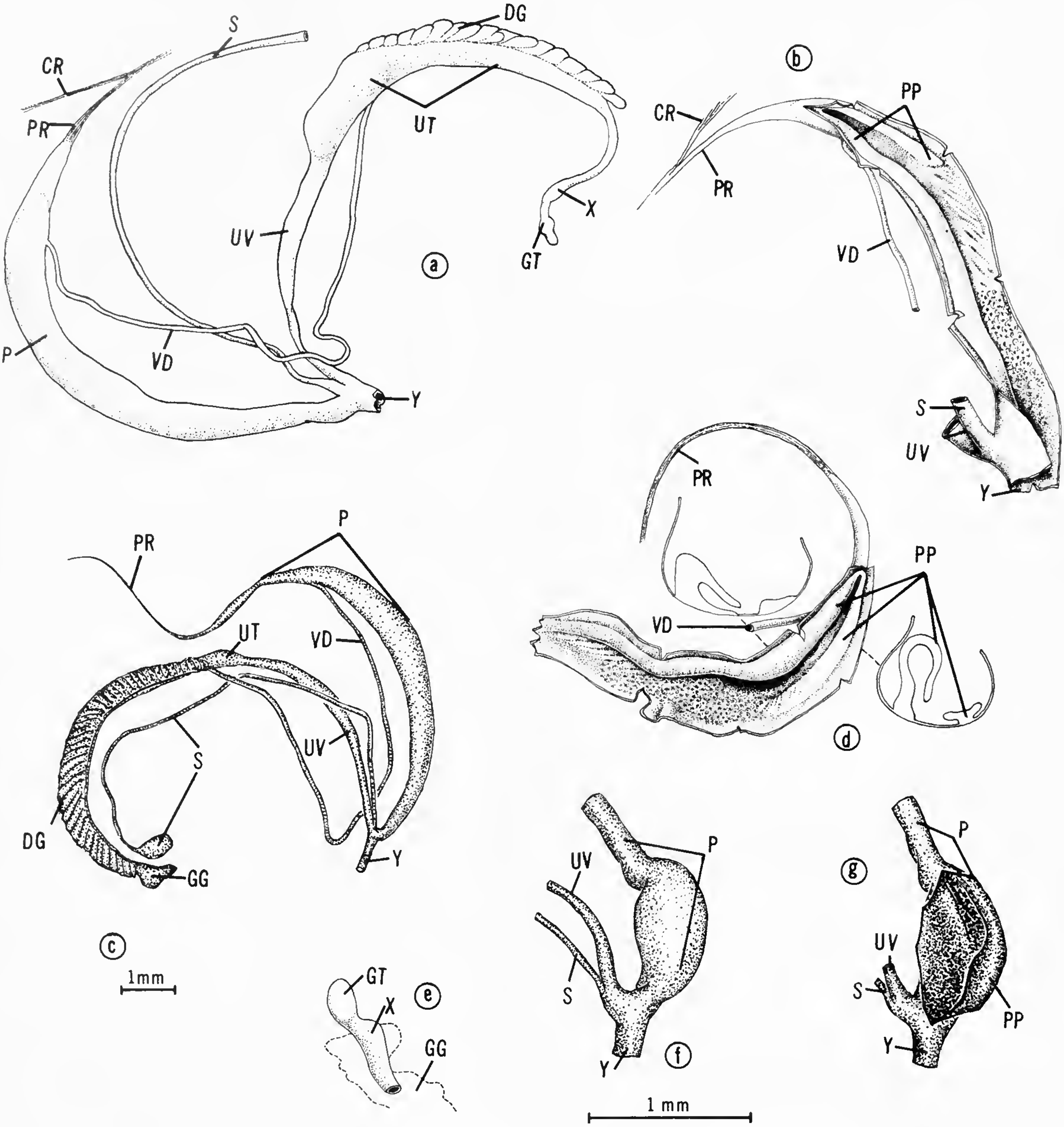

FIG. 147. Anatomy of *Planudonta*: **a-b**, *P. intermedia*. Mt. Ooumu, Nukuhiva, Marquesas. BPBM 96057. *a*, genitalia, *b*, interior of penis; **c-e**, *P. concava*. Mt. Ooumu, Nukuhiva, Marquesas. *c*, genitalia, *d*, interior of penis, *e*, talon and carrefour; **f-g**, *P. subplanula*. Puokoko. Nukuhiva, Marquesas. BPBM 95936. *f*, terminal genitalia, *g*, interior of penis. (See Appendix for explanation of abbreviations.)

with broad, somewhat irregularly spaced, reddish flammulations that become narrowed and strongly zigzagged near periphery, becoming broader again on shell base and in umbilicus. Aperture ovate, with evenly rounded outer margin, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly almost one-quarter whorl: upper a high, thin lamellar ridge, weakly expanded and serrated above on posterior quarter, with very gradual anterior descension; 2nd parietal distinctly higher posteriorly, expanded and serrated above on posterior quarter, with rather sharp anterior descension to threadlike anterior half that terminates slightly beyond end of upper parietal. Palatal barriers 3, deeply recessed within aperture, low lamellar ridges: 1st basal in position, a short threadlike trace; 2nd an elevated, V-shaped ridge, with gradual anterior descension; 3rd slightly supraperipheral, a low and threadlike trace. Height of holotype 1.58 mm., diameter 4.57 mm.

Holotype. — Marquesas Islands: Nukuhiva, Puokoko on Tunoa Ridge at 3,485 ft. elevation. Collected on ferns or shrubs on November 22, 1929, by members of the Pacific Entomological Survey. BPBM 95936.

Range. — Nukuhiva, Marquesas Islands.

Paratype. — BPBM 98252.

Material. — Nukuhiva: Puokoko on Tunoa Ridge at 3,485 ft. elevation (1 specimen, BPBM 95936); Tovii region at 200 ft. elevation (1 specimen, BPBM 98252).

Remarks. — A specimen from the Tovii region of Nukuhiva (BPBM 98252) is tentatively referred here despite several differences. It is obviously subadult, has a greater H/D ratio than the holotype (table XCIV), much more widely spaced ribbing, lacks the lower parietal, and has only two small palatals. The whorls are also more loosely coiled and more strongly rounded above (table XCV). The similarities are sufficient that I prefer to consider them conspecific.

The only slightly depressed spire, retention of 3 palatals, and very wide umbilicus separate *P. subplanula* from the other species of *Planudonta.*

Unfortunately, the type specimen is not fully grown. While partial descension of the body whorl has occurred, there is no indication of change in the ribbing pattern at the aperture and an estimated additional quarter whorl of growth could occur before cessation of growth as a gerontic individual. An adult size of 5 mm. is quite possible.

Description of soft parts. — Only a fragmentary, very smashed individual was available. No details of muscular or digestive system could be determined and only a small part of the terminal genitalia remained.

Lower part of penis (fig. 147f, P) swollen and twisted, internally (fig. 147g) with two pilasters, one large and hemispherical, one low and broad, that continue apically as two low pilasters. Area between pilasters in swollen area densely papillose. Atrium (Y) long and slender. Shaft of spermatheca (S) and remnant of free oviduct (UV) typical.

Jaw of about 20 rather narrow plates on each side, edges free, middle area partly fused.

Radula with centrals tricuspid, about 6 μ wide and 8-10 μ long. More than 100 rows, with about eight laterals and ten marginals. Latter rectangular, mesocone split with inner cusp distinctly smaller, ectocone split into two to four cusps of variable length, shorter than main mesoconal cusp and always narrower, but sometimes as long as main mesoconal cusp. Laterals without endocone until 6th or 7th, transition to square marginals occurring in three or four rows.

(Based on BPBM 95936, one fragmentary example.)

Planudonta intermedia, new species. Figures 147 a-b; 149c-d.

Description. — Shell small, with 6¼ tightly coiled whorls. Apex and early spire distinctly sunken beneath level of penultimate whorl, last half of body whorl descending rather rapidly below level of penultimate whorl, H/D ratio 0.413. Embryonic whorls slightly less than 1½, sculpture eroded from most of upper surface, with microradial and microspiral traces visible in sutures, visible in umbilicus as typical microradial ribbing, with first half whorl macroscopically smooth. Postnuclear whorls with high, narrow, slightly protractively sinuated radial ribs, 77 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of very fine radial riblets, five to ten between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification, with a secondary sculpture of narrow, rather widely spaced spiral cords. Sutures deep, whorls strongly shouldered above and on basal margin, markedly compressed laterally, with evenly rounded outer margin. Color light yellowish-white, with broad, irregular, strongly zigzagged, reddish flammulations. Umbilicus broadly open, V-shaped, regularly decoiling, contained 1.93 times in the diameter, with flattened walls on which the upper third of each volution lacks any formed sculpture. Aperture compressedly ovate, strongly shouldered above and on basal margin, inclined less than 10° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision, with eleven deeply recessed threadlike traces: upper parietal relatively low, strongly expanded and serrated above on posterior visible three-quarters, with rather gradual anterior descension; 2nd parietal slightly reduced in height, equally expanded and serrated above posteriorly, with more gradual anterior descension; 2nd parietal slightly reduced in height, equally expanded and serrated above posteriorly, with more gradual anterior descension to a threadlike anterior that extends slightly beyond end of upper parietal. Accessory traces located three above upper parietal; four between 1st and 2nd parietal; and six below 2nd parietal. Columellar and palatal walls with numerous, extremely fine threadlike ridges, that extend posteriorly beyond line of vision: one columellar and two palatal traces are slightly more elevated than the remaining, but still are threadlike in character. Height of holotype 1.61 mm., diameter 3.75 mm.

Holotype. — Marquesas Islands: Nukuhiva, near summit of Mt. Ooumu at 4,050 ft. elevation. Collected among dead leaves and wet humus on November 12, 1929, by members of the Pacific Entomological Survey. BPBM 96057.

Range. — Nukuhiva, Marquesas Islands.

Material. — Only the holotype is known.

Remarks. — The apertural barriers recall that of *Taipidon centadentata,* except that in *Planudonta intermedia* the palatal riblets extend posteriorly beyond the line of vision while in *T. centadentata* they are less than one-sixteenth of a whorl in length. The upper columellar and two of the mid-palatal traces are distinctly more elevated than the others. Descension of the body whorl is substantial and there is partial gerontic ribbing pattern just behind the aperture. The specimen probably is fully adult, but gerontic growth could have continued for a small fraction of a whorl.

Planudonta matauuna agrees in having the accessory parietal traces, but their number and length are greatly increased in *P. intermedia.* Its name is derived from the growth pattern and umbilical form, which lie between the patterns of *P. subplanula* and *P. concava.* The penis is unusual only in the very large size of the pilasters.

Description of soft parts. — External features and partial pallial complex without unusual structures.

Apical genitalia not available for study.

Prostate (fig. 147a, DG) shorter and with larger acini than in *P. concava.* Uterus (UT) bipartite, lower portion extending below vas deferens origin.

Vas deferens (VD) typical, entering penis laterally between major pilasters, about 0.43 mm. below penis head. Penial retractor (PR) arising from columellar muscle, inserting onto fleshy extension of penis head. Penis (P) about 4.6 mm. long, slightly tapering, with a short, fleshy extension, internally (fig. 147b) with two nearly circular pilasters (PP) that unite at penis apex. One fades out into a series of

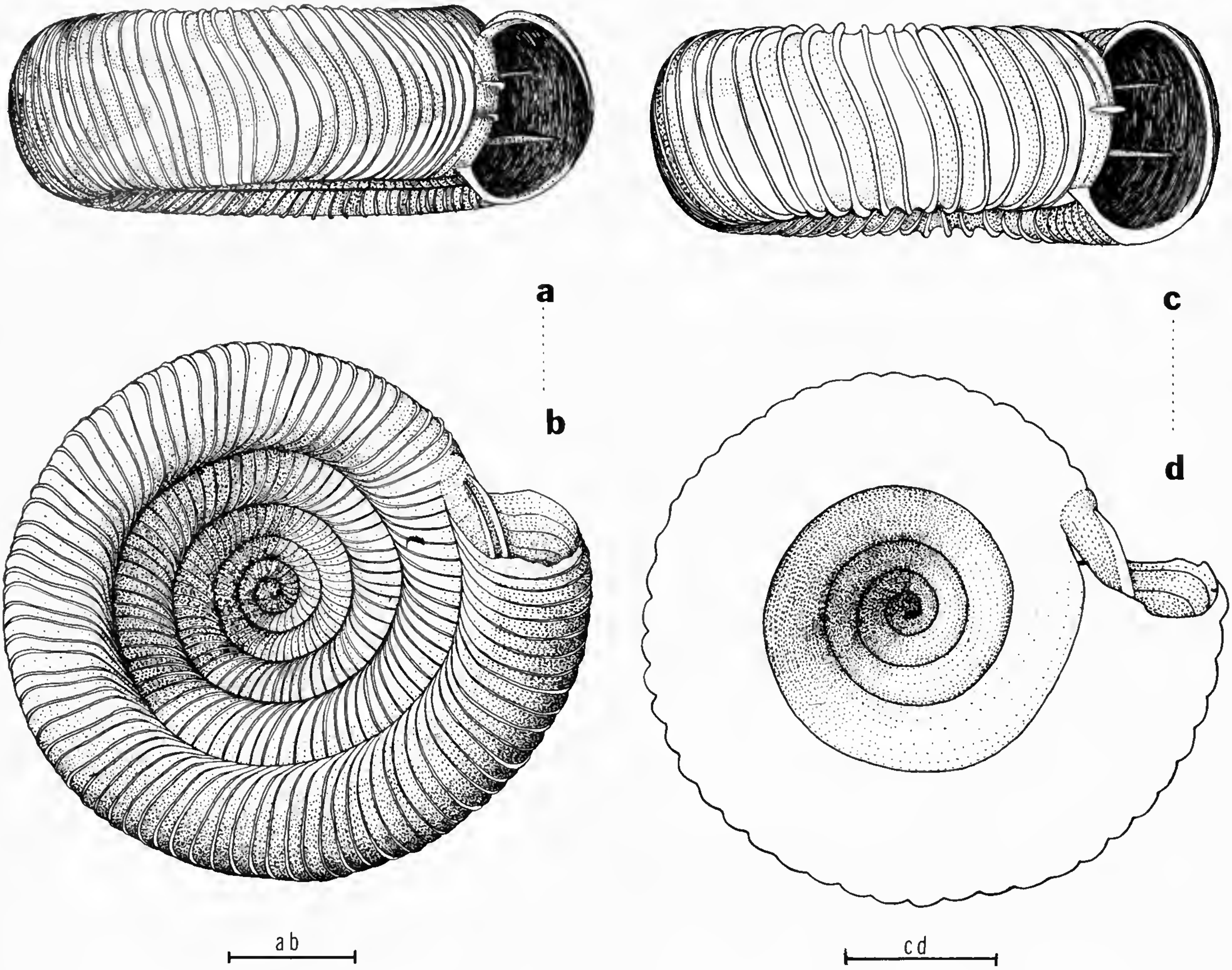

FIG. 148. *Planudonta subplanula,* new species: **a-b**, Puokoko, 3,485 ft., Nukuhiva, Marquesas. Holotype. BPBM 95936; **c-d**, Tovii, Nukuhiva, Marquesas. Paratype. BPBM 98252. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

transverse rugae after upper fifth, other continues to atrium. Atrium (Y) incomplete in only available example.

Free oviduct (UV) not clearly distinguished externally from uterus, internally with much finer pustulations. Spermatheca (S) with head missing, shaft inserting directly into peniovidućal angle.

Free muscle system and digestive system incomplete and not studied.

Jaw and radula not successfully mounted.

(Based on BPBM 96057, one partly extracted specimen.)

Planudonta concava, new species. Figures 147c-e; 149a-b.

Description. — Shell very large, with 6⅝ tightly coiled whorls. Apex and spire deeply and evenly sunken beneath level of first half of body whorl, last half of body whorl descending moderately until below level of penultimate at aperture, H/D ratio 0.364. Apical whorls 1⅜, typical microsculpture visible in sutures, surface worn. Postnuclear sculpture of high, prominent, lamellar, strongly protractively sinuated radial ribs, 69 on the body whorl, whose interstices are 3-5 times their width. Microsculpture of fine radial riblets, six to ten between each pair of major ribs, crossed by barely visible microspirals. Sutures deep, whorls strongly rounded above and shouldered below on basal margin, somewhat compressed laterally, with evenly rounded outer margin. Color light yellow-white, with broad, irregularly spaced, reddish flammulations that become strongly zigzagged near periphery and fade out on shell base. Umbilicus very broadly open, quite shallow, regularly decoiling, contained 1.74 times in the diameter, with upper one-quarter to one-half of each umbilical whorl lacking major sculpture. Aperture ovate, shouldered above on basal margin, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly less than three-sixteenths of a whorl: upper a moderately elevated, V-shaped ridge, not expanded above posteriorly, with rather sharp anterior descension; 2nd parietal a threadlike trace, equal in length to upper parietal, very weakly expanded above on posterior third. A very thick, slightly elevated callus near point where columellar wall dips around umbilical margin gives impression of being an additional parietal. Palatal and columellar walls without barriers. Height of holotype 2.10 mm., diameter 5.79 mm.

Holotype. — Marquesas Islands: Nukuhiva, ridge of Mt. Ooumu at 3,900 ft. elevation. Collected on the ground under dead leaves on November 13, 1929 by members of the Pacific Entomological Survey. BPBM 96102.

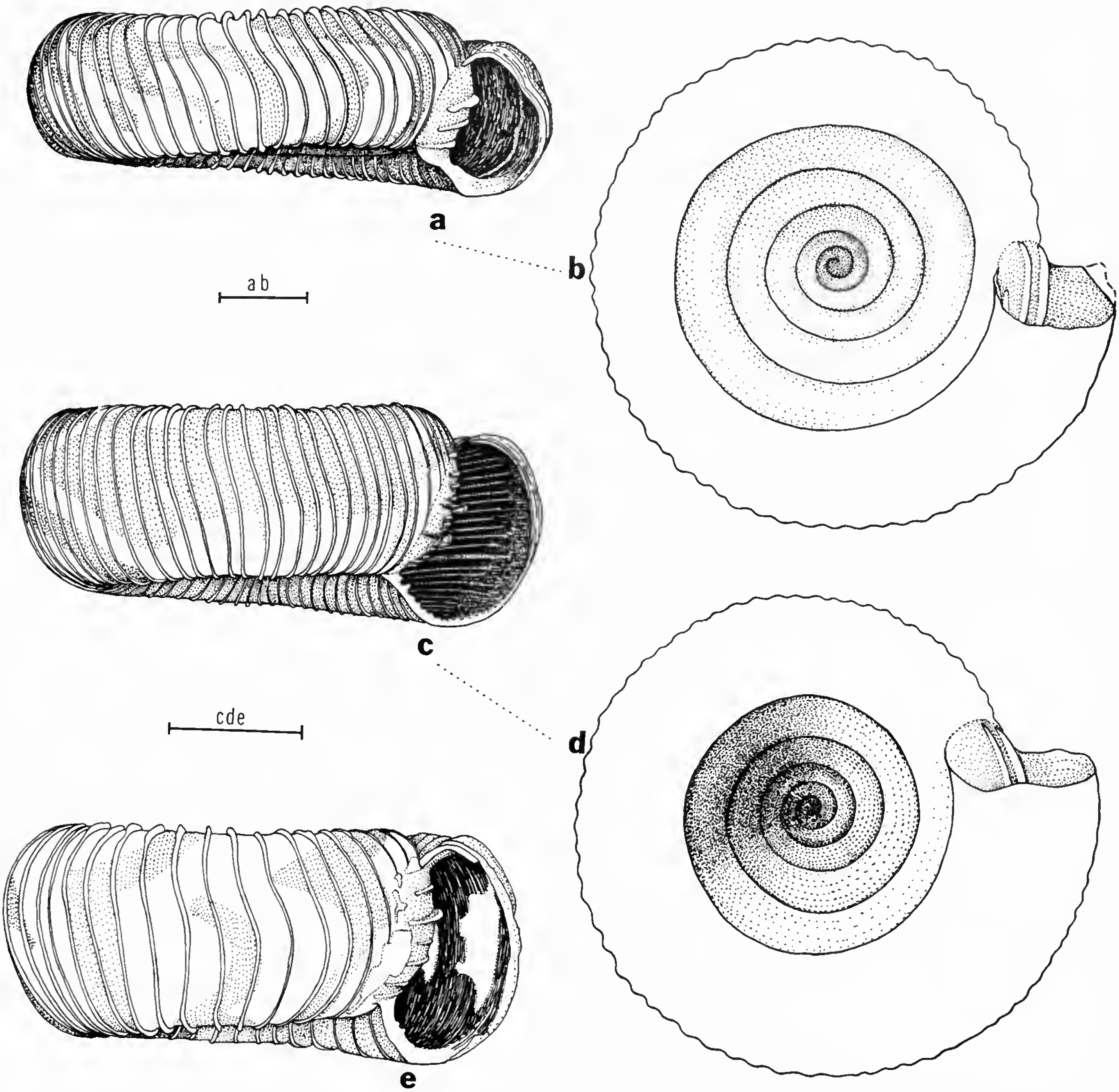

FIG. 149. **a-b**, *Planudonta concava*, new species. Mt. Ooumu, 3,900 ft., Nukuhiva, Marquesas. Holotype. BPBM 96102; **c-d**, *Planudonta intermedia*, new species. Mt. Ooumu, 4,050 ft., Nukuhiva, Marquesas. Holotype. BPBM 96057; **e**, *Planudonta matauuna*, new species. Matauuna, 3,800 ft., Hivaoa, Marquesas. Holotype. BPBM 98789. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Range. – Nukuhiva, Marquesas Islands.

Material. – Only the holotype is known.

Remarks. – The very depressed apex and complete absence of any palatal or columellar barriers separate *Planudonta concava* from the other planorbiform Marquesan endodontids. The comparatively large size of *P. concava* may simply be a function of its being an adult shell while the types of *P. subplanula* and *P. intermedia* may be subadult. The very broad and shallow umbilicus with even depression of the apex and spire differ markedly from the almost flat apex and rather deep umbilicus of *P. subplanula*. The latter retains palatal barriers and has a much narrower zone of riblessness on the umbilical whorls.

The only known specimen of *P. concava* is gerontic with typical breakdown in ribbing pattern just behind the aperture. It is conceivable that existing palatal barriers were resorbed during this gerontic growth (see, for example, *Minidonta simulata*, fig. 70d), but the absence of any parietal reduction and any lip callus or irregularities makes me doubt the possibility of secondary reduction. Descent of the body whorl has proceeded far enough that the columellar wall lies inside the umbilical margin of the penultimate whorl at the aperture. Extensive callus formation has been required to fill in this angle and this growth gives the impression of forming a barrier at the parietal-columellar angle (fig. 149a, b). I am uncertain as to whether a 3rd parietal exists in young shells and has been covered by callus formation, or whether this trace barrier is an artifact of deposition unique to this specimen.

Description of soft parts. — Only a partial extracted specimen was available. External features as in all examined Endodontidae.

Mantle collar thick, without separate lobes, a slender glandular extension onto lung roof. Pneumostome and anus typical.

Pallial region about 6.8 mm. long. Lung roof clear, without granulations. Kidney about 3.03 mm. long, rectal lobe 1.32 mm. and appressed to hindgut. Ureter typical, reflexed posteriorly alongside rectal kidney arm, opening just anterior to rectal kidney arm termination. Heart about 1.5 mm. long, slightly angled to plane of hindgut. Principal pulmonary vein large, running to mantle gland extension.

Ovotestis and hermaphroditic duct not available for study. Albumen gland (fig. 147c, GG) very slender, only partly shown in drawing, much longer than talon. Talon (fig. 147e, GT) with short thick shaft, not tapering, entering top of slightly more swollen carrefour. Prostate (DG) flattened, two or three rows of acini attached to a narrow tube. Uterus (UT) typically bipartite, lower chamber extending well below level of vas deferens origin.

Vas deferens (VD) loosely bound to peniovidućal angle, entering penis laterally between major pilasters, about 0.72 mm. below head. Penial retractor (PR) apparently arising from columellar muscle, inserting directly onto fleshy extension of penis head. Penis (P) about 6.05 mm. long, very slender and tapering gradually, with a firm, slender, fleshy extension well above entrance of vas deferens. Internally (fig. 147d, PP) with two very slender, elevated pilasters above, which merge into a papillose central portion, but reappear as formed, semicircular pilasters just before atrium. Atrium (Y) very long and slender.

Free oviduct (UV) internally much more finely papillose than uterine section, externally not clearly differentiated. Spermatheca (S) with oblong head lying next to albumen gland, slender shaft inserting into peniovidućal angle. Vagina absent.

Free muscle system not studied.

Jaw about 60μ wide, composed of separated plates that are one-third as wide as long in small fragment mounted. Central area not differentiated.

Radula with centrals about 10μ long and 8μ wide, 10-11 laterals and more than 7 marginals. Tooth structure as in *Planudonta subplanula.*

(Based on BPBM 96102, one partial specimen.)

Planudonta matauuna, new species. Figure 149e.

Description. — Shell small, with 5¼ tightly coiled whorls. Apex and spire moderately and evenly depressed below level of penultimate whorl, last half of body whorl descending moderately rapidly to point below level of penultimate whorl at aperture, H/D ratio 0.449. Apical whorls 1¼, traces of typical sculpture visible in sutures of umbilicus, eroded from apex of shell. Postnuclear sculpture of high, prominent, rather widely spaced, slightly protractively sinuated radial ribs, 44 on the body whorl, whose interstices are 4-6 times their width. Microsculpture of fine radial riblets, nine to twelve between each pair of major ribs, crossed by barely visible spiral riblets. Sutures deep, whorls strongly rounded above and on shouldered umbilical margin, compressed laterally, with evenly rounded outer margin. Color light yellow-white, with narrow, irregular, reddish flammulations that become strongly zigzagged on side of shell base. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.07 times in the diameter, upper third of each whorl without typical ribbing. Aperture subovate, strongly compressed laterally, shouldered above and on umbilical margin, inclined about 10° from shell axis. Parietal wall with 2 major barriers, extending posteriorly somewhat more than one-eighth whorl, with four accessory traces: upper parietal a moderately elevated lamellar ridge, weakly expanded above on posterior half, with rather gradual anterior descension; 2nd parietal a low elevated threadlike ridge, not obviously expanded or elevated posteriorly. Accessory traces located near parietal-palatal margin, between 1st and 2nd parietal, with two below 2nd parietal, all short, deeply recessed and threadlike. Columellar wall with two short, inconspicuous threadlike traces that reach only to top of columellar callus. Remnant of palatal wall with three subperipheral, widely spaced, threadlike traces. Height of holotype 1.74 mm., diameter 3.88 mm.

Holotype. — Marquesas Islands: Hivaoa, Matauuna, north of Mt. Temetiu's summit at 3,800 ft. elevation. Collected among dead leaves on March 3, 1930 by members of the Pacific Entomological Survey. BPBM 98789.

Range. — Hivaoa, Marquesas Islands.

Material. — Only the holotype is known.

Remarks. — The holotype of *Planudonta matauuna* is a dead specimen with the umbilical region and part of the body whorl badly broken. The very widely spaced ribbing (ribs/mm. 3.61) and what seems to be a quite distinct pattern of apertural barriers required description of this specimen as a species. The palatal traces (not shown in the type figure) are much shorter and differently placed than the enlarged traces seen in *P. intermedia* (fig. 149c), although the larger parietals of both species are almost identical. Compared with the other *Planudonta, P. matauuna* has a much deeper, cup-shaped umbilicus and very widely spaced radial ribbing. *P. concava,* the only species with similarly spaced ribbing, is much, much larger and has a very shallow, V-shaped umbilicus. Although the type has a subadult lip growth, actual adult size probably differs only slightly, since considerable descension of the body whorl has occurred and, judging from the other *Planudonta,* probably less than one-eighth whorl of growth would be terminal.

Genus **Rikitea,** new genus (Solem & Cooke)

Rather small, widely umbilicated Endodontidae in which the apertural barriers are reduced to 1 extremely large parietal. Columellar and palatal barriers absent. Ribbing prominent, microsculpture unknown. Elevation of apex and whorl count unknown, body whorl descending rapidly. Sutures deep, whorls evenly rounded.

Type species. — *Rikitea insolens,* new species.

At first glance, *Rikitea insolens* would seem to be a relative of *Nesodiscus obolus,* distinguished primarily by the heavy ribbing and enlarged parietal. Comparison of whorl contours, ribbing type, size

TABLE XCV. - RANGE OF VARIATION IN PLANUDONTA, RIKITEA AND NESODISCUS

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D ratio	Whorls	D/U ratio	Pr	C	P
Planudonta										
subplanula	2	84	1.58	4.57	0.346	6 3/8	1.68	2	0	3
intermedia	1	77	1.61	3.75	0.413	6 1/4	1.93	2+11	MANY	MANY
concava	1	69	2.10	5.79	0.364	6 5/8	1.74	2	0	0
matauuana	1	44	1.74	3.88	0.449	5 1/4	2.07	2+4	1+1	3
Rikitea										
insolens	1	48	1.22	2.90	0.421	___	2.20	1	0	0
Nesodiscus										
taneae (Garrett)	246	REDUCED ON BODY WHORL	2.10(1.70-2.94)	4.89(3.86-5.82)	0.428(0.327-0.535)	6+(4 3/4-8 1/8)	2.58(1.92-2.97)	2	0	3-4-5
huaheinensis (Pfeiffer)	159	REDUCED	2.19(2.09-2.48)	5.17(4.90-5.82)	0.424(0.372-0.448)	5 7/8(5 5/8-6 1/4)	2.51(2.27-2.82)	2	0	4
obolus										
f. obolus (Gould)	60	OVER 200	1.90(1.31-2.48)	4.76(4.44-5.03)	0.398(0.273-0.535)	6+(5 1/2-6 1/2)	2.14(1.75-2.69)	1-2	0	0-1-2
f. acetabulum (Pease)	91	OVER 200	2.11(1.77-2.48)	5.12(4.31-5.95)	0.414(0.359-0.461)	6 1/4-(5 7/8-7)	2.02(1.86-2.23)	1-2	0	0-1
f. celsus (Pease)	18	OVER 200	2.84(2.22-3.46)	5.50(5.10-6.28)	0.517(0.406-0.647)	6 7/8-(6 3/8-7 3/8)	2.15(2.00-2.66)	1-2	0	0-1-2
cretaceus (Garrett)	7	VERY REDUCED	2.10(1.84-2.29)	5.62(5.06-6.41)	0.377(0.335-0.429)	6 1/2+(6 1/8-7 1/8)	2.03(1.95-2.09)	1	0	1
fictus (Pease)	1,041	VERY REDUCED	2.77(2.16-3.60)	6.47(5.62-7.32)	0.428(0.337-0.531)	7 7/8+(7 1/8-8 5/8)	1.97(1.84-2.23)	1	0	0-1
fabrefactus (Pease)	75	VERY REDUCED	3.66(2.89-4.67)	7.46(6.84-8.55)	0.490(0.404-0.602)	7+(6 1/4-8)	1.91(1.70-2.17)	0	0	0
f. piceus (Garrett)	6	VERY REDUCED	3.05(2.55-3.40)	6.06(5.82-6.21)	0.505(0.428-0.553)	7 1/8-(6 1/8-7 1/4)	1.99(1.94-2.07)	1	0	1
magnificus	1	UNKNOWN	5.10	11.19	0.454	7 1/8	2.87	1	0	0

(table XCV), parietal barrier structure, and pattern of whorl coiling leaves no choice but to consider them unrelated. In *Nesodiscus obolus* the whorls are distinctly flattened and the periphery angulated, the sutures much shallower; the ribbing reduced to strongly protractively sinuated microradials; the adult size is about 4.75 mm.; the parietal barrier an elevated threadlike ridge that is distinctly supraperipheral; and the whorls are very tightly coiled. *Rikitea insolens* has the whorls evenly rounded and the sutures deep; the ribbing is very prominent and only slightly protractively sinuated; the adult size is less than 3 mm.; the parietal barrier a greatly elevated lamellar blade that is medial; and the whorls, by extrapolation from the remaining part, much more loosely coiled.

Considerable reluctance was felt in describing a genus from a single partial individual, but the differences are so striking that nomenclatural recognition has been given. The single huge parietal barrier finds its parallel only in *Discocharopa* (see Part II). In the absence of the apical whorls and with the worn condition preventing study of the microsculpture, determining the exact relationship that *Rikitea* bears to other genera is not possible. The general form of the sculpture agrees with *Taipidon*, but the pattern of coiling almost certainly is different. *Anceyodonta*, *Minidonta*, and *Gambiodonta* differ in nearly every character of shape and umbilicus, but the form of the parietal barrier and the ribbing could, without difficulty, be derived from the *Minidonta-Anceyodonta* type. The complete absence of accessory traces, columellar and palatal barriers in *Rikitea* is not significant, since the loss of these has occurred several times in different lineages. Probably *Rikitea* is a quite isolated derivative from *Minidonta*, but more complete material will be needed to determine its affinities.

Rikitea insolens, new species (Cooke & Solem). Figure 150.

Description. — Shell smaller than average, apex and early whorls missing so that whorl count is unknown. Descension of last whorl accelerating rapidly, spire probably flat or only slightly elevated. H/D ratio probably about 0.421. Microsculpture worn off entire surface, apical sculpture unknown. Body whorl with 48 very prominent, high, slightly protractively sinuated radial ribs whose interstices are about twice their width (too widely spaced in fig. 150a). Sutures deep, whorls strongly rounded above, with evenly rounded outer margin and slight shouldering of umbilical margin. Aperture nearly circular, inclined about 15° from shell axis. Parietal wall with single, very high, medially placed barrier, extending posteriorly beyond line of vision, with gradual anterior descension on visible anterior quarter until just before termination, when descension becomes abrupt. Barrier worn on surface, but remnants of strong superior expansion and probable serration remain. Height of specimen with apex and most of spire missing 1.22 mm., diameter 2.90 mm.

Holotype. — Gambier Islands: Mangareva, Station 187, Mangareva Islet, north part of Rikitea. Collected by Yoshio Kondo on June 27, 1934. BPBM 141663.

Range. — Mangareva Islet, Mangareva, Gambier Islands.

Material. — Only the holotype is known.

Remarks. — Associated with the single example of *Rikitea insolens* were one specimen each of *Minidonta simulata*, *Anceyodonta subconica*, *A. ganhutuensis*, and *Gambiodonta mangarevana;* two specimens of *Anceyodonta andersoni*; six each of *A. difficilis* and *A. hamyana*; nine of *A. obesa*; and 15 of *A. sexlamellata*. Comparatively little material was obtained from this station and further collecting probably would yield additional specimens of *Rikitea.*

Differences from *Nesodiscus obolus* have been given above under the discussion of the generic affinities. The only other species that might be confused are some of the Hawaiian taxa with reduced apertural barriers, such as *Cookeconcha decussatulus*, *C. lanaiensis*, and *C. jugosus*. All are much larger, with narrower umbilici, different whorl contours, and marked secondary spiral cording.

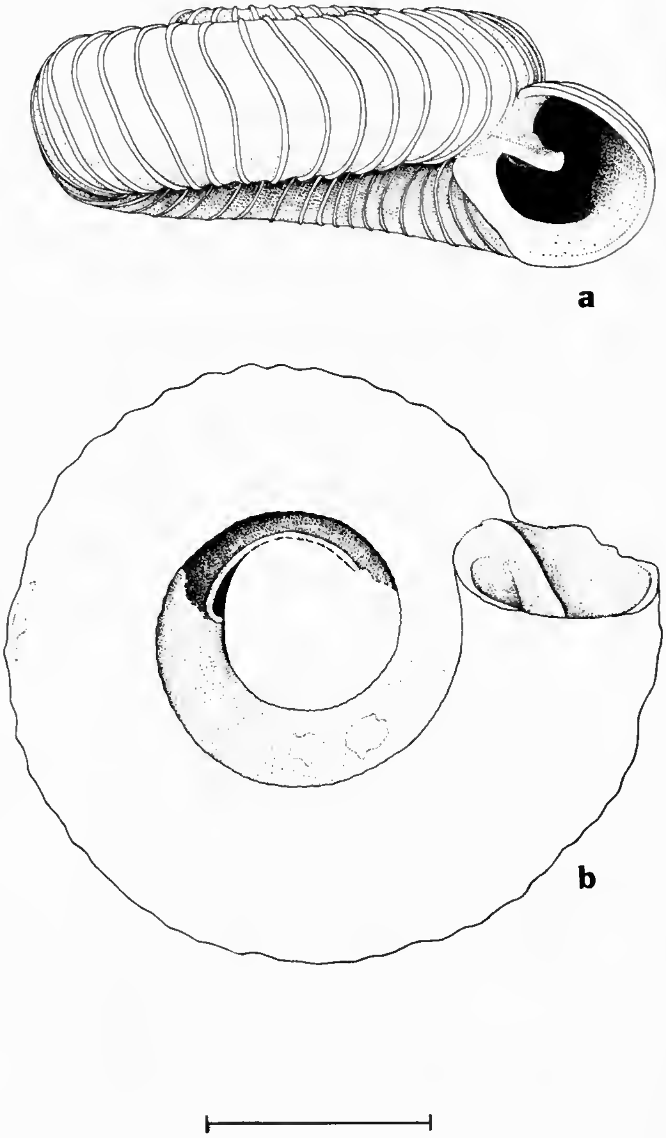

FIG. 150. a-b, *Rikitea insolens*, new species. Station 187, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 141663. *a*, side; *b*, base of shell. Scale line equals 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Rikitea insolens is quite unlike any species of similar size and the name *insolens* refers to its unusual structure. Although much smaller in size, I suspect that *Rikitea* represents the Mangarevan equivalent of the *Nesodiscus* level of organization.

Genus **Nesodiscus** Thiele, 1931

Hand. Syst. Weichtierkunde, 1, (2), p. 571.

Endodontidae with the major apical sculpture consisting of large and broadly rounded radial ribs, apical microsculpture typical. Postnuclear whorls with very fine and crowded ribs in most species, larger ribs present in *magnificus,* restricted to upper spire in *taneae.* All sculpture greatly reduced in *cretaceus* and *fabrefactus.* Apex often markedly protruding, except in *fabrefactus* and *magnificus,* spire rarely flat (form *obolus*), usually moderately elevated and convex, strongly elevated in form *celsus* and strongly elevated with concave sides in *fabrefactus.* Mean H/D ratio much less than 0.500 in all but *celsus* and *fabrefactus.* Body whorl with angled to strongly keeled periphery, rarely rounded in *obolus.* Whorls 6-8, lower counts in the smaller species. Umbilicus very broadly open, U-shaped in *magnificus,* cup-shaped in most species, mean D/U ratio 1.90-2.15 except narrower in *huaheinensis, taneae* and *magnificus.* Size large to very large. Parietal wall generally with 1 low barrier extending posteriorly beyond line of vision, absent in typical *fabrefactus,* a 2nd deeply recessed parietal in *taneae* and *huaheinensis,* rarely in *obolus.* Columellar wall without barriers. Palatal barriers very deeply recessed, variable in number: normally 4 in *taneae* and *huaheinensis;* 1 in *cretaceus* and *fictus;* 0-3 in *obolus;* absent in *fabrefactus* and *magnificus.* Soft parts not examined except in *fictus* and penial complex of *fabrefactus.* Pallial organs and apical viscera typical of family, except for effects of narrowing whorl diameter and lengthening of organs. Penial retractor originating partly from diaphragm, partly from columellar muscle, inserting directly on penis head. Vas deferens entering penis laterally between united pilasters. Penis short, expanded supramedially or slender, depending on degree of pilaster expansion and folding, internally with two equal pilasters united above at penis head. Prostate shorter than free oviduct, vagina not differentiated. Radula and jaw typical.

Type species. — Helix fabrefactus Pease, 1864, by monotypy.

Originally it was proposed as monotypic for the only known species of the Endodontidae that totally lacks apertural barriers. The only extended use of the generic name has been the reference of *Endodonta acuticarinata* Thiele, 1928, to *Nesodiscus* by Ilse Rensch (1937, p. 586, fig. 8). This species is a paryphantid (Solem, 1959b, pp. 155-156) and totally unrelated to the Society Island genus.

Nesodiscus undoubtedly is a derivative from the same stock that produced *Mautodontha boraborensis.* The structural trends which differentiate that species from the generalized *Mautodontha* — increased size and whorl count, deeper recession of the palatal barriers and increased length of the parietals, reduced sculpture, wider umbilicus, and depressed form — all are greatly intensified in *Nesodiscus.* There is a large and distinct gap between *Nesodiscus* and *Mautodontha boraborensis.* The latter retains 4 parietals, the apical sculpture is fine and not coarsened, the ribbing less crowded and more distinct, the periphery is obtusely angled, and the palatal barriers remain quite short. In the most generalized *Nesodiscus,* the apex is protruded and with coarse radial ribs (fig. 31b), there are only 2 parietals (with the lower very deeply recessed), the radial ribbing is reduced (*taneae*) or extremely fine and crowded (*obolus*), the periphery is sharply angulated or keeled, and the much more deeply recessed palatals are very short. While *Mautodontha boraborensis* reaches the size, whorl count, and apparently has the same umbilical mucus closure (see p. 156) found in the Borabora Island *Nesodiscus,* the great majority of its features agree more with *Mautodontha.* It has been classified in that genus. *Minidonta* and *Anceyodonta* from Mangareva are the only other situation in which there are species so nearly transitional between genera in the Endodontidae.

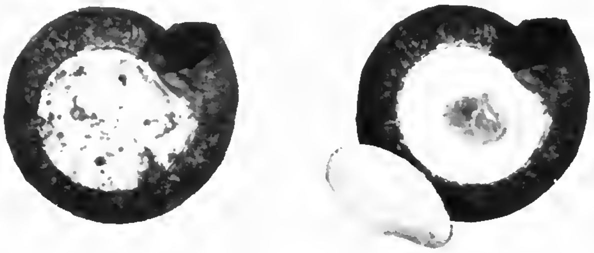

FIG. 151. Umbilical mucus cover in *Nesodiscus taneae.* Borabora, Society Islands. FMNH 116516. Left, closed; right, opened with eggs removed. (MM).

Within *Nesodiscus,* increased size correlates with loss of the lower parietal and most to all of the palatals, continued sculptural reduction (except *magnificus*), flattening of the whorls and increased peripheral and umbilical keeling. In the Boraboran species, *N. taneae, N. cretaceus,* and *N. magnificus,* the eggs are brooded in the umbilicus and sealed in by a mucus membrane (fig. 151). Garrett (1884, p. 42) reported that this membrane was frequent in the Borabora specimens of *N. taneae,* but had not been observed in Maupiti specimens. None of the Huahine, Tahaa, or Raiatean specimens examined during this study showed unmistakable traces of the mucus seal. This may be restricted to Boraboran species.

Except for the large populations of *Nesodiscus fictus* collected during the Mangarevan Expedition, all available material of *Nesodiscus* consisted of small sets in museums that dated from Garrett and Pease, large sets of incredibly mixed species and genera in the Pease collection at the Museum of Comparative Zoology, plus a few dead shells taken by the Mangarevan Expedition. Garrett collected these species by the hundreds. Available specimens represent a small fraction of those collected by Garrett. They had been sorted to varietal name, exchanged one or more times, and hence would be biased strongly for extremes in size and shape. The variation recorded for individual sets (table XCVI) has no necessary relevance to the actual population parameters. The extent and types of bias in the sets of *N. fictus* from Stations 1081 and 1085, as sorted by the Bishop Museum staff in the mid-1930's, is outlined below. I presume that the bias

TABLE XCVI. - LOCAL VARIATION IN NESODISCUS

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
taneae						
Borabora						
BPBM 152386-7, 89-90, BPBM 152366	7	2.49±0.111 (2.11-2.96)	5.36±0.140 (4.87-5.66)	0.465±0.0142 (0.400-0.523)	5 3/8+ (4 3/4-6 3/8)	2.65±0.087 (2.32-2.97)
ANSP 47803	14	2.13±0.042 (1.85-2.42)	5.17±0.056 (4.74-5.53)	0.403±0.0104 (0.327-0.456)	6- (5 3/4-6 3/4)	2.53±0.043 (2.27-2.82)
BPBM 3792	7	2.09±0.162 (1.70-2.94)	4.85±0.123 (4.51-5.49)	0.429±0.0238 (0.369-0.535)	6 (5 3/8-8 1/8)	2.47±0.043 (2.38-2.62)
BPBM 167406	6	1.92±0.089 (1.70-2.22)	4.63±0.133 (4.18-4.97)	0.414±0.0098 (0.389-0.447)	5 7/8- (5 1/2-6 1/4)	2.73±0.036 (2.61-2.82)
BPBM 3178	5	2.17±0.070 (1.90-2.29)	4.27±0.044 (4.18-4.38)	0.508±0.0188 (0.433-0.531)	5 1/2 (5 1/4-5 5/8)	2 43±0.139 (1.92-2.67)
Maupiti						
BPBM 3359	6	2.05±0.055 (1.90-2.22)	5.00±0.082 (4.84-5.36)	0.410±0.0122 (0.388-0.460)	6+ (5 7/8-6 1/8)	2.80±0.016 (2.74-2.85)
ANSP 47846 (Types)	9	1.88±0.059 (1.72-2.28)	4.73±0.081 (4.47-5.07)	0.397±0.0090 (0.354-0.451)	5 7/8+ (5 5/8-6 1/8)	2.66±0.032 (2.54-2.84)
huaheinensis						
Huahine						
BPBM 2232	6	2.20±0.084 (1.90-2.48)	5.22±0.147 (4.97-5.82)	0.422±0.0102 (0.372-0.441)	6- (5 5/8-6 1/4)	2.47±0.053 (2.27-2.62)
obolus						
Form obolus						
BPBM 3786	6	1.45±0.083 (1.31-1.83)	4.71±0.074 (4.51-5.03)	0.307±0.0127 (0.278-0.364)	5 3/4+ (5 1/2-6 1/4)	1.85±0.026 (1.75-1.93)
Form acetabulum						
BPBM 3446	8	2.10±0.089 (1.83-2.48)	5.17±0.107 (4.71-5.69)	0.406±0.0134 (0.338-0.437)	6 1/4+ (6-7)	1.92±0.022 (1.86-2.05)
Form celsus						
BPBM 3484	6	2.71±0.223 (2.22-3.59)	5.64±0.176 (5.10-6.27)	0.481±0.0370 (0.406-0.647)	6 5/8+ (6 3/8-7)	2.15±0.106 (2.00-2.66)
cretaceus						
BPBM 2230	2	2.52±0.228 (2.29-2.75)	6.14±0.262 (5.88-6.41)	0.409±0.0198 (0.389-0.429)	6 7/8+ (6 3/4-7 1/8)	2.09±0.0050 (2.08-2.09)

TABLE XCVI, CONTINUED

ANSP 47832	4	1.85±0.076 (1.62-1.95)	5.11±0.383 (4.01-5.73)	0.365±0.0145 (0.335-0.405)	6 1/4- (5 5/8-6 1/2)	2.00±0.032 (1.95-2.09)
fictus						
BPBM 4956	5	3.09±0.210 (2.48-3.53)	6.89±0.116 (6.67-7.32)	0.447±0.0295 (0.369-0.529)	8- (7 5/8-8)	2.02±0.054 (1.91-2.21)
BPBM 152284, -5, -7, (adult) Sta. 1085	37	2.62±0.042 (2.16-3.27)	6.36±0.034 (6.01-6.73)	0.412±0.0064 (0.337-0.531)	7 5/8+ (7 1/4-8)	1.95±0.011 (1.83-2.08)
BPBM 139791 (adult) Sta. 1081	25	2.78±0.046 (2.42-3.27)	6.38±0.041 (5.95-6.93)	0.436±0.0070 (0.385-0.521)	8- (7 5/8-8 1/2)	1.93±0.013 (1.84-2.11)
BPBM 139790[1] Sta. 1081	11	3.05±0.104 (2.42-3.59)	7.02±0.051 (6.80-7.32)	0.435±0.0145 (0.346-0.509)	8 1/4 (8-8 5/8)	1.92±0.021 (1.84-2.04)
fabrefactus						
USNM 42427	4	3.19±0.142 (2.94-3.59)	7.16±0.043 (7.06±7.25)	0.445±0.0180 (0.413-0.495)	6 5/8 (6 1/2-7)	1.90±0.028 (1.85-1.98)
BPBM 115345	12	3.50±0.063 (3.20-3.92)	7.28±0.100 (6.80-7.91)	0.483±0.0107 (0.437-0.545)	7 (6 1/2-7 3/8)	1.89±0.023 (1.70-1.98)
BPBM 165099	5	3.83±0.182 (3.40-4.44)	7.44±0.180 (7.12-8.10)	0.514±0.0148 (0.469-0.548)	7 1/4- (6 7/8-7 1/2)	1.99±0.049 (1.88-2.17)
BPBM 2229	5	4.16±0.169 (3.66-4.64)	7.95±0.146 (7.71-8.50)	0.523±0.0219 (0.474-0.602)	7 3/8 (6 7/8-8)	1.90±0.013 (1.74-1.97)
fabrefactus form piceus						
BPBM 4994	5	3.15±0.067 (3.01-3.40)	6.08±0.068 (5.82-6.21)	0.520±0.0112 (0.495-0.553)	7 1/8 (6 7/8-7 1/4)	1.98±0.025 (1.94-2.07)

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1. Selected large individuals as segregated by BPBM staff.

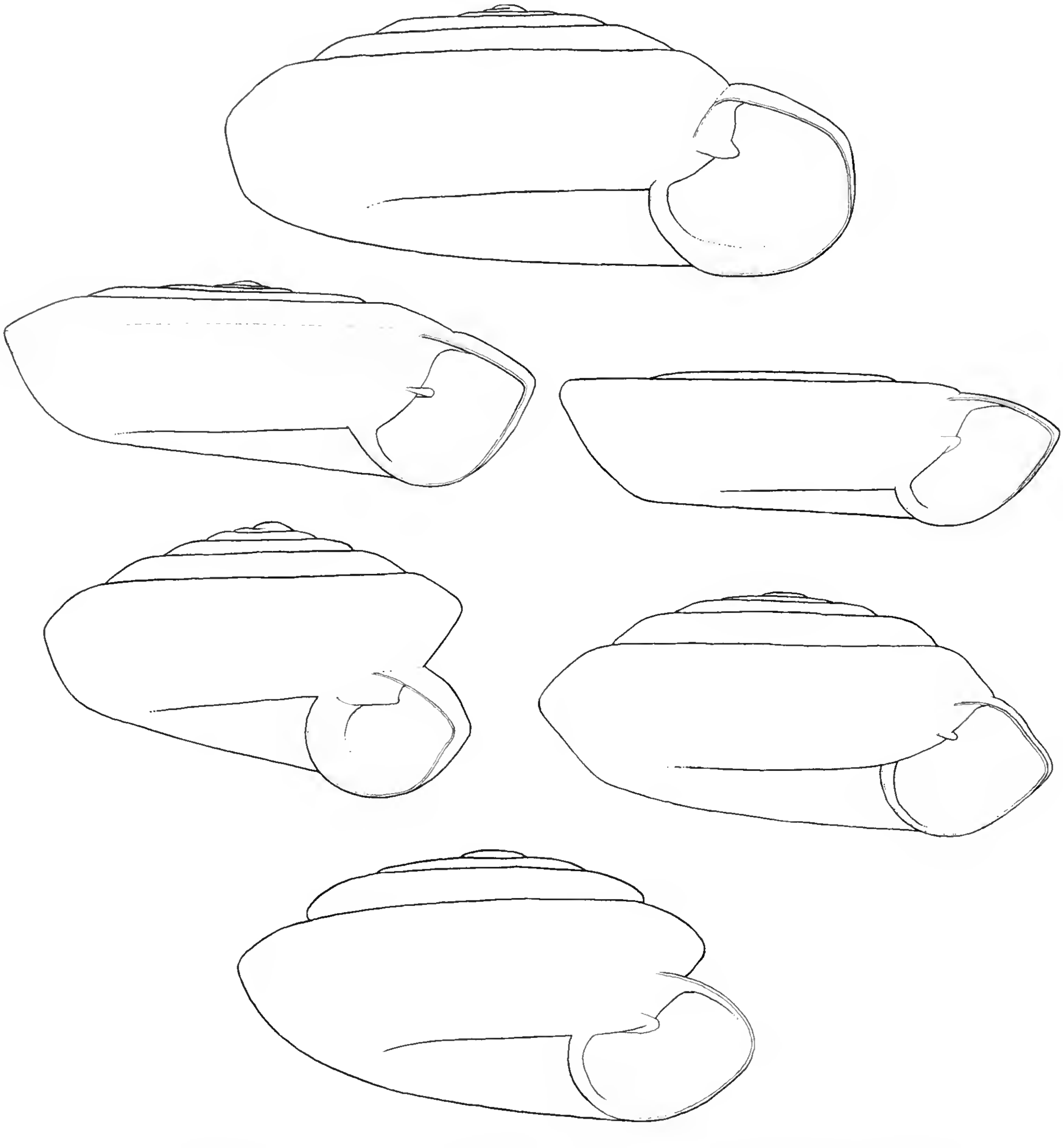

FIG. 152. Shape variation in *Nesodiscus taneae*. Material from the W.H. Pease collection, BPBM 170951. (MM).

present in the labelled sets of *obolus, acetabulum,* and *celsus* are at least as large and roughly equivalent.

Since I had comparatively little new material and only a fraction of the specimens studied by Garrett, I have deferred to Garrett's judgment in recognizing specific limits. In certain cases – *taneae* and *huaheinensis; cretaceus* and *fictus; fabrefactus* and *piceus;* and the forms of *obolus* – reliance on the mixed material in the Pease collection would have led to erroneous conclusions.

Variation within the species is quite large (fig. 152) and the difficulties of seeing and counting apertural barriers make use of the key and identification of juveniles or oddly shaped specimens difficult. To some extent, the species are separable through use of measurements taken at three whorls, four whorls, and five whorls (table XCVII). The distance was measured from the suture line opposite the first apical whorl ending to the suture marking the end of the particular whorl (fig. 153) with the whorls lying parallel to the ocular micrometer. This character obviously separates such confusing forms as *N. fictus* and *N. cretaceus,* and can resolve the possibly puzzling individuals of the *piceus-fictus* pair. On the average, *N. obolus* is smaller

TABLE XCVII. - EARLY WHORL SIZE IN NESODISCUS

Name	Number of Specimens	Diameter At 3W	 4W	 5W
taneae				
BPBM 3359	6	1.09±0.018 (1.06-1.16)	1.58±0.020 (1.52-1.66)	2.17±0.041 (2.09-2.35)
BPBM 3792	6	1.16±0.026 (1.06-1.23)	1.68±0.048 (1.49-1.82)	2.32±0.069 (2.05-2.52)
BPBM 152388	2	1.23±0.066 (1.16-1.29)	1.67±0.083 (1.59-1.76)	2.28±0.099 (2.19-2.38)
huaheinensis				
BPBM 2232	6	1.23±0.051 (1.06-1.39)	1.76±0.071 (1.59-1.95)	2.41±0.097 (2.12-2.72)
obolus form *obolus*				
BPBM 3786	6	1.02±0.038 (0.93-1.19)	1.49±0.036 (1.42-1.66)	2.13±0.056 (2.02-2.38)
form *acetabulum*				
BPBM 3446	6	1.03±0.017 (0.96-1.06)	1.45±0.026 (1.36-1.52)	1.96±0.055 (1.79-2.12)
form *celsus*				
BPBM 3484	6	1.06±0.012 (1.03-1.09)	1.46±0.020 (1.39-1.52)	2.03±0.029 (1.92-2.09)
cretaceus				
ANSP 47832 BPBM 2230	3	1.13±0.027 (1.09-1.18)	1.55±0.027 (1.51-1.60)	2.10±0.030 (2.04-2.14)
fictus				
BPBM 4956	5	0.94±0.013 (0.89-0.96)	1.30±0.016 (1.26-1.32)	1.73±0.019 (1.69-1.79)
fabrefactus				
BPBM 2229	7	1.33±0.021 (1.23-1.39)	1.76±0.038 (1.59-1.85)	2.35±0.072 (2.05-2.55)
form *piceus*				
BPBM 4994	5	1.11±0.025 (1.03-1.16)	1.44±0.032 (1.32-1.52)	1.87±0.044 (1.72-1.99)
magnificus				
HOLOTYPE	1	1.74	2.53	3.42

than *N. taneae* or *N. huaheinensis* in respect to the early whorl size, but there is some overlap. More than in any other genus of the Endodontidae, certain identification requires the availability of series.

Anatomical data were available for only two of the most specialized species, *N. fictus* and *N. fabrefactus*. Binney (1885, p. 89, pl. 2, fig. L; reprinted by Pilsbry, 1893-1895, p. 25, pl. 9, fig. 22) figured a few radular teeth of *Nesodiscus huaheinensis,* but these showed no unusual features. There were six laterals and 12 marginals. Only fragmentary material of *N. fabrefactus* was seen, but there was excellent material of *N. fictus.* That species has a mean whorl count 7⅞+) exceeded only by *Kleokyphus hypsus* (8) and *Libera incognata* (8+). Two other species, *Libera jacquinoti* and *L. streptaxon* have about 7⅝ whorls, and the Fijian *Priceconcha tuvuthaensis* has about 7⅜ whorls. All other species are significantly lower in whorl count. The great whorl count increase combines with the very widely open umbilicus to greatly reduce individual whorl cross-sectional area when compared to a species of similar size with fewer whorls and a narrower umbilicus. Hence, there is less space available and many organs are both narrowed and elongated. The prostatic acini, for example, normally are three or four times as long as they are wide; in *N. fictus* they are almost square. The pericardial arm of the kidney (fig. 154b) is greatly narrowed compared with the ureter. The albumen gland is proportionately very long and several times the length of the talon-carrefour, and the buccal mass is more cyclindrical than usual with more posterior buccal retractor insertions.

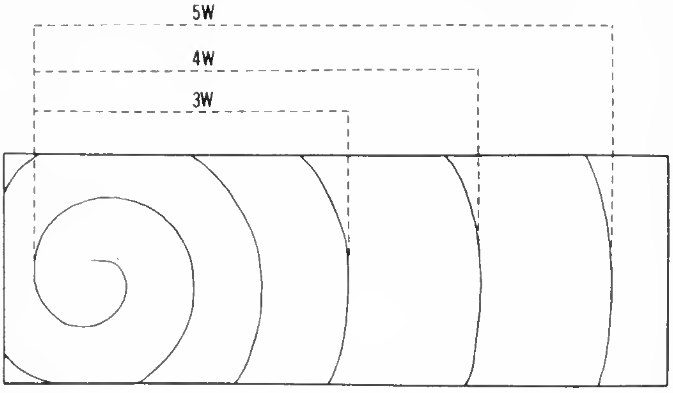

FIG. 153. Method of early whorl measurement in *Nesodiscus*.

These are just a few of the elongations and changes, specializations resulting from whorl increment. Differences found in the *Nesodiscus* with lower whorl counts, such as *N. taneae,* should be viewed with the realization that most obvious changes in *N. fictus* are the result of adaptation to whorl volume factors.

Systematically important features indicate no particular specialization. There are two essentially equal-size penial pilasters, the penial retractor inserts directly on the penis head, the short vaginal area is not structurally differentiated, and the vas deferens enters the penis laterally. Despite the volume changes, the ovotestis orientation is typical. Thus *Nesodiscus* is at the same level of anatomical complexity as *Mautodontha, Minidonta,* and *Endodonta.* Apparently, there is character displacement between *N. fictus* and *N. fabrefactus,* since they differ markedly in penial length and the extent of pilaster swelling in the penial mid-region. This was observed in specimens collected at the same station.

Within *Nesodiscus* there is a relatively clear pattern of increasing specialization and obvious complementarity of species. *N. taneae* and *N. huaheinensis* are nearest to *Mautodontha,* retaining 4 palatals and a relatively narrow umbilicus. *N. taneae* has more rounded whorls and retains traces of major radial ribbing, thus being a little less specialized than *N. huaheinensis.* The two are very similar and obviously closely related. *N. obolus* shows more specialization, with very fine and crowded sculpture, widening of the umbilicus, loss of the lower parietal and all palatals, plus increased peripheral angulation, but still retaining slightly rounded whorls. In their increasing umbilical angulation, reduction of sculptural prominence, flattening of the whorls, and protrusion of the peripheral keel, both *N. cretaceus* and *N. fictus* show specializations over the first three species, but their retention of a single rather large and only moderately recessed palatal barrier is unexpected since

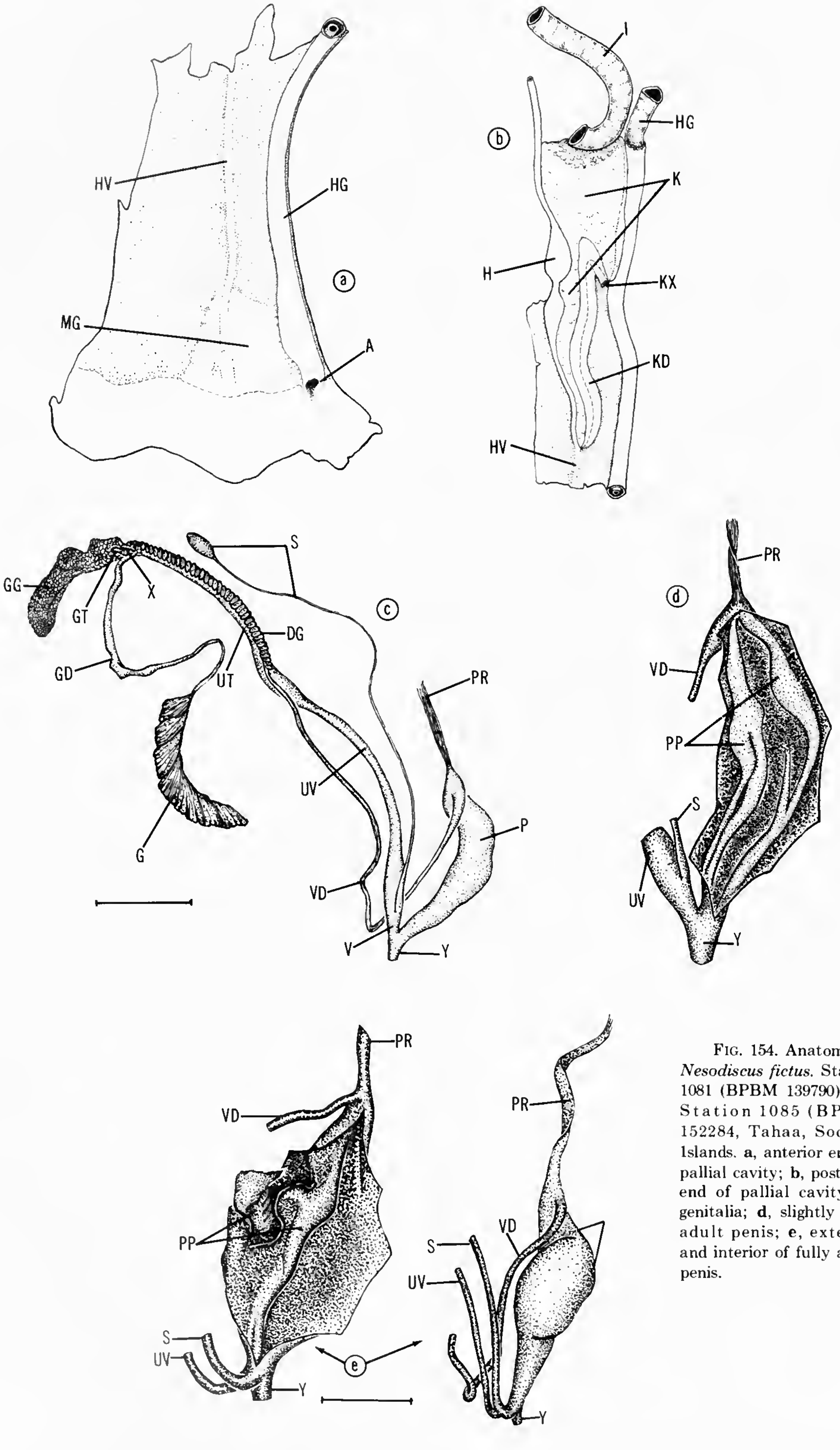

FIG. 154. Anatomy of *Nesodiscus fictus*. Station 1081 (BPBM 139790) and Station 1085 (BPBM 152284, Tahaa, Society Islands. **a**, anterior end of pallial cavity; **b**, posterior end of pallial cavity; **c**, genitalia; **d**, slightly subadult penis; **e**, exterior and interior of fully adult penis.

the more generalized species cited above have the palatals deeply recessed and reduced in size. The differences between *cretaceus* and *fictus* are more in degree than in kind (see the "*Diagnosis*" for each species), except for apex size, and they seem to represent a second complementary pair. *N. fabrefactus*, with its change in whorl and spire contour, greater sculptural reduction, prominent umbilical keel, complete loss of apertural barriers (except in form *piceus*), and great size is the most specialized species. Derivation from the same ancestral stock that produced *N. fictus* is extremely likely.

A somewhat linear progression is evident, with *obolus* forming a lateral branch from a *taneae-huaheinensis* type ancestor; *cretaceus* and *fictus* evolving in a different branch from the same stock and reaching a more complex level of organization; while *fabrefactus* evolved from close to the *fictus-cretaceus* level of separation. *Nesodiscus magnificus* would seem to be a separate line of specialization, since it retains a rounded umbilical margin, major radial sculpture (probably), a narrower umbilicus, and changes in whorl contour that are attributable to the extreme peripheral keel protrusion rather than to compression and flattening. Reduction of the apertural barriers to a single parietal in *N. magnificus* could be merely a parallel development and does not suggest any direct affinity to the *cretaceus-fictus-fabrefactus* series.

The above information and suggested pattern of derivation corresponds well with distributional data. If Tahaa-Raiatea is viewed as the center of origin for *Nesodiscus*, then the presence of the most generalized species, *taneae* and *huaheinensis*, on the "periphery" of Huahine to the east, Borabora and Maupiti north and west is a typical dispersal pattern. The relative proximity of Tahaa and Borabora, which lie nearer the distributional center, ties in with the very similar *N. cretaceus* and *N. fictus* found on these islands. The most specialized species, *N. fabrefactus*, lives on both Raiatea and Tahaa.

More than is usual for the Endodontidae, species of *Nesodiscus* inhabit two islands. *N. taneae* is found on both Borabora and Maupiti; *N. obolus* on Raiatea and Huahine; *N. fabrefactus* on Raiatea and Tahaa. *N. fictus* and *N. cretaceus* are distinct, but dissection of the latter might demonstrate a very close relationship. Only *N. huaheinensis* and *N. magnificus* are unquestionably limited to a single island.

The exclusive nature of the *Nesodiscus* and *Libera* distributions may be more than coincidence. Both have evolved efficient ways of brooding eggs, *Libera* by a secondarily narrowed brood chamber and *Nesodiscus* by use of a mucus seal over a widely open umbilicus (at least in the Borabora species). Whether an accident of dispersal or competitive factors have kept them isolated is unknown.

KEY TO THE GENUS *Nesodiscus*

1. Aperture with at least one barrier 2
No apertural barriers .... *Nesodiscus fabrefactus* (Pease, 1864)
2. Adult or 7 whorl diameter less than 8 mm. 3
Adult or 7 whorl diameter more than 10 mm.
Nesodiscus magnificus, new species
3. Aperture with 2 parietals, lower deeply recessed; 3 or more palatals 4
Aperture with 1 parietal; only rarely more than 1 palatal 5
4. Wide radial ribs visible on upper spire (fig. 155d); Maupiti or Borabora .... *Nesodiscus taneae* (Garrett, 1872)
No major radial ribs (fig. 155a); Huahine.
Nesodiscus huaheinensis (Pfeiffer, 1853)
5. Single palatal only moderately recessed (fig. 159e); shell surface macroscopically smooth 6
Usually no palatals, if present, very deeply recessed; shell surface with crowded, fine ribs.
Nesodiscus obolus (Gould, 1846)
6. Sides of spire convex 7
Sides of spire concave.
Nesodiscus fabrefactus, form *piceus* (Garrett, 1884)
7. Mean diameter about 5.6 mm.; mean whorl count about 6½; Borabora .... *Nesodiscus cretaceus* (Garrett, 1884)
Mean diameter about 6.5 mm.; mean whorl count about 7⅞; Tahaa .... *Nesodiscus fictus* (Pease, 1864)

Nesodiscus taneae (Garrett, 1872). Figures 151; 152; 155d-f.

Pitys taneae Garrett, 1872, Proc. Calif. Acad. Sci., **4**, p. 204 – Maupiti, Society Islands, found on the ground in damp forests; Garrett, 1873, Proc. Acad. Nat. Sci., Philadelphia, **1873**, p. 234, pl. 3, fig. 65.

Patula janeae Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 93 – typographical error for *taneae* Garrett; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 481.

Helix taneae (Garrett), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 482.

Endodonta taneae (Garrett), 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 42 – Borabora and Maupiti, Society Islands.

Helix boraborensis "Pease", Garrett, 1884, *loc. cit.*, p. 42 – a nude name in the synonymy of *taneae* Garrett.

Helix (*Endodonta*) *taneae* (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 62, pl. 11, figs. 95-97.

Endodonta garrettii Ancey, 1889, Le Naturaliste, (2), **11**, (53), p. 118 – Borabora (?), Society Islands; Pilsbry, 1892, Man. Conchol., (2), **8**, p. 95 - name only.

Endodonta (*Endodonta*) *garrettii* Ancey, Pilsbry, 1893, *op. cit.*, (2), **9**, p. 25.

Endodonta (*Endodonta*) *taneae* (Garrett), Pilsbry, 1893, *loc. cit.*, p. 26.

Diagnosis. – Shell variable in size, normally relatively small, diameter 3.86-5.82 mm. (mean 4.89 mm.), with 4⅜ - 8⅛ normally to very tightly coiled whorls. Apex and spire normally are moderately and almost evenly elevated, slightly rounded above, occasionally flattened or strongly elevated, last whorl usually descending slightly more rapidly, sometimes drastically deflected, H/D ratio 0.327-0.535 (mean 0.428). Umbilicus broadly open, rather narrow for genus, varying from U-shaped to V-shaped in outline, regularly decoiling, contained 1.92-2.97 times (mean 2.58) in the diameter, sides of whorls distinctly flattened to strongly rounded. Postnuclear sculpture of low, rather widely spaced, slightly protractively sinuated radial ribs, becoming reduced on lower spire and absent from all of body whorl. Microsculpture of fine radial riblets, eight to twelve between each pair of major ribs near termination of latter on lower spire, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification. Sutures shallow, whorls compressed to flattened laterally above periphery, which varies from having a protruded keel to being obtusely angulated, generally sharply angulated or keeled, compressed laterally below periphery with strongly rounded basal margin, umbilical margin sharply rounded to prominently angulated, generally the former. Aperture subquadrangular to subcircular, depending upon whorl contours, inclined about 25 - 30° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision: upper moderately elevated and bladelike, somewhat expanded and more strongly elevated on visible posterior third, with anterior two-thirds evenly elevated until just before edge of parietal callus; 2nd normally recessed almost to limit of vision, equally high posteriorly, in gerontic specimens visible only by partial destruction of palatal wall. Columellar wall without barriers. Palatal barriers normally 4, occasionally upper missing or additional subperipheral barrier present, recessed almost one-quarter whorl behind lip and extending posteriorly a little less than three-sixteenths of a whorl: lower basal in position, moderately elevated, with gradual anterior descension; 2nd and 3rd evenly spaced on lower palatal wall, distinctly higher than 1st, with progressively more gradual anterior descension and further anterior prolongation; 4th, when present, supraperipheral, midway between periphery and parietal-palatal margin, slightly lower than 2nd, with much more gradual anterior descension and longer anterior extension.

The presence of at least a few major radial ribs on the upper spire, more prominent microradial sculpture, and generally greater convexity to the upper palatal walls combine to separate *Nesodiscus taneae* from the otherwise extremely similar *N. huaheinensis*. *Nesodiscus obolus* differs in its total lack of widely spaced major radial sculpture, generally much wider umbilicus, presence of only a single parietal barrier, and in having at most 3 very deeply recessed palatals.

Description (*taneae*). — Shell smaller than average, with slightly less than 6⅛ normally coiled whorls. Apex markedly protruded, early whorls of spire flat, lower whorls descending regularly, last whorl slightly more rapidly, H/D ratio 0.451. Apical whorls 1½, sculpture partially eroded, but traces of low, broadly rounded radial ribs remaining. Postnuclear whorls with low, broadly rounded, somewhat irregularly spaced, protractively sinuated radial ribs, becoming reduced to absent on body whorl. Microsculpture of fine radial riblets crossed by much finer and more crowded spiral riblets. Sutures shallow, whorls flat above the acutely angled periphery, evenly rounded below to slight shouldering at baso-umbilical margin. Color light yellow horn with darkish, irregular flammulations. Umbilicus widely open, U-shaped, regularly decoiling, contained 2.74 times in the diameter, whorls strongly rounded inside. Aperture subquadrangular, flattened laterally above periphery and on basal margin, inclined about 25° from shell axis. Parietal barriers 2: upper a threadlike ridge for first quarter whorl, suddenly becoming higher and weakly expanded above for posterior fifth of length; lower parietal very deeply recessed, slightly lower elevated portion opposite posterior part of upper parietal, barely visible from aperture. Columellar wall without barriers. Palatal barriers 4, deeply recessed: 1st palatal at baso-columellar margin, a deeply recessed crescentic ridge barely visible from aperture; 2nd and 3rd palatals high lamellar ridges, short, extending one-sixteenth of a whorl, posterior end clearly visible from aperture, with gradual anterior descension; 4th palatal supraperipheral, a high lamellar ridge, very deeply recessed, although extending slightly further anteriorly than 1st palatal. Height of lectotype 2.27 mm., diameter 5.04 mm.

Lectotype. — Society Islands: Maupiti. Collected by Andrew Garrett. ANSP 47846.

Description (*garrettii*). — Shell small, with 6⅜ rather tightly coiled whorls. Apex and spire slightly and evenly elevated, last whorl not descending more rapidly, H/D ratio 0.397. Apical sculpture eroded. Postnuclear whorls with sculpture of low, rather crowded, fine, almost vertical radial ribs on spire, becoming worn off on most of shell. Traces of microsculpture as fine radials crossed by extremely fine spirals on part of spire and in umbilicus. Most of surface worn. Sutures shallow, whorls flatly and evenly rounded above obtusely angulated periphery, compressed laterally and almost flat down to strongly rounded basal margin. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.29 times in the diameter, margin distinctly shouldered, whorls slightly flattened inside. Color light yellow brown, mid-spire with bright, sharply defined, narrow to broad, dark reddish markings, mostly absent from body whorl. Aperture subcircular, compressed laterally above and flattened below periphery, inclined about 20° from shell axis. Parietal barriers 2, lower deeply recessed: upper an elevated bladelike ridge, extending posteriorly beyond line of vision, elevated and weakly expanded on visible posterior quarter, with sharp anterior descension; 2nd recessed almost one-quarter whorl, elevated portion higher than upper, extending posteriorly beyond line of vision. Columellar wall without barriers. Palatal barriers 5, recessed three-sixteenths of a whorl, extending less than one-eighth whorl: lower basal in position, slender, low; 2nd, 4th, and 5th with progressively more gradual anterior descension, rather low, 5th supraperipheral; 3rd lower, shorter, lying close to the 4th palatal. Height of holotype 1.68 mm., diameter 4.23 mm.

Holotype. — Society Islands. Probably Borabora. Institut Royal des Sciences Naturelles de Belgique, Brussels, ex Dautzenberg, Ancey.

Range. — Maupiti and Borabora Islands, Society Islands.

Paratypes — ANSP 290111, BPBM 3359.

Material. — Society Islands: Maupiti (27 specimens, BPBM 3359, ANSP 47846, ANSP 290111, FMNH 46406, FMNH 90608, FMNH 91904, FMNH 117055). Borabora (58 specimens, BPBM 2762, BPBM 3178, BPBM 3792, BPBM 115340, BPBM 167406, FMNH 46609, FMNH 47803, FMNH 90619, FMNH 91853): south slope Pahio-Temanu ridge (Stations 1091, 1092, 1093) at 600-800 ft. elevation (50 specimens, BPBM 152342, BPBM 152366-7, BPBM 152386-90). Locality unknown (111 specimens, BPBM 170946, BPBM 170951, BPBM 170954, FMNH 46260, FMNH 91116).

Remarks. — Variation within *Nesodiscus taneae* is the largest known for any species of Endodontidae. The few specimens seen from Maupiti are relatively uniform in size and shape, but those found on Borabora vary amazingly (fig. 152). It is quite possible that detailed study of local populations would have revealed a complex of species confused under this name, but Garrett believed that they represented one variable form. The only recent field collections, from the Pahio-Temanu cliff region on Borabora (Stations 1091, 1092, 1093), yielded dead shells of three different types. The material collected by Garrett long since has been split into small lots and dissipated among many collections. It is impossible to use these fragmentary sets to determine relationships of the varieties outlined below. Transitional examples were seen, but the probability of sub-specific differentiation remains for investigation.

On Maupiti Island, the type locality, the shells are acutely keeled and relatively flattened above (although less so than in *N. huaheinensis*). Below the periphery the shell angles sharply toward the umbilicus which has an obtusely rounded or only slightly keeled margin, and the shells are comparatively

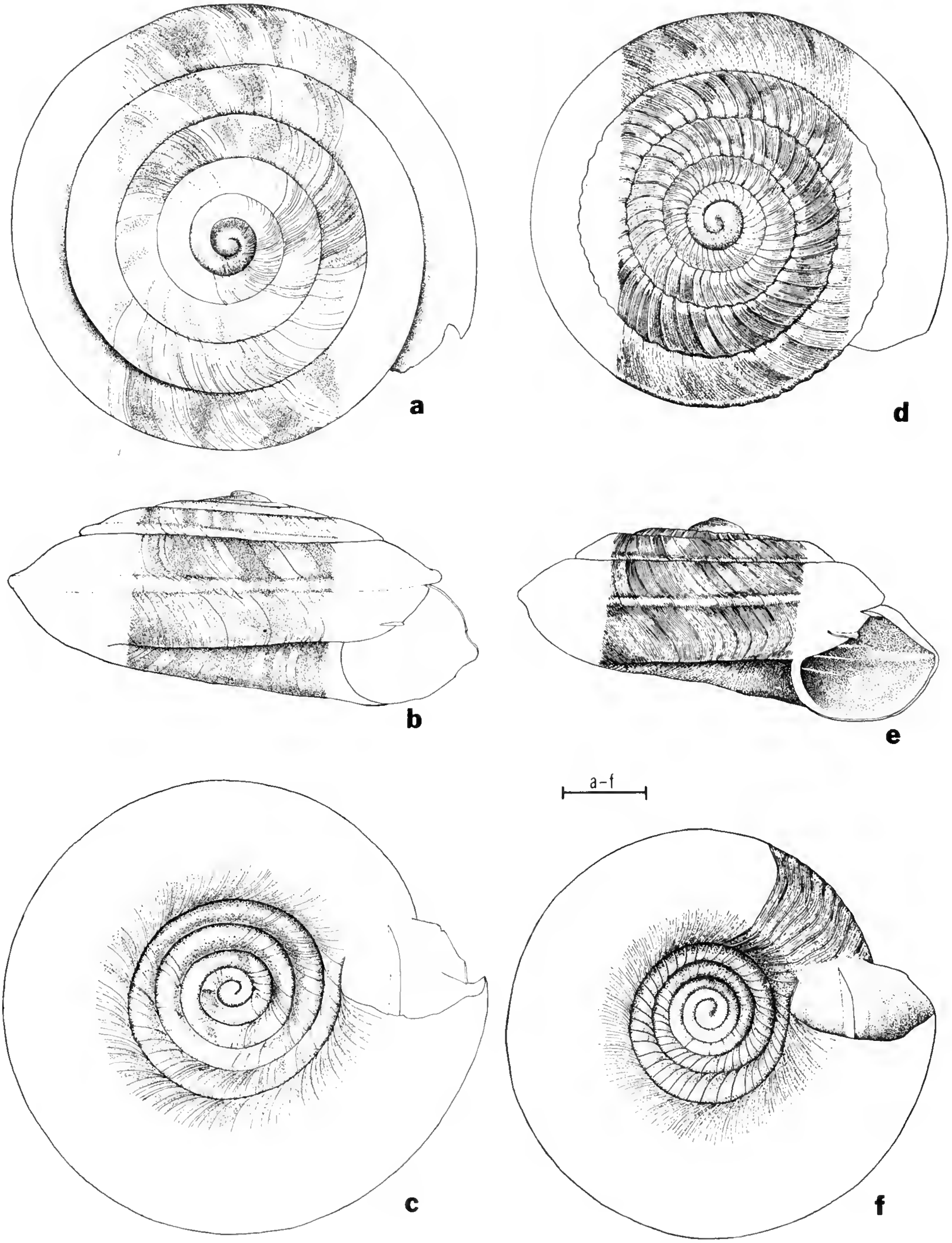

FIG. 155. **a-c**, *Nesodiscus huaheinensis* (Pfeiffer, 1853). No locality. BPBM 170947; **d-f**, *Nesodiscus taneae* (Garrett, 1872). Maupiti, Society Islands. Lectotype. ANSP 47846. Scale lines equal 1 mm. (SH).

uniform in size (table XCVI). All observed specimens have at least traces of the major radial ribs on the spire (fig. 155d).

On Borabora, it is possible to recognize the normal Maupiti form with the same size range and sculpture (table XCVI), but with the shell often slightly more elevated (BPBM 2762, BPBM 115340, BPBM 170951). There are also three additional more or less distinguishable forms. Form A is larger (mean diameter 5.44 mm.), with less sharply angled peripheral margin and more rounded lower body whorl. Occasionally a shell will be seen in which the whorls are much narrower, more tightly coiled, and with the spire slightly more elevated. Form B is smaller (diameter 4.27 mm.), more elevated (mean H/D ratio 0.508), and has sinuated nodular swellings on the later whorls, which probably are remnants of ribbing. Sometimes the sculpture is present only on part of the shell. In field collections, mixed sets occur (part of BPBM 152367). Form C is an apparently rare variant in which the periphery is only slightly angled or evenly rounded. This latter form was described as *Endodonta garrettii* Ancey, 1889. A new description of the holotype is given above. The great majority of Mangarevan Expedition shells were form A, but material transitional to B was also present. Mixed sets of *N. taneae* and *N. huaheinensis* originating from the Pease collection in the Museum of Comparative Zoology contained many variations (fig. 152).

Garrett (1884, p. 42) mentioned that the umbilical brood chamber cover (fig. 151) was extremely common on Boraboran shells, although not found in his Maupiti examples. One specimen had the brood chamber cover intact, and upon opening was found to have two eggs inside.

Nesodiscus huaheinensis (Pfeiffer, 1853). Figure 155a-c.

Helix huaheinensis Pfeiffer, 1853, Zeits. Malak., **10**, pp. 55-56 — Huahine, Society Islands; Pfeiffer, 1853, Monog. helic. viv., **3**, p. 640; Pfeiffer, 1868, *op. cit.*, **5**, p. 222; Pfeiffer, 1876, *op. cit.*, **7**, p. 260.

Endodonta huaheinensis (Pfeiffer), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474; Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), pp. 37-38, pl. 2, figs. 26, a, b, c.

Patula huaheinensis (Pfeiffer), Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 93; Binney, 1885, Ann. N. Y. Acad. Sci., **3**, p. 89, pl. 2, fig. L (radula).

Helix aranea "Behn" Pfeiffer, 1876, Monog. helic. viv., **7**, p. 260 — A manuscript name quoted in the synonymy of *huaheinensis*.

Helix (Endodonta) huaheinensis Pfeiffer, Tryon, 1887, Man. Conchol., (2), 3, p. 61, pl. 11, figs. 92-94.

Endodonta (Endodonta) huaheinensis (Pfeiffer), Pilsbry, 1893, *op. cit.*, (2), **9**, pp. 25, 26, pl. 9, fig. 22 (radula).

Diagnosis. — Shell smaller than average, diameter 4.90-5.82 mm. (mean 5.17 mm.), with $5\frac{5}{8}$ - $6\frac{1}{4}$ normally coiled whorls. Apex usually slightly protruding above level of moderately and almost evenly elevated spire, last whorl descending only slightly more rapidly, H/D ratio 0.372-0.448 (mean 0.424). Umbilicus widely open, relatively narrow for genus, U-shaped to V-shaped, regularly decoiling, contained 2.27-2.82 times (mean 2.51) in the diameter, internal whorls normally strongly rounded. Postnuclear whorls without major ribbing, occasionally irregular growth striae. Microsculpture of very wide and crowded radial riblets, crossed by barely visible and extremely crowded spiral riblets. Sutures shallow, whorls flatly rounded down to normally acutely angled periphery, lower palatal margin laterally compressed, with strongly rounded basal and umbilical margin that may be obtusely angulated. Aperture subquadrangular, flattened above, strongly compressed laterally below acutely to right-angled periphery, inclined about 25 - 30° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision: upper high and bladelike, weakly expanded and serrated above on posterior visible third, anterior two-thirds evenly elevated until just before anterior end; 2nd parietal recessed almost one-quarter whorl, slightly reduced in height posteriorly, frequently not visible from aperture without breaking palatal wall. Columellar wall without barriers. Palatal barriers normally 4, barely visible from aperture, recessed almost one-quarter whorl: lower basal in position, moderately elevated, often recessed beyond line of vision; 2nd and 3rd on lower palatal wall, slightly more elevated, extending posteriorly less than three-sixteenths of a whorl, with progressively more gradual anterior descension; 4th supraperipheral, midway between periphery and parietal-palatal margin, extending further anteriorly and more elongated than 2nd palatal.

The total absence of major radial ribbing, much less distinct microsculpture, and generally flatter whorls separate *Nesodiscus huaheinensis* from its close relative, *N. taneae*. All other species of *Nesodiscus* are immediately separable in having a reduced number of apertural barriers.

Type. — Unknown. No specimens that could be connected with Pfeiffer were seen. Until localized material with soft parts are available, I prefer to withhold neotype selection.

Range. — Huahine, Society Islands. Abundant in all the large valleys (Garrett, 1884, p. 37).

Material. — Society Islands (81 specimens, BPBM 170941, BPBM 170947, BPBM 170952, BPBM 170966, FMNH 8293, FMNH 62594): Huahine (77 specimens, BPBM 2232, BPBM 87512, BPBM 115344, BPBM 165096, FMNH 46354, FMNH 90616, FMNH 91845, FMNH 91872, FMNH 91145, FMNH 117046, Cardiff); about 100 yd. inland (Station 1008) at 6 ft. elevation, Tiva, Huahine Iti (1 specimen, BPBM 151564).

Remarks. — The dimensions of *Nesodiscus huaheinensis* and *N. taneae* overlap completely and there is no significant difference in the means (table XCV). In *N. huaheinensis* the spire whorls are more flattened, and there is never any widely spaced radial sculpture. Garrett, who collected many specimens of both species, considered *taneae* and *huaheinensis* distinct species, although he made no direct comparisons.

The only specimen collected in this century (BPBM 151564) is from 100 yd. inland at Tiva, Huahine Iti. Unfortunately, it is a dead juvenile.

Nesodiscus obolus (Gould, 1846). Figures 156a-f; 157; 158a-c.

Helix (Pitys) obolus Gould, 1846, Proc. Boston Soc. Nat. Hist., **2**, p. 175 — Tahiti, Society Islands (error); Pfeiffer, 1848, Monog.

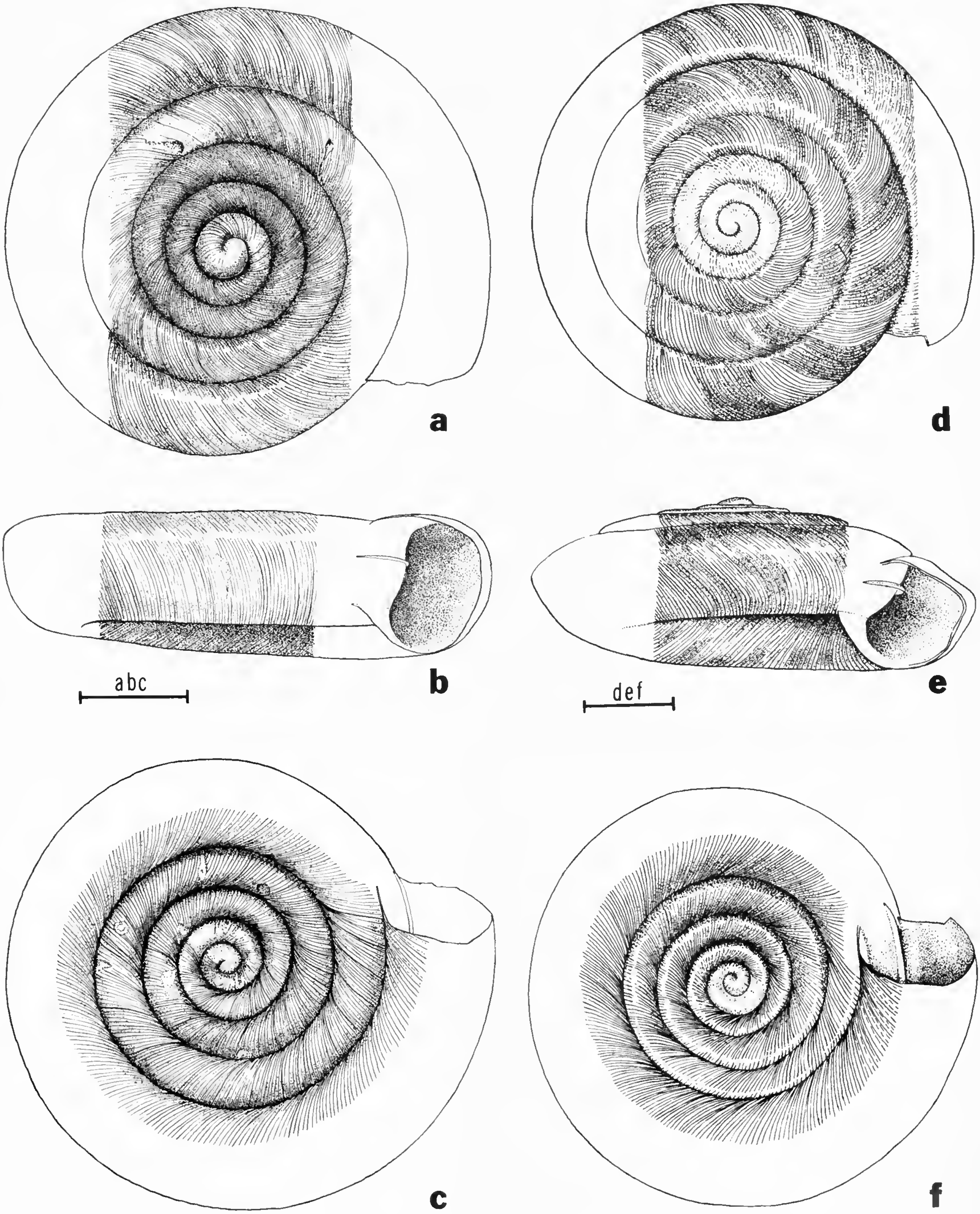

FIG. 156. **a-c**, *Nesodiscus obolus* form *obolus* (Gould, 1846). Raiatea, Society Islands. BPBM 3786, Garrett; **d-f**, *Nesodiscus obolus* form *acetabulum* (Pease, 1861). Tahiti, Society Islands (error). Lectotype. ANSP 47844. Scale lines equal 1 mm. (SH).

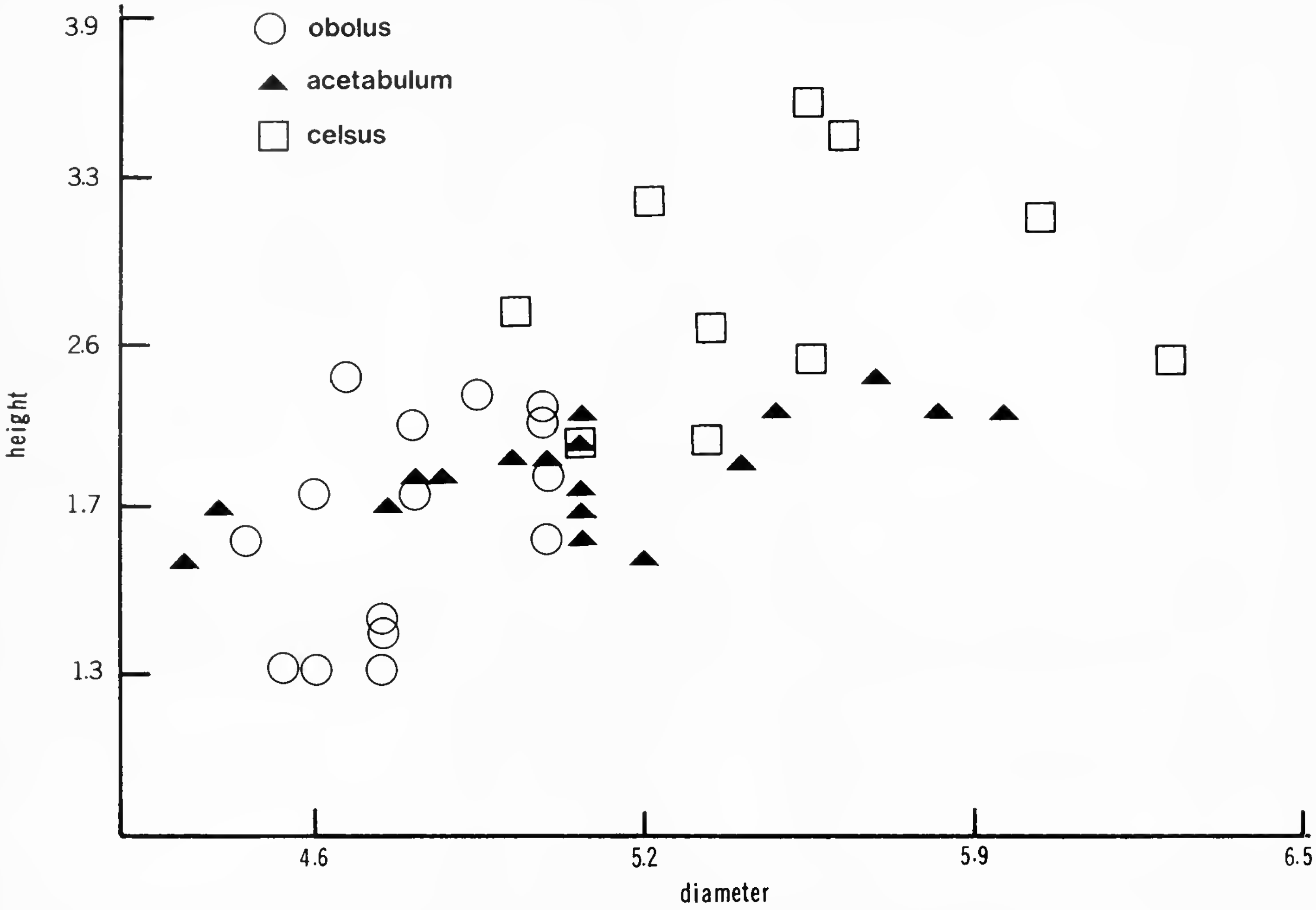

FIG. 157. Scatter diagram of height and diameter in *Nesodiscus obolus*.

helic. viv., **1**, p. 187; Gould, 1852, U.S. Explor. Exped., Wilkes, **12**, pp. 53-54; Pfeiffer, 1853, Monog. helic. viv., **3**, p. 145; Pfeiffer, 1859, *op. cit.*, **4**, p. 156; Gould, 1860, U.S. Explor. Exped., Wilkes, Atlas of Shells, pl. 4, figs. 50, a, b, c; Gould, 1862, Otia Conch., p. 22; Pfeiffer, 1868, Monog. helic., viv., **5**, p. 222; Pfeiffer, 1876, *op. cit.*, **7**, p. 261; Johnson, 1964, Bull. U.S. Nat. Mus., **239**, p. 117.

Pitys obolus (Gould), H. and A. Adams, 1858, Genera Recent Mollusca, 2, p. 113.

Endodonta obolus (Gould), von Martens, 1860, Die Heliceen, 2nd ed., p. 90; Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), pp. 39-41 – Raiatea and Huahine, Society Islands. Corrects locality of *obolus* to Raiatea and of *acetabulum* to Huahine.

Helix acetabulum Pease, 1861, Proc. Zool. Soc. London, **1861**, pp. 242-243 – Tahiti, Society Islands (error); Pfeiffer, 1868, Monog. helic. viv., **5**, p. 222; Pfeiffer, 1876, *op. cit.*, **7**, p. 260.

Pithys ? *celsa* Pease, 1870, Jour. de Conchyl., **18**, p. 396 – Raiatea, Society Islands.

Endodonta celsa (Pease), 1871, Proc. Zool. Soc. London, **1871**, pp. 455, 474.

Endodonta acetabulum (Pease), 1871, Proc. Zool. Soc. London, **1871**, p. 474.

Patula barffi "Garrett" Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 93 – A nude name for *acetabulum*.

Patula intermixta "Mousson" Schmeltz, 1874, *loc. cit.*, p. 93 – A nude name for *celsa*.

Helix celsa (Pease), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 260.

Helix (*Endodonta*) *obolus* (Gould), Tryon, 1887, Man. Conchol., (2), 3, p. 61, pl. 11, figs. 77-79 – The synonym *barffi* is misspelled "*bariffi*".

Endodonta (*Endodonta*) *obolus* (Gould), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 25, pl. 4, fig. 39.

Diagnosis. – Shell smaller than average, diameter 4.31-6.28 mm. (mean 5.08 mm.), with 5½-7⅜ tightly coiled whorls. Shape and spire elevation quite variable, apex flat or barely protruding (*obolus*), moderately and almost evenly elevated with slight additional protrusion of apex (*acetabulum*), or strongly elevated and rounded above (*celsus*), last whorl not descending more rapidly to descending slightly more rapidly, H/D ratio 0.273-0.647 (mean 0.432). Umbilicus broadly open, cup-shaped to U-shaped, regularly decoiling, contained 1.75-2.69 times (mean 2.09) in the diameter, rarely with any angulation to basal-umbilical margin. Postnuclear whorls with sculpture of extremely fine and crowded radial ribs, too numerous to count, whose interstices are usually equal to their width, becoming interrupted on body whorl by irregular growth wrinkles. Microsculpture visible under 96× magnification as exceedingly fine lattice of approximately coequal radial and spiral riblets. Sutures impressed, whorls flatly to moderately strongly rounded down to obtusely rounded to sharply keeled periphery, lower palatal margin rounded to compressedly flattened, basal margin strongly rounded. Aperture subcircular to quadrangular, inclined about 25 - 40° from shell axis. Parietal wall with one supraperipheral, raised and threadlike barrier, extending posteriorly for about one-half whorl; rarely a single very weak and deeply recessed lower parietal can be seen in the extreme posterior of the aperture. Many specimens opened for one-quarter whorl showed no trace of 2nd parietal. Columellar wall without barriers. Palatal wall normally without barriers, occasionally with one or two short and weak, deeply recessed threadlike traces visible approximately one-quarter whorl behind aperture.

The absence of any prominent and widely spaced major radial ribbing, presence of only a single parietal, and usually no palatal barriers serve to distinguish

Nesodiscus obolus from either *N. taneae* or *N. huaheinensis*. The three species show overlap in respect to any individual measurement, but by reference to more than one measurement, presence or absence of sculpture on the spire, and the apertural barriers, any specimen is immediately identifiable as belonging to one of the three species.

Description (*obolus*). – Shell smaller than average, with slightly more than 5⅜ tightly coiled whorls. Apex slightly protruded above level of first postnuclear whorl, entire spire sunken beneath level of body whorl, H/D ratio 0.273. Apical whorls 1⅝, sculpture completely eroded by fungus action. Postnuclear sculpture of low, very irregular, somewhat protracted radial ribs with occasional traces of stronger growth lines. Microsculpture mainly eroded with traces of very fine and crowded radial riblets crossed by much finer and more crowded spiral riblets. Sutures deeply impressed, whorls strongly shouldered above, flattened to slightly concave above acutely angled periphery, slightly concave below periphery to evenly rounded basal-umbilical margin. Color light yellow horn, with regularly spaced, rather prominent, somewhat sinuated, reddish flammulations. Umbilicus saucer-shaped, regularly decoiling, contained 1.85 times in the diameter. Aperture subquadrate, flattened above and on lateral margin, evenly rounded below, inclined about 20° from shell axis. Parietal wall with single supramedial, V-shaped barrier, extending posteriorly beyond line of vision. Palatal barriers 3, deeply recessed within aperture: lower palatal recessed almost one-quarter whorl, high and bladelike, extending beyond line of vision; 2nd palatal subperipheral, not as deeply recessed, anterior portion low and threadlike, extending beyond line of vision; upper palatal midway between periphery and parietal margin, equally recessed as 2nd palatal, anterior portion low and threadlike, extending beyond line of vision. Height of lectotype 1.38 mm., diameter 5.06 mm.

Lectotype of obolus. – Society Islands: Tahiti (error). Redpath Museum, McGill University number 12953.

Description (*acetabulum*). – Shell of average size, with slightly more than 6 tightly coiled whorls. Apex slightly elevated, whorls of spire descending gradually and evenly, H/D ratio 0.385. Apical whorls 1⅜, sculpture of low, broadly rounded radial ribs. Remaining whorls with irregular growth wrinkles and a microsculpture of barely visible radial and spiral riblets. Sutures shallow, whorls flatly rounded above periphery, somewhat flattened laterally and on umbilical margin. Color very light yellow-white with frequent prominent, reddish flammulations extending into the umbilicus. Umbilicus broadly open, U-shaped, regularly decoiling, contained 2.00 times in the diameter, with the whorls strongly rounded inside. Aperture subquadrangular, with acutely rounded periphery, obtusely rounded basal margin, inclined slightly more than 30° from shell axis. Parietal wall with single, low, bladelike barrier, extending posteriorly beyond line of vision. No columellar or palatal barriers visible. Height of lectotype 1.97 mm., diameter 5.04 mm.

Lectotype of acetabulum. – Tahiti (error), Society Islands. ANSP 47844.

Description (celsus). – Shell of average size, with 7⅛ tightly coiled whorls. Apex and spire moderately and almost evenly elevated, very slightly rounded above, last whorl not descending more rapidly, H/D ratio 0.492. Apical whorls 1½, sculpture completely eroded. Postnuclear whorls with surface badly pitted and scarred, sculpture visible occasionally as very fine and crowded radial riblets, made quite irregular by growth striae. Microsculpture visible in spots as a microlattice of extremely fine and crowded riblets. Sutures impressed, whorls moderately rounded above, compressed laterally, with a marked supraperipheral sulcus visible above obtusely angled periphery, with almost evenly rounded and only slightly compressed lower palatal wall. Baso-umbilical margin weakly and obtusely angulated, walls of umbilicus evenly and strongly rounded. Color very light yellow horn, with irregular,

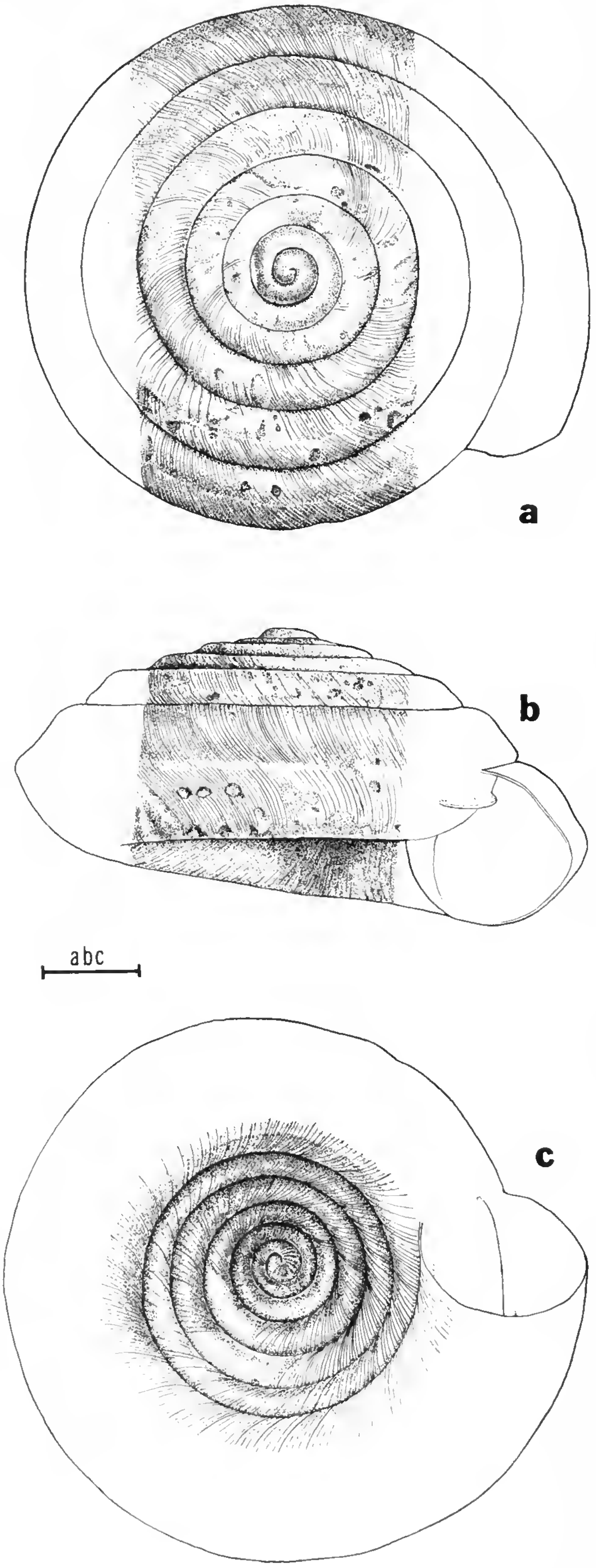

FIG. 158. **a-c**, *Nesodiscus obolus* form *celsus* (Pease, 1870). Raiatea, Society Islands. Lectotype. BPBM 3484 ex Garrett. Scale line equals 1 mm. (MM).

reddish flammulations that become very irregular and fade out on body whorl. Umbilicus broadly open, cup-shaped, later whorls decoiling less rapidly than earlier, contained 2.17 times in the diameter. Aperture subquadrangular, markedly flattened laterally above periphery, inclined about 35° from shell axis. Parietal wall with single supraperipheral raised barrier, extending posteriorly beyond line of vision, posterior visible quarter slightly more elevated, with relatively sharp anterior descension. Columellar wall without barriers. No palatal barriers visible from aperture. Height of lectotype 3.03 mm., diameter 6.15 mm.

Lectotype of celsus — Raiatea, Society Islands. BPBM 3484, ex Andrew Garrett.

Range. — Huahine and Raiatea, Society Islands. Widely dispersed over both islands (Garrett, 1884, p. 39).

Paratypes. — ANSP 290105 (*acetabulum*); BPBM 3484 (*celsus*).

Material. — Form *obolus*. Raiatea (6 specimens, BPBM 3786, Redpath Museum). Huahine (21 specimens, BPBM 165097, Cardiff). No locality (33 specimens, BPBM 170932, BPBM 170937, BPBM 170940, BPBM 170953).

Form *acetabulum*. — Raiatea (6 specimens, BPBM 3785). Huahine (17 specimens, BPBM 3446, BPBM 115341-2, Cardiff). No locality (68 specimens, BPBM 170896, BPBM 170933-4, BPBM 170940, BPBM 170943, ANSP 47844, ANSP 290105, FMNH 46274, FMNH 46247, FMNH 46395, FMNH 91889, FMNH 91762, FMNH 117052).

Form *celsus*. — Raiatea (10 specimens, BPBM 3484, BPBM 165098). No locality (8 specimens, BPBM 170939, BPBM 170973, BPBM 171012).

Remarks. — All available material consisted of small museum sets dating from the collections of Garrett prior to the mid-1880's. These had been segregated into the varieties *obolus*, *acetabulum*, and *celsus*. None were accompanied by exact locality data. Garrett (1884, pp. 39-41) reviewed the previous descriptions, corrected mistakes in type locality citations by Pease, and then stated (p. 40) "Having ... collected hundreds of specimens, both on Raiatea and Huahine, I do not hesitate, after a careful study of the numerous examples, to add both *acetabulum* and *celsus* to the synonymy of *obolus*."

The differences between the three forms (tables XCV, XCVI, XCVII) are mainly in the spire elevation and placement of the peripheral angulation or keel. In form *obolus* (fig. 156b) the spire is flat or barely elevated and the peripheral angulation is situated on the upper quarter of the body whorl; in form *acetabulum* (fig. 156e) the spire is slightly to moderately elevated and the peripheral angulation is at or slightly above the body whorl midpoint; while in form *celsus* (fig. 158b) the apex and spire are almost evenly and quite prominently elevated, with the peripheral angulation at or even slightly below the body whorl midpoint. Proportionate umbilical width is not materially altered by this change in spire height, but the umbilical depth is very shallow in *obolus* and progressively greater in *acetabulum* and *celsus*. The greater spire elevation of the two latter is reflected in their increased H/D ratio and in the partial separation of *celsus* in a height-diameter scatter diagram (fig. 157). The greater overlap of *obolus* and *acetabulum* simply reflects the minor alteration in H/D ratio caused by a flattened instead of a slightly elevated spire. Possibly subspecific separation would be discovered through study of local populations.

Compared with both *N. taneae* and *N. huaheinensis*, the parietal barrier in *N. obolus* is both lower and longer, extending more than one-half whorl in all individuals opened. One example had a short 2nd parietal that would not be visible from the unbroken aperture, but eight others did not. The actual frequency of 2 parietals in this species is unknown. Similarly, about 20 per cent of those specimens opened or subadult showed 1 or 2 low palatal barriers recessed about one-quarter whorl. Checking for their presence or absence required breaking off almost one-quarter of the body whorl and destruction of more than a few specimens was not considered justified.

Garrett stated that the Huahine specimens were less variable than those from Raiatea. Too little museum material retained island designations to enable verification of this observation.

Some specimens of *acetabulum* or *celsus* could be confused with *N. huaheinensis*. The latter has only microradial ribbing, while *obolus* shows reticulated microribbing between the very crowded major ribs. Doubtful specimens can be separated by checking the number and position of palatal barriers.

In order to stabilize the nomenclature, I have selected lectotypes for all three varieties. Because of the known mixing of sets in the Pease collection (now at the Museum of Comparative Zoology) one lectotype was chosen from a set in the Garrett collection at the Bernice P. Bishop Museum and another from the Academy of Natural Sciences, Philadelphia collection. The chosen specimens match the original descriptions. Since Garrett collected both type sets for Pease, his material can be considered to represent Pease's original concept. Lots of Pease material in the Museum of Comparative Zoology are often obvious mixtures of several species from different islands. Selection of lectotypes from these mixtures thus would represent pure guesswork.

Nesodiscus cretaceus (Garrett, 1884). Figure 159a-c.

Pitys ficta "Pease" Schmeltz, 1877 (not Pease, 1864). Cat. Mus. Godeffroy, **6**, p. 81 — Borabora, Society Islands (name only).

Endodonta cretacea Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 41, pl. 2, figs. 27, a, b — Borabora, Society Islands at 600 ft. elevation.

Helix (Endodonta) cretacea Garrett, Tryon, 1887, Man. Conchol., (2), **3**, pp. 66-67, pl. 11, figs. 98-100.

Endodonta (Endodonta) cretacea Garrett, Pilsbry, 1893, *op. cit.*, (2), **9**, p. 25.

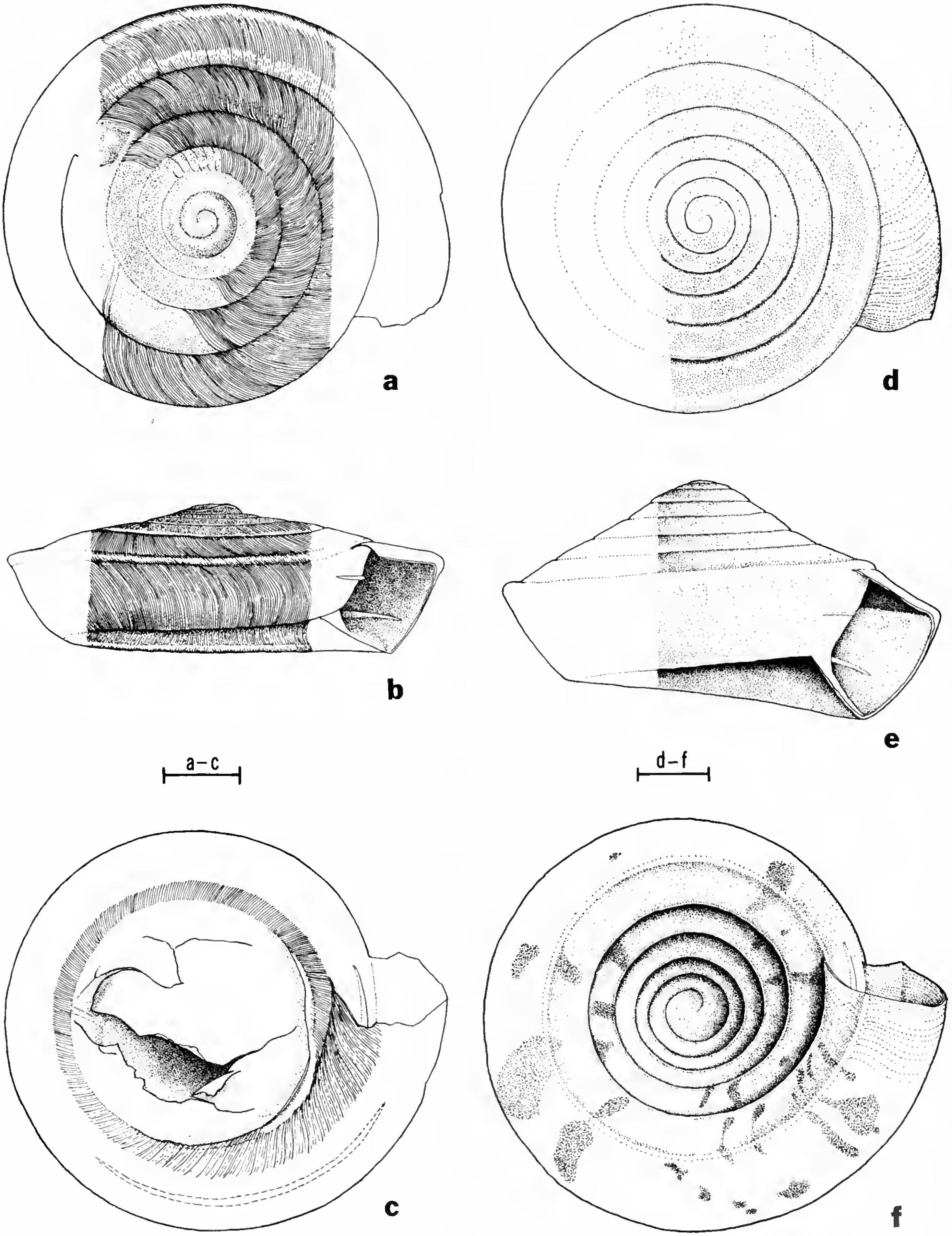

FIG. 159. **a-c**, *Nesodiscus cretaceus* (Garrett, 1884). Society Islands. Lectotype. ANSP 47832; **d-f**, *Nesodiscus fabrefactus* var. *piceus* (Garrett, 1884). Raiatea, Society Islands. Lectotype. BPBM 4994. Scale lines equal 1 mm. (*a-c*, MM; *d-f*, SH).

Diagnosis. — Shell somewhat smaller than average, diameter 5.06-6.41 mm. (mean 5.62 mm.), with 6⅛-7⅛ tightly coiled whorls. Apex slightly protruding above moderately and evenly elevated spire, last whorl not descending more rapidly, H/D ratio 0.335-0.429 (mean 0.377). Umbilicus widely open, V-shaped, regularly decoiling, contained 1.95-2.09 times (mean 2.03) in the diameter, interior walls almost completely flattened. Postnuclear whorls with very low, irregular, crowded and indistinct radial riblets, accentuated on body whorl near aperture by intrusion of growth striae. No microsculpture visible on any specimen examined. Sutures reduced to a thin line, whorls flat down to peripheral keel or with a weak to prominent supraperipheral sulcus, periphery protruded into an acutely angled keel, lower palatal wall flatly rounded down to right or obtusely angled basal margin, columellar wall flat or at most flatly rounded. Aperture quadrangular, flattened above periphery and on columellar margin, lower palatal margin faintly rounded, inclined about 30 - 40° from shell axis. Parietal wall with single, supramedial barrier, extending posteriorly beyond line of vision, posterior visible third greatly elevated, but not expanded above, anterior visible half a raised threadlike ridge with gradual anterior descension. Columellar wall without barriers. Lower palatal wall with a single, submedial, rather deeply recessed bladelike barrier, extending posteriorly beyond line of vision, with gradual anterior descension.

The Borabora Island *Nesodiscus cretaceus* differs from the Raiatean *N. fictus* in its larger apex, much lower whorl count, smaller size, and reduced barrier size. *N. fabrefactus* is much larger, with very sharply angulated baso-columellar margin and generally lacks all apertural barriers.

Description. — Shell smaller than average, with a little more than 6½ tightly coiled whorls. Apex and spire slightly elevated, sides of spire flat, H/D ratio 0.335. Apical whorls 1⅝, sculpture eroded. Remaining whorls with growth wrinkles and a microsculpture of fine radial ribs crossed by even finer and more crowded spiral riblets. Sutures very shallow, whorls flat above the acutely angled periphery, only slightly rounded down to right-angled basal margin, which then slants evenly into the umbilicus. Color very light yellow-white with a few narrow, reddish flammulations. Umbilicus broadly open, U-shaped, regularly decoiling, contained 1.99 times in the diameter, with whorls only slightly rounded inside. Aperture quadrangular with parietal margin slightly shorter than palatal, inclined about 30° from shell axis. Parietal wall with single barrier, high and threadlike for first three-sixteenths of a whorl, becoming a narrow, low, bladelike structure posteriorly and passing beyond line of vision from aperture. No columellar barrier. Palatal wall with single, low, bladelike barrier, extending from one-sixteenth of a whorl behind the aperture to beyond the line of vision, located almost midway between periphery and basal margin. Height of lectotype 1.91 mm., diameter 5.69 mm.

Lectotype. — Society Islands: Borabora at 600 ft. elevation. Collected by Andrew Garrett. ANSP 47832.

Range. — Borabora, Society Islands. One area at 600 ft. elevation (Garrett, 1884, p. 41).

Paratypes. — ANSP 290093, BPBM 2230.

Material. — Society Islands (4 specimens, ANSP 47382, ANSP 290093): Borabora (3 specimens, BPBM 2230, Brussels).

Remarks. — Only the smaller size, larger apex, and lower whorl count really serve to separate *Nesodiscus cretaceus* from Borabora and *N. fictus* from Tahaa. The apertural barriers are very similar and there are no significant differences in shape and sculpture. The "dentate" variety of *N. fabrefactus*, form *piceus*, is recognized by the concave sides to the spire and very sharp angulation at the baso-columellar margin.

N. cretaceus was cited by Garrett (1884, p. 41) as being common at a restricted locality. Only seven specimens were located in museum collections and no new material was obtained by the Mangarevan Expedition.

Nesodiscus fictus (Pease, 1864). Figures 154; 160d-f.

Helix ficta Pease, 1864, Proc. Zool. Soc. London, **1864**, p. 669 — no locality; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 223; Pfeiffer, 1876, *op. cit.*, 7, p. 260.

Endodonta ficta (Pease), Pease, 1871, Proc. Zool. Soc. London, **1871**, pp. 455, 474 — Raiatea, Society Islands; Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 38, pl. 2, figs. 25, a, b — Tahaa, Society Islands.

Patula ficta (Pease), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 207 — Raiatea, Society Islands.

Helix (Endodonta) ficta Pease, Tryon, 1887, Man. Conchol., (2), **3**, p. 62, pl. 12, figs. 5-7.

Endodonta (Endodonta) ficta (Pease), Pilsbry, 1893, *op. cit.*, *(2)*, **9**, p. 25.

Diagnosis. — Shell relatively large, diameter 5.62-7.32 mm. (mean 6.47 mm.), with 7⅛-8⅝ very tightly coiled whorls. Apex normally moderately and almost evenly elevated, slightly rounded above, occasionally only slightly elevated, body whorl not descending more rapidly, H/D ratio 0.337-0.531 (mean 0.428). Umbilicus widely open, cup-shaped, regularly decoiling, contained 1.84-2.23 times (mean 1.97) in the diameter, inner whorls moderately rounded. Postnuclear sculpture of extremely fine and crowded radial ribs, becoming irregular on body whorl because of growth striae. Microsculpture occasionally visible under 96× magnification as a lattice of coequal radial and spiral riblets. Sutures shallow, whorls flatly rounded down to prominent supraperipheral sulcus, periphery slightly to moderately protruded into an acutely angled keel, lower palatal margin almost flat down to strongly rounded, almost right-angled basal margin, with columellar wall slightly but distinctly rounded. Aperture subquadrangular, flatly rounded on all margins, inclined about 30 - 40° from shell axis. Parietal wall with single, supramedial, relatively low, bladelike barrier, extending posteriorly beyond line of vision, entire visible length with approximately equal height. Columellar wall without barriers. Palatal wall almost always with a low, extremely deeply recessed, submedial, threadlike barrier that extends posteriorly beyond line of vision. Many adult specimens have the palatal barrier recessed beyond the line of vision from the aperture, but a very few specimens seem to have lost this barrier.

The convex spire outline, distinguishable radial sculpture, normal presence of a lower palatal, distinct rounding to the umbilical wall and higher whorl count combine to distinguish *Nesodiscus fictus* from *N. fabrefactus*, which is also found on Tahaa Island. The differences from *Nesodiscus cretaceus*, except for the whorl count, larger apex, and smaller size of the latter, are primarily in degree. *N. fictus* has a less strongly angled umbilical margin and much more prominent apertural barriers than are found in *N. cretaceus*.

Description. — Shell larger than average, with 7¾ tightly coiled whorls. Apex slightly protruding, whorls of spire descending gradually, sides of spire distinctly convex, H/D ratio 0.467. Nuclear whorls 1⅝, sculpture eroded. Remaining whorls with narrow, very crowded, irregular radial riblets interrupted by irregular growth wrinkles. Occasional traces of faint microspiral ribbing can be detected. Sutures shallow, whorls flat above the slight supraperipheral sulcus; periphery rounded, slightly protruding; subperipheral and columellar margins flatly rounded. Color mainly leached from shell, slight traces of reddish flammulations remaining. Umbilicus widely open, broadly U-shaped, contained 1.98 times in the diameter, whorls flatly rounded inside with slight indentation of sutures. Aperture

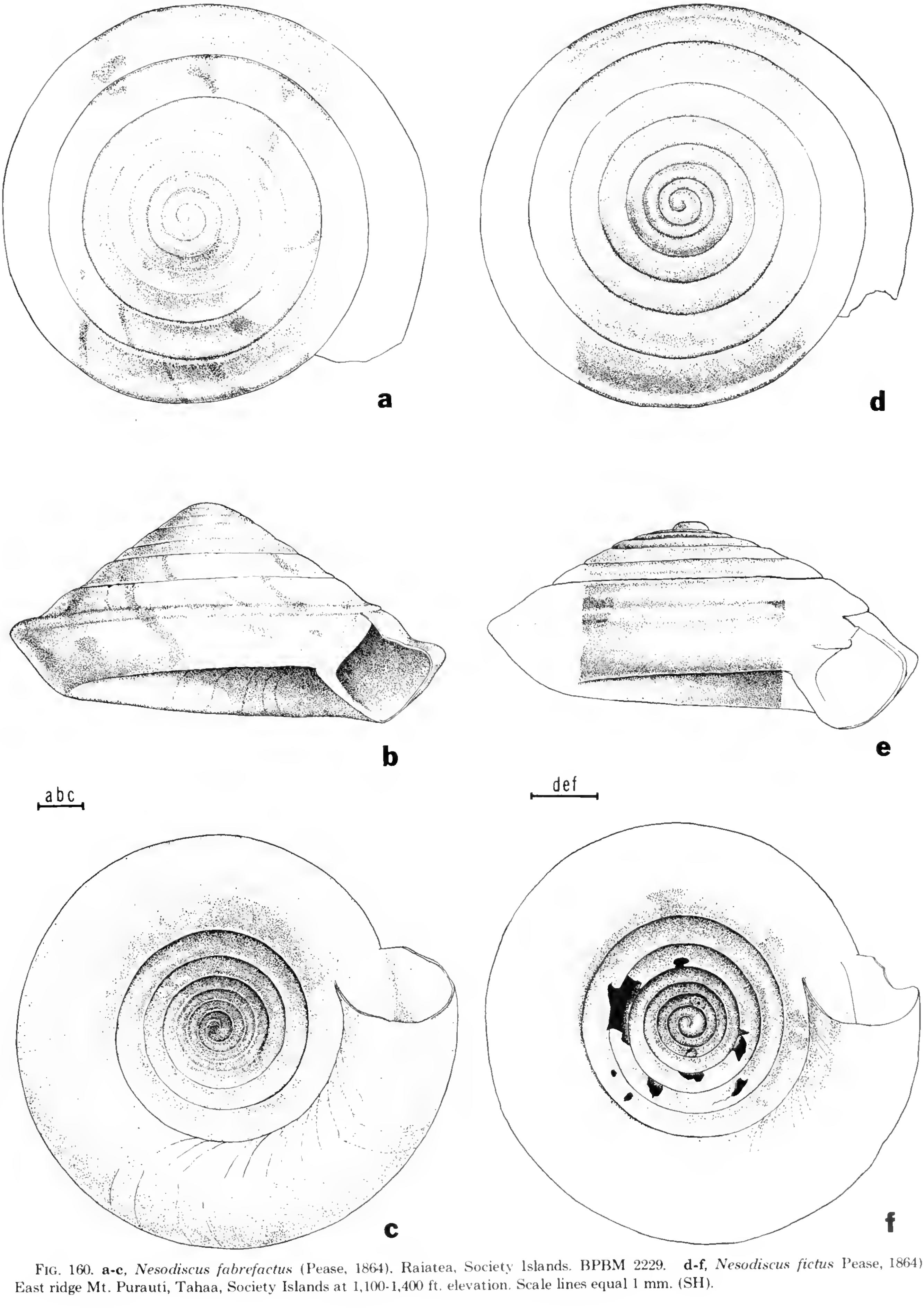

FIG. 160. **a-c**, *Nesodiscus fabrefactus* (Pease, 1864). Raiatea, Society Islands. BPBM 2229. **d-f**, *Nesodiscus fictus* Pease, 1864). East ridge Mt. Purauti, Tahaa, Society Islands at 1,100-1,400 ft. elevation. Scale lines equal 1 mm. (SH).

subquadrangular, lower palatal wall only slightly longer than parietal, inclined about 25° from shell axis. Parietal wall with single, slightly supramedial, threadlike raised barrier, extending posteriorly beyond line of vision. Columellar wall without barriers. Lower palatal wall with a single, submedial barrier, deeply recessed and barely visible from aperture, extending posteriorly beyond line of vision. Height of lectotype 2.86 mm., diameter 6.12 mm.

Lectotype. — Pacific Islands (= Raiatea). USNM 24213, ex W. H. Pease "from type."

Range. — Tahaa, Society Islands.

Material. — Tahaa (5 specimens, BPBM 4956, FMNH 91834): valley southeast of Mt. Purauti (Station 1085) at 800 ft. elevation (265 specimens, BPBM 152284-92); east ridge of Mt. Purauti (Station 1081) at 1,200-1,400 ft. elevation (719 specimens, BPBM 139790-800, BPBM 145081-2, BPBM 152254). No locality (52 specimens, BPBM 166000, BPBM 170935, BPBM 170942, BPBM 170949, BPBM 170964, BPBM 170972, FMNH 46356, FMNH 46386, FMNH 117048, USNM 24213).

Remarks. — In the original paper describing *Helix ficta* and *Helix fabrefacta,* Pease stated that specimens were sent both to the Cumingian collection and the Smithsonian Institution. No specimens of this species were located in the Cuming collection now at the British Museum (Natural History). Only one example was found in the United States National Museum that dated from this period. Although labelled as "*Discus fabrefactus* Pease," this can still be considered as the type of *Helix ficta* Pease. Carpenter transmitted Pease's manuscript for publication. The original shell label is in Carpenter's handwriting. In a footnote to Pease's description Carpenter had stated that he thought that *fabrefacta* and *ficta* were identical. Thus, the identification of this specimen as *fabrefactus* is easily explained as being a personal judgment of Carpenter. I have no hesitation in considering this specimen a lectotype rather than a neotype.

The extreme predominance of *N. fictus* at these two stations does suggest that some form of zonation, geographical or altitudinal, may exist between the two species. Without much more data and collecting efforts, no conclusions are possible.

As mentioned in the diagnosis, *N. fictus* and *N. cretaceus* have much in common, with the latter being smaller, having fewer whorls and less conspicuous barriers. They are obviously complementary species.

This was the only species of *Nesodiscus* for which abundant material that was accurately localized could be studied. Data from three samples are included in Table XCVI. The large size, abundant material (265 specimens from Station 1085 and 719 from Station 1081), and small pill boxes used in the Bishop Museum mollusk collection combined to produce minor biases. Thus the specimens in BPBM 139790 represented the 11 largest individuals selected from 719, and the 25 from BPBM 139791 represented a very small portion of the 428 individuals catalogued as "normal adults." The 37 shells from BPBM 152284-5-7 included 18 of 96 "normal adults" and seven (BPBM 152287) previously selected by the BPBM staff for their relatively low spire. Hence the slightly reduced height and H/D ratio of the Station 1085 sample is biased by the inclusion of low-spired individuals. Similarly, the greater height and diameter of BPBM 139790 shells is caused by conscious selection for large size. It is significant that the H/D ratios and D/U ratios are virtually identical for the Station 1081 samples, and that the diameters for the Station 1081 and Station 1085 "normal adults" are essentially identical.

At Station 1081, 450 (71.5 per cent) of 630 live collected or recently dead specimens were adult, 180 (28.5 per cent) were juvenile; at Station 1085, 107 (59.2 per cent) of 181 were adult, 74 (40.8 per cent) juvenile. Time permitted only a partial use of this material in studying variation. Allowing for the obvious biases documented above, there are no differences between the two populations revealed by the measurements utilized.

Description of soft parts. — Foot and tail slightly more than one-half shell diameter in length, not narrower in proportion. Sole undivided, truncated anteriorly, bluntly rounded posteriorly. Pedal grooves typical, equal in prominence, no caudal horn or middorsal groove present. Slime network of irregularly rectangular units, quite prominent in tail region. Head projecting in front of foot termination. Ommatophores typical, eyespot small. Gonopore in typical position.

Body color yellow-white, without darker markings.

Mantle collar thin, a large glandular extension (MG) onto pallial roof (fig. 154a). Pneumostome and anal opening typical, no mantle lobes developed.

Pallial region (fig. 154a, b) extending slightly more than one whorl apically, stretched out length about 13.1 mm. Lung roof clear, without granulations. Kidney (fig. 154b, K) about 2.7 mm. long, rectal arm equal to half total length, pericardial arm very slender and much less than width of ureter in section opposite heart. Base of kidney squarely rounded, lying above loop of intestine. Ureter (KD) arising at apex of kidney, reflexing at angle of rectal and pericardial arms, opening anterior of rectal kidney arm termination, next to hindgut. Heart (H) lying parallel to hindgut, about 1.38 mm. long. Principal pulmonary vein (HV) unbranched, extending into glandular extension of mantle collar.

Ovotestis (fig. 154c, G) of palmately clavate alveoli, generally less developed than in figured example, lying at a slant to the shell axis, extending three-quarters of a whorl above stomach reflexion. Hermaphroditic duct (GD) very long and slender, reflexing near base of albumen gland before entering carrefour. Albumen gland (GG) long and slender, of small acini. Talon (GT) long and slender, much shorter than albumen gland, fingerlike. Carrefour not differentiated. Prostate (DG) scarcely longer than wide, two rows of acini, duct barely visible. Uterus (UT) very slender, typically bipartite, external differentiation very indistinct.

Vas deferens (VD) greatly enlarged from prostate duct, loosely bound to peniovidueal angle, entering penis laterally about 0.33 mm. below penis head, usually between pilaster junction. Penial retractor (PR) arising from columellar muscle with partial attachment to diaphragm, inserting directly on head of penis. Penis (P) about 2.2-2.4 mm. long, moderately to strongly swollen medially, internally (fig. 154d, e) with two pilasters that unite apically above vas deferens insertion, complexly expanded and/or folded in medial expanded area, tapering down into atrium. Atrium (Y) short.

Free oviduct (UV) much longer than prostate, slightly enlarged above spermathecal insertion. Spermatheca (S) with head next to base of albumen gland, shaft inserting just above peniovidncal angle. Vagina (V) not structurally differentiated.

Free muscle system very elongated, but typical in structure and points of fusion.

Buccal mass slender, elongated, generative sac quite small. Buccal retractors split, inserting only slightly in front of posterior buccal mass margin. Esophagus slender and elongated, entering stomach just above pallial cavity origin. Stomach extending just over one whorl apically, reflexing normally to intestine which follows typical coiling pattern compressed in approximately one-eighth whorl between pallial cavity apex and full expansion of stomach. Hindgut at parietal-palatal margin a little less than one-eighth whorl above pallial cavity apex, without change in diameter from apical portion to anus.

Digestive gland extending over 3½ whorls above termination of ovotestis, very slender and elongated. Salivary glands very narrow, lying along esophagus, not united above or touching.

(Based on BPBM 152284, BPBM 139790, five adults, 6.3-6.8 mm. in diameter, with 7¼-7½ whorls.)

Nesodiscus fabrefactus (Pease, 1864). Figure 160a-c.

Helix fabrefactus Pease, 1864, Proc. Zool. Soc. London, **1864**, p. 669 – no locality; Pfeiffer, 1868, Monog. helic. viv., 5, p. 190; Pfeiffer, 1869, Novit. Conchol., 3, pp. 505-506, pl. 108, figs. 28-31; Pfeiffer, 1876, Monog. helic. viv., 7, p. 210.

Endodonta fabrefacta (Pease), 1871, Proc. Zool. Soc. London, **1871**, p. 474 – Raiatea, Society Islands; Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), pp. 38-39 – Tahaa and Raiatea, Society Islands.

Patula conicava "Mousson" Schmeltz, 1874, Cat. Mus. Godeffroy, 4, p. 72 – A nude name; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 480 – name only.

Helix (*Goniodiscus*) *fabrefactus* Pease, Tryon, 1887, Man. Conchol., (2), **3**, p. 45, pl. 5, figs. 81-82.

Endodonta (*Endodonta*) *fabrefacta* (Pease), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 25, pl. 5, figs. 52-53.

Nesodiscus fabrefactus (Pease), Thiele, 1931, Hand. Syst. Weichtierk., 1, (2), p. 571, fig. 656; Zilch, 1959, Hand. Paläzool., (6), 2, (2), p. 212, fig. 747.

Diagnosis. – Shell very large, diameter 5.56-8.50 mm. (mean 7.13 mm.), with 6¼-8 tightly coiled whorls. Apex and early spire moderately to strongly elevated, sides of spire usually distinctly concave, occasionally flat, body whorl not descending to descending moderately more rapidly, H/D ratio 0.404-0.602 (mean 0.493). Umbilicus broadly open, regularly decoiling, last portion flaring slightly, producing a convex outline, contained 1.70-2.17 times (mean 1.92) in the diameter, with inner margins flat to very gently rounded. Surface essentially smooth, except for vague, irregular radial growth wrinkles, plus exceedingly fine microreticulated secondary sculpture under 96× magnification. Sutures an indented line, whorls flatly rounded down to moderately prominent supraperipheral sulcus, periphery an acutely angled and protruded keel, lower palatal wall flat to gently rounded, baso-umbilical margin right-angled, columellar wall almost completely flat. Aperture subquadrangular, inclined 30-40° from shell axis, more than 45° from shell axis in gerontic individuals. Apertural walls without any trace of barriers in nominate race. Variety *piceus* differs in having a parietal and a palatal barrier, located as in *N. fictus.*

Nesodiscus fabrefactus, in its typical form, is readily recognizable by its total absence of apertural barriers, concave outline to the spire, and extremely sharp angulation at the baso-columellar margin. Variety *piceus,* in which a long parietal and deeply recessed palatal are present, differs from *N. fictus* by its concave spire outline and sharp baso-columellar margin. *N. cretaceus* from Borabora differs in its spire outline, prominent barriers, and much less sharply angled baso-columellar margin.

Description. – Shell large, with slightly more than 7 tightly coiled whorls. Apex and spire strongly elevated, rounded above, slightly convex on lower portion, H/D ratio 0.495. Apical whorls 1⅜, sculpture eroded. Remaining whorls with irregular growth wrinkles and very fine radial microriblets. Sutures very shallow, whorls flat above supraperipheral sulcus; periphery and umbilical margins strongly angulated, the former slightly protruding. Whorls flatly rounded on lower palatal and umbilical margins. Color leached from shell. Umbilicus broadly open, U-shaped, regularly decoiling, contained 1.98 times in the diameter, whorls flattened inside, sutures only slightly indented. Aperture subquadrangular, upper palatal margin sinuated, inclined about 30° from the shell axis. No apertural barriers. Height of neotype 3.59 mm., diameter 7.25 mm.

Neotype. – Society Islands: Raiatea. USNM 42427, ex W. H. Pease.

Range. – Confined to four large valleys on Raiatea and one on the east coast of Tahaa, Society Islands (Garrett, 1884, p. 38).

Paratypes. – USNM 42427.

Material. – Society Islands: Raiatea (47 specimens, BPBM 2229, BPBM 115345, BPBM 165099, FMNH 90612, FMNH 90634, FMNH 91859, USNM 42427). Tahaa: valley southeast of Mt. Purauti (Station 1085) at 800 ft. elevation (3 specimens, BPBM 9574, BPBM 152293); east ridge of Mt. Purauti (Station 1081) at 1,200-1,400 ft. elevation (7 specimens, BPBM 139801-2). No locality (18 specimens, BPBM 170970-1, FMNH 46404, FMNH 91107).

Remarks. – Whether the form discussed below as variety *piceus* is a geographic race or simply an individual variation is unknown. Juvenile examples of *fabrefactus* did not show any traces of apertural barriers and I am inclined to consider it a subspecific taxon. There is a great size difference in whorl width between *fabrefactus* and *piceus* (table XCVII). Unfortunately, its geographic status cannot be determined.

Nearly all individuals examined had concave spire outlines, only a few were flat, and none showed the typical convexity seen in all other *Nesodiscus.* In lacking all apertural barriers, *Nesodiscus fabrefactus* is unique among the Endodontidae. While *N. magnificus* and several Hawaiian *Cookeconcha* have only a single parietal, *N. cretaceus, N. fictus,* and *N. obolus* have a single parietal plus one or more additional barriers. The slight keeling or sharp angulation of the baso-columellar margin is equally distinctive.

No specimen dating from Pease's original description could be located in either the British Museum (Natural History) or in the Smithsonian Institution, places where Pease is believed to have donated the types. It must be assumed that original material, if extant, cannot be identified as such. I have chosen a neotype from specimens received by the Smithsonian

Institution from W. Harper Pease prior to January, 1885. Since they had the locality Raiatea, the specimens evidently were sent after 1871, when Pease corrected his error in locality. They may have come from the original set, or else from material subsequently collected by Andrew Garrett. In either case, they represent the original concept of this species.

Unfortunately, the only soft parts available were mixed with examples of *N. fictus,* which overwhelmingly predominated at the stations involved. Apparently, the typical pattern of character displacement is present, with the presumed *fictus* having a swollen, shorter (2.2-2.4 mm. long) penis with enlarged pilasters, and the putative *fabrefactus* a slender, longer (3.1-3.3 mm.) penis with little or no pilaster enlargement.

Description of soft parts. — Only fragmentary extracted individuals were available. Apparently, BPBM 139801 contained a mixture of *fictus* and *fabrefactus* soft parts, since two penial types were present. One conformed to the *fictus* type, the other was longer, 3.1-3.3 mm., more slender, with only a very weak expansion of the pilaster about one-third of way from head. No other features of the fragments differed from the structures in *fictus.* In view of the uncertain identity of these soft parts, no figures have been prepared.

Nesodiscus fabrefactus var. **piceus** (Garrett, 1884). Figure 159d-f.

Endodonta fabrefacta var. *picea* Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, 9, (1), p. 39 — west side of Raiatea, Society Islands.

Endodonta (*Endodonta*) *fabrefacta* var. *picea* Garrett, Pilsbry, 1893, Man. Conchol., (2), 9, p. 25 — name only.

Diagnosis. — Shell of average size, diameter 5.82-6.21 mm. (mean 6.06 mm.), with 6⅞-7¼ tightly coiled whorls. Apex and spire as in the typical form, last whorl not descending, H/D ratio 0.428-0.553 (mean 0.505). Umbilicus as in typical form, contained 1.94-2.07 times (mean 1.99) in the diameter. Sculpture, whorl contour, peripheral keel, and aperture as in typical form. Parietal wall with single, threadlike, almost medial barrier, slightly elevated posteriorly. Lower palatal wall with deeply recessed, single ridgelike barrier, extending posteriorly beyond line of vision, more elevated than parietal.

In all features of shape, sculpture, and whorl contour, form *piceus* is identical with the nominate variety. The possession of a relatively low and inconspicuous parietal, plus a distinct palatal, both occupying the same position as in *Nesodiscus cretaceus* and *N. fictus,* combine to separate *piceus* from the nominate form of *Nesodiscus fabrefactus.*

Description. — Shell of average size, with 7⅛ tightly coiled whorls. Apex and spire moderately and evenly elevated, sides of spire distinctly concave, body whorl not descending more rapidly, H/D ratio 0.543. Embryonic whorls and early spire with surface sculpture completely eroded. Lower spire macroscopically smooth, part of body whorl with irregular growth lines and traces of microradial ribbing. Sutures not indented, whorls flat down to relatively prominent supraperipheral sulcus. Periphery distinctly protruded into an acutely angled keel, lower palatal margin strongly compressed laterally, flatly rounded down to keeled baso-columellar margin, with columellar wall flatly rounded. Color light yellow-white, with irregular and widely scattered reddish flammulations below periphery of body whorl and in umbilicus. Umbilicus broadly open, regularly decoiling, last two whorls somewhat flaring outward, contained 2.07 times in the diameter. Aperture quadrangular, inclined about 30° from shell axis. Parietal wall with single, medial, threadlike barrier, extending posteriorly beyond line of vision, becoming weakly elevated on visible posterior quarter. Columellar wall without barriers. Lower palatal wall with single, deeply recessed, bladelike barrier, extending posteriorly beyond line of vision and much higher than parietal. Height of lectotype 3.39 mm., diameter 6.21 mm.

Lectotype. — Society Islands: Raiatea. West side of island. Collected by Andrew Garrett. BPBM 4994.

Range. — West side of Raiatea, Society Islands.

Material. — Raiatea (6 specimens, BPBM 4994, BPBM 9573).

Remarks. — The possession of a distinct parietal and one palatal separates *Nesodiscus fabrefactus* form *piceus* from the typical variety. The actually smaller size of the former (mean diameter of *piceus* is 6.06 mm., of *fabrefactus* 7.46 mm.) is confirmed by the essentially identical whorl count (table XCV) and much wider early whorls (table XCVII) in the nominate race. I suspect that *piceus* probably is a valid subspecies, but without new collections its status as a variety should be maintained. Form *piceus* probably is nearer the ancestral species and *fabrefactus* is a derived taxon. The probability of a dwarfed *fabrefactus* regaining apertural barriers that are identical in shape and position to those found in *N. cretaceus* and *N. fictus* seems quite small. It is much more probable that with increasing size the reduced barriers still present in *piceus* were lost by *fabrefactus.*

Nesodiscus magnificus, new species. Figure 161a-c.

Diagnosis. — The very large size, 11 mm. in diameter with 7 whorls, relatively narrow and flat-sided umbilicus, D/U ratio 2.87, strongly protruded keel, and convex spire, H/D ratio 0.454, combine with the single supramedial parietal barrier and complete absence of columellar or palatal barriers to separate *Nesodiscus magnificus* from other Society Island species. The only species that even approaches it in size, *Nesodiscus fabrefactus,* has the sides of the spire concave, the umbilicus much wider (D/U ratio less than 2.25), and the baso-columellar margin keeled or very strongly angled.

Description. — Shell very large, with 7⅛ normally coiled whorls. Apex and spire strongly elevated, rounded above, body whorl not descending more rapidly, H/D ratio 0.454. Apical whorls and early spire with sculpture completely eroded. Lower spire badly worn, showing occasional traces of low, rounded, indistinct radial ribs, whose interstices are about twice their width. No trace of microsculpture visible on shell surface. Sutures consisting of an impressed line slightly below outer edge of keel, whorls concave down to strongly protruded threadlike keel, supra- and subperipheral sulci prominent, lower palatal wall flatly rounded down to very strongly rounded baso-columellar margin, with columellar wall strongly flattened. All color leached from shell. Umbilicus broadly open, U-shaped, slightly decoiling, last whorl decoiling a little more rapidly, contained 2.97 times in the diameter, inside whorls strongly flattened, sutures indented. Aperture subquadrangular, inclined about 40° from shell axis. Parietal wall with single, supramedial, bladelike barrier, extending posteriorly beyond line of vision, posterior visible quarter slightly more elevated, anterior portion a raised lamellar ridge until shortly before anterior termination. No columellar or palatal barriers. Height of holotype 5.10 mm., diameter 11.19 mm.

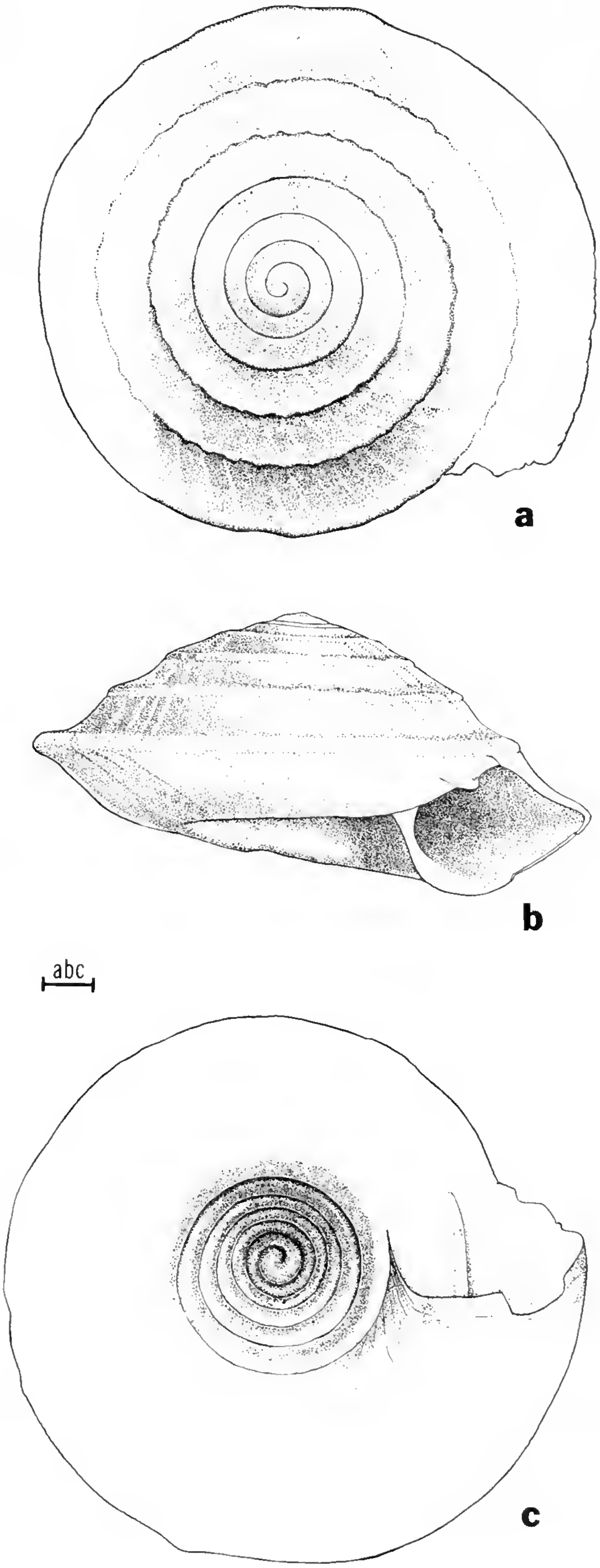

FIG. 161. a-c, *Nesodiscus magnificus*, new species. Station 1091, south slope of Pahio-Temanu ridge, Borabora, Society Islands at 800 ft. elevation. Holotype. BPBM 152341. Scale line equals 1 mm. (SH).

Holotype. – Society Islands: Borabora, Station 1091, south slope of Pahio-Temanu ridge, at 800 ft. elevation. Collected by Gessler and St. John on a ledge over rock overhang, on October 13, 1934. BPBM 152341.

Range. – Borabora, Society Islands.

Material. – Only the holotype is known.

Remarks. – Only the Hawaiian *Nesophila tiara* (Mighels, 1845) and the Mangareva Island *Gambiodonta grandis* exceed the size of *Nesodiscus magnificus*. An occasional specimen of *Endodonta fricki* (Pfeiffer, 1858) will reach 10 mm. in diameter, but otherwise only *Libera jacquinoti* from an unknown locality and possibly *Nesodiscus fabrefactus* reach 9 mm. in diameter (see Garrett, 1884, p. 38).

Nesodiscus magnificus shows several differences from the common *Nesodiscus* pattern. The keel is much sharper and more strongly protruded, producing an actual concavity on the upper palatal wall; the umbilicus is narrower, typically U-shaped and with the whorls much more strongly flattened internally than in the other more narrowly umbilicated species; sculptural remnants approach the *N. taneae* pattern rather than those very fine and crowded ribs seen in the other taxa; the baso-columellar margin is strongly rounded, but not keeled or angled; and the apex is not distinctly protruded above the spire.

Unfortunately, only the one dead, quite worn individual collected in leaf litter is known.

Genus **Nesophila** Pilsbry, 1893

Man. Conchol., (2), **9**, p. 27.

Medium-sized to very large Endodontidae with moderately to greatly reduced sculpture. Apex and spire slightly to moderately elevated, last whorl descending a little more rapidly. Umbilicus widely open, regularly decoiling, with distinctly angulated margin and flattening of the inner whorls. Periphery of body whorl rounded to obtusely angulated, usually compressed laterally above and below. Parietal wall with many threadlike lamellar traces that extend posteriorly beyond line of vision. Columellar and palatal walls without barriers. Pallial region typical. Genitalia with short, ovoid talon, a very short vagina, and simple uterus. Penial retractor attached partially to diaphragm, partially to columellar muscle apex. Penis long, nearly uniform in diameter, with two large pilasters connected above and below, forming an elongately oval, "donut"-shaped stimulatory pad. Jaw of completely fused plates centrally, traces of sutures visible at outer edge. Radular teeth typical in form, except outer marginals tending to square basal plates, large in size.

Type species. – *Helix tiara* Mighels, 1845 (original designation).

Described as a section of *Endodonta* to be used for all Polynesian species in which the columellar and palatal barriers were lost, *Nesophila* is restricted here to a small complex from Kauai. The species share a widely open umbilicus with margined shoulder, rounded or obtusely angulated periphery, complete loss of palatal and columellar barriers, with the parietals split into a number of threadlike traces. Many species of *Cookeconcha* have lost the columellar and palatal barriers, but retain 1 or 2 large to threadlike parietals. Derivation of *Nesophila* from a generalized *Cookeconcha*-type ancestor requires, essentially, only increase in size, reduction in sculpture, intensification of contour trends, and splitting of the parietals.

Somewhat similar modifications of apertural barriers are seen in other parts of the Pacific. *Australdonta radiella* from Rurutu and Tubuai, Austral Islands, has lost the columellar and palatals, with the parietals split into 7-17 threadlike traces, only one of which is enlarged. The Rapan *Opanara megomphala* has less drastically split parietals, but the palatal and columellar wall covered with threadlike traces. The Marquesan *Taipidon centadentata* and *Planudonta intermedia* still retain a few elevated parietals and palatals, but have most of the palatals split into threads. Examination of anatomical and other shell features indicates that the barrier similarities are convergent, since each form shows clear relationships to local species.

The morphologic gaps between *Endodonta, Cookeconcha,* and *Nesophila* are much larger than the gaps between species within the genera.

Nesophila tiara (Mighels, 1845). Figure 165c-g.

Helix tiara Mighels, 1845, Proc. Bost. Soc. Nat. Hist., **2**, p. 19 – Kauai; Pfeiffer, 1848, Mon. helic. viv., **1**, p. 85; Pfeiffer, 1850, Zeit. Malak., **6**, pp. 70-71; Pfeiffer, 1853, Mon. helic. viv., **3**, pp. 98-99; Pfeiffer, 1853, Syst. Conchyl. Cab., (1), **12**, (3), p. 293, pl. 125, fig. 9-11 (plate issued in 1853); Reeve, 1854, Conchol. Icon., *Helix*, pl. 109, fig. 611; Pfeiffer, 1859, Mon. helic. viv., **4**, p. 93; Pfeiffer, 1868, Mon. helic. viv., **5**, p. 156; Pease, 1871, Proc. Zool. Soc., London, **1871**, p. 475; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 163; Tryon, 1887, Man. Conchol., (2), **3**, p. 38, pl. 8, figs. 25-27; Johnson, 1949, Occ. Pap. Moll., **1**, (14), p. 229, pl. 27, fig. 23.

Endodonta tiara (Mighels), von Martens, 1860, Die Heliceen, ed. 2, p. 90; Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Patula (Stepsanoda) (sic) tiara (Mighels), Clessin, 1881, Nomen. Helic. viv., p. 94.

Charopa tiara (Mighels), Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 175; Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 15.

Endodonta (Nesophila) tiara (Mighels), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 291.

Diagnosis. – Shell very large, diameter 10.72-12.55 mm. (mean 11.29 mm.), with 5¼-5⅝ normally coiled whorls. Apex and spire slightly and almost evenly elevated, body whorl descending slightly more rapidly, H/D ratio 0.500-0.630 (mean 0.560). Umbilicus widely open, V-shaped, regularly decoiling, margin distinctly angled with inner whorls flattened, contained 2.91-3.28 times (mean 3.14) in the diameter. Apical whorls smooth, without trace of sculpture under 96× magnification. Postnuclear whorls basically with irregular growth wrinkles, which obscure an apparent pattern of very low and inconspicuous radial ribs on most of spire, becoming completely dominated by growth wrinkles on body whorl. No microsculpture visible. Sutures impressed, whorls compressed laterally above and below rounded periphery, umbilical margin angulated, columellar wall distinctly flattened. Aperture subcircular, compressed laterally above and below rounded periphery, inclined about 25 - 30° from shell axis. Parietal barriers 7-11, usually 9, approximately equal-sized threadlike traces extending posteriorly beyond line of vision. Columellar and palatal walls without barriers.

Range. – Kauai, Hawaiian Islands.

Lectotype. – Kauai, Hawaiian Islands. MCZ 176994.

Material. – Hawaiian Islands (2 specimens, FMNH 7678, FMNH 91893): Kauai (2 specimens, FMNH 46399); upper Kaapoko, Hanalei at 1,300 ft. elevation (2 specimens, BPBM 93905); south branch, north fork, Wailua River, Wailua (3 specimens, BPBM 81310).

Remarks. – The very large size of *Nesophila tiara* serves to separate it from the other described species, which range from 4-7 mm. in diameter with essentially identical whorl counts. Study of the abundant *tiara* material in the Bernice P. Bishop Museum may lead to recognition of several subspecies on Kauai.

The anatomy of *N. tiara* basically is the same as that of *Endodonta fricki*. The position of the ovotestis lying perpendicular (fig. 165d) to the plane of coiling, rather than at an angle (fig. 163c) to the plane of coiling as in most Endodontidae, probably is a simple correlative of the very large size with low whorl count reached by *Nesophila tiara*. The greater development of the penial pilasters with stronger lateral extensions of the free edges probably is a result of a similar cause. Possibly the smaller, shorter talon of *N. tiara* may have more systematic significance.

Description of soft parts. – Foot and tail long and slender, length about equal to shell diameter, very slightly tapering posteriorly, bluntly rounded behind. Sole undivided. Pedal grooves deep, rather high on side of foot, no caudal horn or middorsal groove present. Slime network prominent, proportionately very fine. Head projecting in front of truncated foot. Ommatophores long, with large eyespots. Gonopore directly behind right rhinophore, a very narrow vertical slit.

Body color yellowish-white, without darker markings.

Mantle collar (MC) thick, without any glandular extension onto pallial roof. Pneumostome (LP) masked by thickened edges of mantle collar, no mantle lobes as such developed. Anus (A) opening above pneumostome in angle of mantle collar.

Pallial region (fig. 165c) extending about three-quarters of a whorl apically, nearly 13 mm. long. Lung roof clear, without granulations. Kidney (K) elongately triangular, about 5-6 mm. long, with very short portion reaching hindgut. Ureter (KD) on inner margin of kidney, opening at point where kidney touches hindgut. Heart (H) about half length of kidney, lying parallel to hindgut. Principal pulmonary vein (HV) rather wide, without obvious branching, reaching to edge of mantle collar. Hindgut (HG) not tapered, following parietal-palatal margin only to apex of pallial cavity, then curving outwards across albumen gland.

Ovotestis (fig. 165d, e, G) of many palmately clavate clumps of alveoli strung in overlapping clusters along a single collecting tubule, stopping well short of soft parts apex. Individual clusters at right angle to plane of coiling. Hermaphroditic duct (GD) very slender at first, moderately expanded medially, narrowing considerably just before reflexing slightly to enter carrefour. Albumen gland (GG) small, lying above head of prostate and uterus. Talon (fig. 165f) with ovoid head and short shaft before entering carrefour (X), lying partially at inner margin of albumen gland, partially buried in albumen gland. Carrefour short and inconspicuous. Prostate (DG) with several rows of large acini opening into a narrow tube, upper section partially wrapped around uterus. Uterus (UT) bipartite, slender upper section partially enfolded by prostatic acini, lower expanded chamber very thinwalled, tapering gradually to free oviduct well below end of prostate.

Vas deferens (VD) slender, lightly bound to penioviducal angle, entering penis a little more than 1 mm. below penial apex, below free edge of one pilaster. Penial retractor (PR) arising from diaphragm at apex of pallial cavity opposite base of spermathecal head, inserting directly onto penis head. Some fibers from point of origin also run to columellar muscle. Penis (P) slightly tapered apically, mostly with equal diameter until sharp constriction just before atrium, 8.2-10.0 mm. long, internally (fig. 165g) with two large pilasters, united apically and basally, both with their outer edges free and elongated, inner margins usually crenulated. Atrium (Y) short and rather wide.

Free oviduct (UV) much shorter than prostate, but much longer than shown in Figure 165d. Ratio of prostate length to postprostatic-free oviduct length about 5:4.5. Spermatheca (S) with head outside and below albumen gland above apex of pallial cavity, shaft inserting onto free oviduct above penis junction. Vagina (V) short, but distinctly recognizable as a morphologic unit.

Free muscle system typical, but massive, particularly the tail fan. Right ommatophoral retractor passing through penioviducal angle, uniting with right rhinophoral retractor about three-eighths of way to columellar margin. Tentacular retractors unite laterally on each side of tail fan about halfway from head to apex of columellar muscle. Columellar muscle extending one-eighth whorl above tip of albumen gland.

Buccal mass as in *E. fricki*. Buccal retractors split, uniting just posterior to buccal mass, joining columellar muscle at its apex. Stomach starting less than 1 mm. above apex of pallial cavity, extending one whorl apically. Intestinal coiling as in *E. fricki*. Hindgut typical, except for slight extension above apex of pallial cavity.

Digestive glands as in *E. fricki*. Salivary glands typical, uniting weakly above esophagus.

Jaw about 0.7 mm. long, of completely fused plates, except at outer margins where traces of sutures can be detected. Concentric striations very prominent.

Radula with central about 14μ long, 9-10μ wide, with 8 laterals and more than 8 marginals. Outer marginals with basal plates more nearly square than usual.

(Based on BPBM 81310, four whole and several fragmentary examples.)

Nesophila baldwini (Ancey, 1889)

Charopa baldwini Ancey, 1889, Bull. Soc. Malacol. France, 6, p. 176 – Sandwich Islands; Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 15.

Endodonta baldwini (Ancey), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 26.

Endodonta (Nesophila) baldwini (Ancey), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 289 – Hawaiian Islands.

Range. – Probably Kauai, Hawaiian Islands.

Material. – None.

Remarks. – The type specimen, about 4 mm. in diameter with 4¾ whorls, was obtained by Ancey from John H. Thomson and possibly originated with A. A. Gould. The description is that of a small *Nesophila* and there is little doubt that it belongs to this group.

Nesophila distans (Pease, 1866)

Helix distans Pease, 1866, Amer. Jour. Conchol., **2**, (4), p. 290 – Sandwich Islands; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 262; Tryon, 1887, Man. Conchol., (2), **3**, p. 60.

Patula (Endodonta) distans (Pease), Clessin, 1881, Nomen. helic. viv., p. 95.

Pitys distans (Pease), Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 185; Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16.

Endodonta distans (Pease), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27.

Endodonta (Nesophila) distans (Pease), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 290 – Kauai.

Range. – Kauai, Hawaiian Islands.

Material. – None.

Remarks. – About 7 mm. in diameter, with 4-5 whorls, this undoubted species of *Nesophila* is intermediate in size between the smaller *baldwini* and large *tiara*.

Nesophila capillata (Pease, 1866)

Helix capillata Pease, 1866, Amer. Jour. Conchol., **2**, p. 292 – Sandwich Islands; Pfeiffer, 1876, Mon helic. viv., **7**, p. 197.

Pitys capillata (Pease), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474 – Kauai.

Patula (Gonyodiscus) capillata (Pease), Clessin, 1881, Nomen. Helic. viv., p. 92.

Charopa capillata (Pease), Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 175; Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 15 – Kilauea and Kealia, Kauai.

Endodonta (Nesophila) capillata (Pease), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 289.

Nesophila capillata (Pease), Cockerell, 1925, Nautilus, **38**, (3), p. 82 – head of Anahola Valley, near waterfall, Kauai, Hawaiian Islands.

Diagnosis. – Shell large, diameter 4.24-4.75 mm. (mean 4.46 mm.), with 4⅝-5 normally coiled whorls. Apex and most of spire slightly and evenly depressed below level of penultimate whorl, body whorl descending rapidly, distinctly below level of penultimate whorl, H/D ratio 0.488-0.517 (mean 0.500). Umbilicus widely open, V-shaped, regularly decoiling, contained 2.34-2.63 times (mean 2.51) in the diameter, with sides distinctly flattened. Postnuclear sculpture of widely spaced, low, narrow, protractively sinuated radial ribs, 39 - 44 (mean 41.0) on the body whorl, whose interstices are 5-9 times their width. Microsculpture of very fine, rather widely spaced radial riblets, six to ten between each pair of major ribs, with barely visible traces of extremely crowded spiral riblets. Secondary spiral sculpture of about 10 narrow spiral cords that "notch" both major and micro-radials and are located from upper shoulder to umbilical margin, but not on shell base or near suture. Sutures deep, whorls strongly rounded above, shouldered on umbilical margin, with laterally compressed and evenly rounded outer margin. Aperture subcircular, compressed laterally, inclined about 10° from shell axis. Parietal wall usually with eleven or twelve threadlike traces that extend posteriorly beyond the line of vision, occasionally with only eight traces. Columellar and palatal walls without barriers.

The smaller size, distinct radial ribbing, and peculiar secondary spiral cording at once separate *Nesophila capillata* from the much larger *N. tiara* with its greatly reduced radial ribbing and lack of secondary spiral cording. While the Oahu *Cookeconcha hystrix* has almost identical sculpture, the palatal barriers and 2 large parietals distinguish that species.

Description. – Shell large, with 5 normally coiled whorls. Apex and spire slightly and regularly depressed below level of penultimate whorl, body whorl descending rapidly, H/D ratio 0.517. Apical whorls 1¼, macroscopically smooth above, umbilical side showing smooth first part, then very fine radial ribbing. Postnuclear whorls with low, narrow, widely spaced, sharply outlined, protractively sinuated radial ribs, 44 on the body whorl, whose interstices are 5-9 times their width. Microsculpture of fine radial riblets, six to ten between each pair of major ribs, with barely visible traces of extremely crowded spiral riblets under 96× magnification. Secondary microsculpture of

11 widely spaced, narrow, spiral cords that "notch" both major and microradials, present from top of whorl shoulder down to umbilical margin, but absent from umbilicus and suture areas. Sutures deep, whorls strongly rounded above, slightly shouldered on umbilical margin, evenly rounded on laterally compressed outer margin, sides of umbilicus flattened. Color light yellow horn, with broad, irregular, zigzagged, reddish flammulations that fade out on shell base. Umbilicus broadly open, V-shaped, regularly decoiling, contained 2.47 times in the diameter, with whorl sides distinctly flattened. Aperture subcircular, compressed laterally, strongly rounded above and below, inclined about 10° from shell axis. Parietal wall with twelve threadlike traces that extend posteriorly beyond line of vision, spacing irregular, those on lower part closer together than those on upper. No columellar or palatal barriers. Height of lectotype 2.45 mm., diameter 4.75 mm.

Lectotype. — Sandwich Islands (=Hawaiian Islands). ANSP 1975a, ex A. D. Brown, W. H. Pease.

Range. — Kauai, Hawaiian Islands.

Paratype. — ANSP 1975.

Material. — Hawaiian Islands (8 specimens, BMNH, ANSP 1972, ANSP 1975, FMNH 155932).

Remarks. — The much larger *Nesophila tiara* lacks the secondary spiral cording, has the main radial sculpture reduced, and the microsculpture absent. Its umbilical walls are less clearly flattened and the parietal traces usually number nine, instead of the eleven to twelve recorded in *N. capillata*.

Cookeconcha hystrix (Pfeiffer, 1846) from Mt. Konahuanui, Oahu, has exactly the same type of sculpture as in *N. capillata,* except that the major radials are more elevated and less widely spaced. Numerous shape and barrier changes distinguish the two species, but the essentially exact correspondence in sculpture emphasizes the unitary nature of the Hawaiian endodontid radiation.

Genus **Kondoconcha,** new genus

Endodontidae with typical apical and microsculpture, major radial ribs prominent on mid-spire, greatly reduced on lower spire and absent from body whorl and shell base. Whorls about 6⅜, rather tightly coiled. Apex and spire moderately and evenly elevated, body whorl often strongly deflected below periphery, which is nearly right angled with a weak supraperipheral sulcus. Umbilicus narrowly open, U-shaped, barely decoiling. Parietal barriers 2, each with at least one accessory ridge on each side, plus several short accessory traces on parietal wall. Columellar barrier very large, parallel to plane of coiling, with a lower accessory trace. Palatal barriers 5, with many accessory traces. Anatomy unknown.

Type species. — *Kondoconcha othnius*, new species.

In general appearance, *Kondoconcha* could be confused with the more narrowly umbilicated *Nesodiscus,* such as *N. taneae* and *N. huaheinensis*, or the Hawaiian *Endodonta binaria* (Pfeiffer, 1856). Its numerous apertural barriers and typical microsculpture distinguish it from the *Nesodiscus,* while the many accessory traces, completely different barrier form, and umbilical shape effectively separate it from any species of *Endodonta.* The presence of only 2 parietals and the angulated periphery suggest that *Kondoconcha* might be related to *Orangia*. The normally sculptured genus *Orangia* also differs significantly in its unusual form of umbilical closure and complete absence of accessory traces. *Orangia* species also have (except rarely) only 4 palatals. Of the Rapan species, only *Opanara bitridentata* and *O. duplicidentata* have accessory traces. Both differ in details of barrier structure, have normal sculpture, and either wider (*duplicidentata*) or differently shaped (*bitridentata*) umbilici. *Kondoconcha* shares the size, 2 parietal barriers, shape and peripheral angulation of *Orangia,* has the accessory traces found in a few *Opanara,* but differs from all Rapan species in its marked sculptural reduction and presence of lateral accessory barriers on both the upper and lower side of each parietal (fig. 108c, d).

I consider that the similarities to *Orangia* are the result of parallel evolution, since both, almost certainly, were derived from an *Opanara*-type ancestral stock. The totally different sculpture and umbilical structure of *Orangia* (fig. 123a, b) when compared with *Kondoconcha* (fig. 162a, c) is striking. Combined with the difference in apertural barriers, generic recognition is required.

Although three sets of partly extracted soft parts were borrowed for study, no satisfactory data on anatomy was obtainable. Three whole specimens had dried out at a previous time, while the fragmentary examples were squashed flat. A single penis, minus retractor and an unknown portion of its lower shaft, was separated from one fragment. It seemed to have the two high and narrow pilasters, but could not be figured and its conditon was too poor for formal description. What could be seen was fully consistent with the hypothesized derivation from *Opanara*, but the evidence is very meager.

So much of this study was possible only because of the labors by Yoshio Kondo that dedication of this very striking genus to him is a small token of appreciation.

Kondoconcha othnius, new species. Figures 108 c-d; 162.

Diagnosis. — Shell large, diameter 3.81-4.24 mm. (mean 4.06 mm.), with 6⅛-6¾ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, sometimes slightly flattened above, last whorl barely to strongly deflected below periphery, H/D ratio 0.548-0.601 (mean 0.567). Umbilicus narrow, U-shaped, scarcely decoiling, contained 5.00 - 6.40 times (mean 5.55) in the diameter. Postnuclear sculpture of broad, prominent, low, protractive radial ribs that become greatly reduced in prominence on the lower spire and are absent from body whorl. Base of shell smooth and shiny, without traces of radial sculpture. Microsculpture of exceedingly fine and crowded radial riblets crossed by even finer and more crowded spiral riblets. No secondary microsculpture. Sutures shallow, whorls strongly rounded above to weak supraperipheral sulcus, periphery nearly right angled, weakly protruded, lower palatal margin strongly and evenly rounded to sharply rounded baso-columellar margin. Aperture ovate, flattened laterally above protruded periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly more than one-quarter whorl, each with lateral accessory ridges, plus three to five (usually three) short accessory traces on the

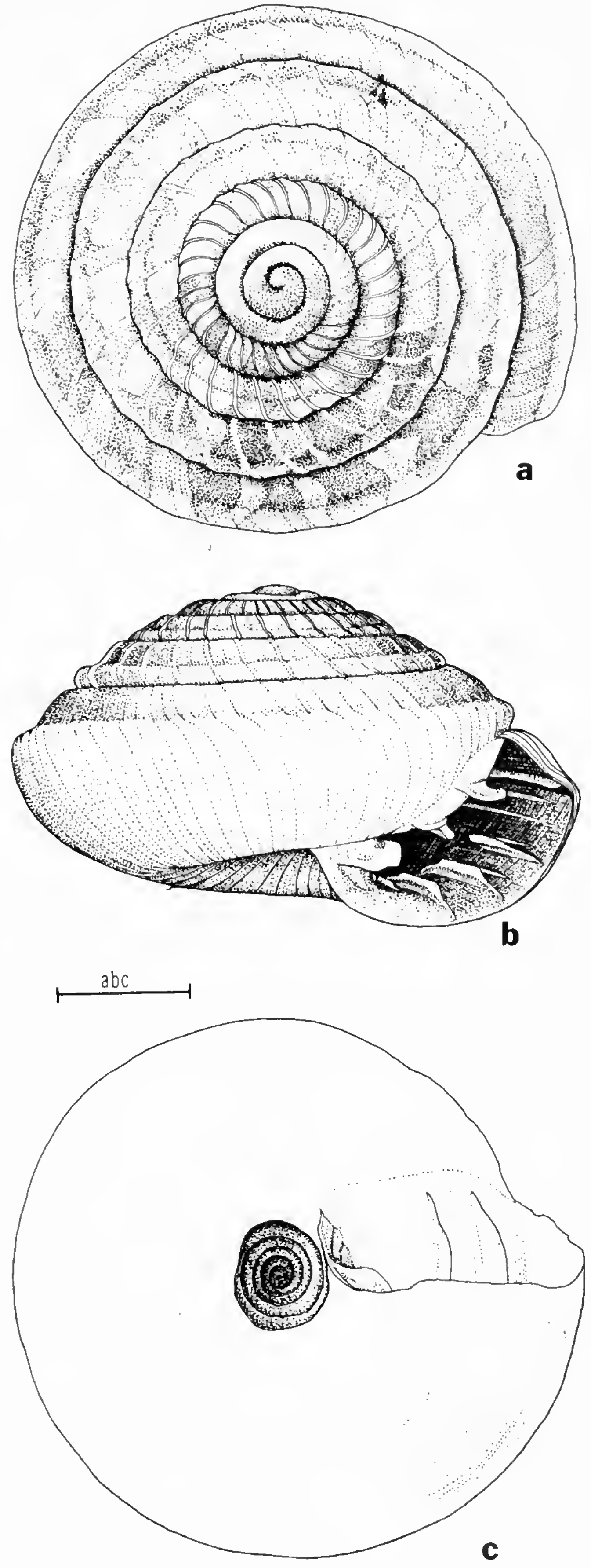

FIG. 162. **a-c**, *Kondoconcha othnius*, new species. Station 346, Mt. Tavaitahu, Rapa Island, Austral Islands. Holotype. BPBM 142462. Scale line equals 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

parietal wall; upper parietal very high and slender, expanded and serrated above on posterior five-eighths, with gradual anterior descension, and a low ridgelike, expanded and serrated accessory lamella on each side of main blade (fig. 108c-d); 2nd parietal slightly lower than 1st, more strongly expanded and serrated above on posterior half, with sharp descension to a strongly elevated threadlike ridge that terminates opposite anterior end of upper parietal, with weak threadlike accessory denticles on upper and lower basal edges of barrier. Accessory traces short, threadlike, deeply recessed within aperture, one situated above upper parietal, one between 1st and 2nd parietal, and one below 2nd parietal. Additional parietal traces occasionally developed above 1st and below 2nd parietal. Columellar barrier very high and bladelike, broadly expanded and serrated above posteriorly, lying parallel to plane of coiling, with extremely abrupt anterior descension nearly to edge of lip margin; a deeply recessed, threadlike, expanded accessory trace situated just above baso-columellar margin. Palatal barriers 5, extending posteriorly nearly three-sixteenths of a whorl, with eight to ten accessory traces, 4th palatal greatly reduced in size, first 3 very large; 1st palatal high, bladelike, expanded, serrated, and flattened above, with gradual anterior descension; 2nd palatal equal in height to 1st, expanded and serrated portion shorter, with more gradual anterior descension; 3rd palatal slightly higher than 2nd, expanded and serrated portion further reduced in length, with more gradual anterior descension; 4th palatal a raised threadlike ridge, only weakly expanded and serrated above, subperipheral, situated slightly below level of upper parietal; 5th palatal larger than 4th, supraperipheral, a raised lamellar ridge, weakly expanded and serrated above, less recessed within aperture. Palatal traces variously located, normally one below 1st palatal, two above 5th palatal, and one or two between each pair of palatals.

The essentially complete loss of ribbing on the shell base, great reductions of radial ribbing on the lower whorls, and development of accessory traces on the sides of the parietal barriers are a combination of characters unique among the Endodontidae. The only species with which *Kondoconcha othnius* can be confused are *Endodonta binaria* (Pfeiffer, 1856) from Kauai, Hawaiian Islands, which differs in the form and length of the apertural barriers, and possibly some of the *Orangia*, which differ in having a closed umbilicus and normal radial sculpture.

Description. — Shell rather large, with 6¾ relatively tightly coiled whorls. Apex and spire strongly and evenly elevated, very slightly rounded above, last whorl deflected below periphery, H/D ratio 0.601. Embryonic whorls with sculpture eroded. Whorls 2¾-5 with low, indistinct, broad radial ribs, that after 5th whorl become indistinguishable except for occasional irregularities on periphery. Base of shell smooth and shiny, without trace of microsculpture. Microsculpture of extremely fine radial and even finer and more crowded spiral riblets. Sutures shallow, whorls rounded down to prominent supraperipheral sulcus. Periphery almost right angled, slightly protruded, lower palatal and basal margin strongly and evenly rounded. Color light greenish-horn, with broad, irregular, reddish flammulations that fade out on last part of body whorl and are greatly reduced on shell base. Umbilicus very narrow, scarcely decoiling, last whorl with irregular outline, contained 6.40 times in the diameter. Aperture ovate, slightly flattened laterally above protruded periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly more than one-quarter whorl, with three short, recessed accessory traces on the parietal wall and two accessory ridges on the sides of both major parietals: upper parietal high and bladelike, slender, expanded and serrated above on posterior five-eighths, with gradual anterior descension until just before anterior end, and two accessory ridges, one on upper and one on lower side of main blade base; 2nd parietal with posterior elevated portion reduced in height, more strongly expanded and serrated above, with sharp anterior descension to an elevated ridgelike anterior termination, weak threadlike accessory traces on each side of main lamellar blade base. Columellar barrier very high, broadly expanded and serrated above, lying parallel to plane of coiling, abruptly descending almost to edge of columellar lip, a single deeply recessed raised threadlike ridge at columellar basal margin as an accessory trace. Palatal barriers 5, with eight accessory traces present: lower palatal high, bladelike, expanded, serrated and flattened above, with gradual posterior and anterior descension; 2nd and 3rd palatals with expanded elevated portions reduced in length, more gradual anterior descension; 4th palatal a raised threadlike ridge, subperipheral, with exceedingly gradual anterior descension; 5th palatal supraperipheral, much higher than 4th, but lower than 3rd, with gradual anterior descension, an elevated lamellar blade. Palatal traces deeply recessed, located one below 1st palatal, one between each pair of major palatals and three above the 5th palatal. Height of holotype 2.54 mm., diameter 4.21 mm.

Holotype. — Austral Islands: Rapa Island. Station 346, hillside west of Mt. Tevaitahu at 750 ft. elevation. Collected under stones in forest by Donald Anderson on July 9, 1934. BPBM 142462.

Range. — Mt. Tevaitahu and Morongoto, Rapa Island, Austral Islands.

Paratypes. — Same as list of material.

Material. — Rapa Island: hillside west of Mt. Tevaitahu (Station 346) at 750 ft. elevation (31 specimens, BPBM 142462-7); hillside (Station 360) at Morongoto (2 specimens, BPBM 144245).

Remarks. — Juvenile specimens of less than four whorls had the prominent radial ribbing present on the shell base. Subadult and adult examples had the base essentially devoid of sculpture, quite smooth and shining. Only six of the 31 specimens from Station 346 were adult and both of the Morongoto specimens were juvenile.

The columellar barrier is larger than the palatal, accessory ridges are present on the sides of the major parietals, there is great reduction of the radial sculpture, and a complete absence of radial sculpture on the shell base. These features combine to make *Kondoconcha othnius* the most distinctive species of Endodontidae found on Rapa Island. Comparisons with *Orangia* and *Opanara* are given above under the generic discussions. The barrier structure is the same seen in other Rapan genera, except for the large number of accessory traces and the addition of these laterally on the parietals.

The Hawaiian *Endodonta binaria* (Pfeiffer, 1856) is strikingly similar in general appearance, having the same shape and identical sculptural reduction on the upper surface. Although obviously more depressed and with a wider umbilicus than *K. othnius* (tables LXXXI, XCVIII), the convergent nature of the similarities in shape and sculpture is clearly revealed by the widely different form of the barriers and subperipheral sculpture. *K. othnius* has barriers identical to those seen in the Rapan taxa, essentially simple in form and roundly expanded and serrated above; *E. binaria* has the bifurcately expanded parietals and palatals typical of *Endodonta* (fig. 167g). *Kondo-*

TABLE XCVIII. - LOCAL VARIATION IN ENDODONTA

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Aperture		
ekahanuiensis Ekahanui, Waianae FMNH 154483	2	1.47±0.008 (1.46-1.48)	2.77±0.041 (2.73-2.81)	0.531±0.0410 (0.520-0.542)	4 3/4	3.48±0.160 (3.32-3.64)	2	1	4+1
binaria FMNH 46567	2	1.92±0.083 (1.84-2.01)	4.26±0.149 (4.11-4.41)	0.452±0.0035 (0.448 0.455)	5 7/8+ (5 3/4-6 1/8)	3.46±0.110 (3.35-3.57)	2	1	4+2
concentrata FMNH 46613, FMNH 73192, FMNH 90627	7	2.38±0.051 (2.17-2.60)	5.06±0.086 (4.70-5.43)	0.471±0.0039 (0.458-0.487)	5 1/4- (5-5 1/2)	4.90±0.147 (4.43-5.50)	2	1	4+0-1
laminata FMNH 46455 FMNH 117042	6	2.55±0.043 (2.47-2.70)	6.22±0.069 (6.05-6.55)	0.411±0.0088 (0.377-0.436)	6 3/8- (6 1/4-6 1/2)	3.50±0.103 (3.12-3.84)	2	1	4+$\underline{3}$-4-$\underline{6}$
lamellosa Oahu, FMNH 73199, FMNH 91143, FMNH 91839, FMNH 154481	15	2.83±0.053 (2.50 3.09)	6.44±0.299 (5.86 7.24)	0.439±0.0051 (0.402-0.472)	6+ (5 3/8-6 1/2)	4.18±0.134 (3.18-5.10)	2	1	5+$\underline{1}$-2
Mt. Konahuanui, Oahu, FMNH 46275, FMNH 116901	4	2.89±0.081 (2.70 3.09)	6.61±0.275 (6.05 7.37)	0.439±0.0062 (0.420 0.446)	5 7/8+ (5 3/8-6 5/8)	4.21±0.329 (3.61-4.84)	2	1	5+2
kamehameha FMNH 73198, FMNH 90629	4	3.13±0.043 (3.03-3.22)	6.91±0.194 (6.38-7.30)	0.453±0.0120 (0.432-0.485)	6 1/8- (5 7/8-6 3/8)	3.42±0.106 (3.23-3.69)	2	1	$\underline{3}$-4
marsupialis FMNH 116902	2	3.45±0.231 (3.22-3.68)	7.20±0.186 (6.64-7.76)	0.480±0.0050 (0.475-0.485)	6 3/8 (6 1/4-6 1/2)	5.11±0.517 (4.59-5.62)	2	1	5+0-1-$\underline{2}$[1]
fricki Makalea, Waianae FMNH 53042, FMNH 111526	22	3.66±0.082 (2.96-4.61)	8.99±0.108 (8.03-9.67)	0.407±0.0056 (0.357-0.476)	6 1/2 (6-7)	3.60±0.049 (3.17-4.10)	2	1	4+$\underline{1}$-2
Miscellaneous exact localities	14	3.55±0.070 (3.09-3.82)	8.99±0.166 (8.22-10.1)	0.396±0.0080 (0.329-0.437)	6 1/2+ (6 1/8-6 7/8)	3.72±0.071 (3.32-4.17)	2	1	4+$\underline{1}$-2-$\underline{3}$

1. Summarized from Cooke (1928).

concha othnius has essentially no subperipheral sculpture on the body whorl; *E. binaria* has prominent radial sculpture and very strong secondary spiral cording. While neither has been dissected, the differences between *Endodonta fricki* and the Rapan genera are marked and I have no doubt that the similarities are convergent.

Genus **Endodonta** Albers, 1850

Die Heliceen, ed. 1, p. 89.

Endodontidae with typical apical sculpture, secondarily reduced in *concentrata, marsupialis, fricki,* and *lamellosa.* Postnuclear whorls rarely with wide, prominent radial ribs (*ekahanuiensis*), reduced on body whorl (*binaria*) or lower spire (*laminata*), or (most frequently) shell surface macroscopically smooth. Apex and spire weakly (*kamehameha*) to moderately elevated, H/D ratio relatively low, above 0.500 only in *ekahanuiensis.* Body whorl flattened above and below a threadlike keel or knife-edge periphery (*concentrata, kamehameha, fricki*). Whorls 5⅞-6½, reduced only in *concentrata* (5¼-) and *ekahanuiensis* (4¾). Umbilicus widely open, U-shaped, last whorl barely (*concentrata, kamehameha*), regularly (*laminata*), or more rapidly decoiling, modified into brood pouch only in *marsupialis.* Size slightly smaller than average (*ekahanuiensis*) to very large (*fricki*). Parietal barriers 2, relatively long, generally weakly to strongly bifid above, simple only in *laminata* and *kamehameha.* Columellar barrier rather large, reaching lip margin (*concentrata, marsupialis*) or midway across callus, lying parallel to plane of coiling or slightly slanted downwards (*marsupialis, ekahanuiensis*). Palatal barriers 4 or 5 (*lamellosa, marsupialis*), bifid only in *binaria,* usually with one or two accessory traces (absent in *kamehameha* and sometimes *concentrata*), generally four in *laminata.* Pallial region typical endodontid, with short rectal kidney arm. Hermaphroditic duct uncoiled. Talon with small, globular head and tapered shaft. Uterus bipartite. Vas deferens entering penis subapically. Latter of variable length, internally with two longitudinal pilasters of varying size that combine or fade out near atrium. Spermathecal shaft joining free oviduct at or just above rather elongated atrium. Penial retractor originating from columellar muscle above buccal retractor origin, inserting directly onto head of generally rather long penis. Jaw of partly fused, very narrow lamellar plates, which are individually wider than in *Cookeconcha,* but are still too indistinct for accurate counting. Radula typical in structure.

Type species. – *Helix lamellosa* Ferussac, 1824 (by subsequent designation of von Martens, 1860, p. 90).

The carinated periphery, marked tendency toward reduction of shell sculpture, generally bifid upper parietal barrier, and U-shaped, rather flat-sided umbilicus are distinctive shell features of *Endodonta.* Of the other Hawaiian genera, *Nesophila* is distinguished by its large size, absence of any columellar or palatal barriers, and splitting of the parietals into seven to eleven threadlike traces; *Cookeconcha* by its generally rounded or laterally compressed periphery (except *stellulus*), retention of marked radial ribbing, and marked tendency toward loss of palatal and columellar barriers. That *Endodonta* is a derivative of *Cookeconcha*-type ancestors is made reasonably certain by the presence of bifid upper parietals in the *C. henshawi* complex and a general tendency for loss of the apical sculpture in *Cookeconcha.* These characteristics are not seen in other Pacific Island Endodontidae and I have no doubt that *Cookeconcha, Nesophila,* and *Endodonta* form a monophyletic group.

Similarities between *Endodonta* and extralimital genera are gross and recognizable as parallel or convergent in nature. The Society Islands genus *Nesodiscus* has a similar tendency toward loss of sculpture, but the widely open umbilicus is cup-shaped, regularly decoiling, and occasionally serves as a brood chamber through secretion of a mucus membrane across the opening. The character of the keeling is quite different in *Nesodiscus*; the parietal barriers are not bifid; and the palatal barriers are much different in shape and very deeply recessed. *Nesodiscus* is a derivative of *Mautodontha,* with *M. boraborensis* relatively intermediate in structure. The Rapan *Kondoconcha othnius* is strikingly similar to *Endodonta binaria* in form, barrier count, and sculpture, but even casual inspection of the apertural barriers in the two species shows very different structure and shape.

The treatment below is not intended as a formal revision of *Endodonta.* It is based only on material in the Field Museum of Natural History collection and attempts to provide an indication of variational patterns within this material. Previously recorded knowledge was not sufficient to allow an assessment of how *Endodonta* was related to Polynesian genera. Hence this brief survey was necessary in order to place *Endodonta* within the family. Slightly more than 2,100 sets of *Endodonta,* containing at least 25,000 specimens, are preserved in the Bernice P. Bishop Museum. Particularly in regard to the forms from the Waianae Mountains, there is a bewildering amount of variation, both intra- and supraspecific, that offers a magnificent opportunity for the study of microevolution. An accurate guess as to the actual number of species in *Endodonta* is impossible. On the basis of Cooke's sorting, about 78 species and an additional 55 geographic races have been segregated (table II). Eventual recognition of at least 100 species-level taxa will be necessary.

A full diagnosis for each species is given where material was available. No examples of *E. apiculata* Ancey, 1889 and *E. rugata* (Pease, 1866) were seen. Literature references to these species are included for completeness. Under each species, some comparative remarks are made, primarily concerned with advanced *versus* primitive characters. Since only a small fraction of existing (or recently extinct) species are covered below, no formal comparisons or keys have been constructed. To avoid giving an erroneous impression of size and sculpture range in *Endodonta,* description of a single new species, *E. ekahanuiensis,* is included.

Three species, *E. lamellosa, E. fricki,* and *E. marsupialis,* have been dissected. Differences of systematic importance are few, primarily concerning penis length, pilaster size and shape, plus the point of vas deferens insertion. The penial, oviducal, and vas deferens coilings cited by Cooke (1928, pp. 22, 23, 26) are artifacts caused by withdrawal of the animal into

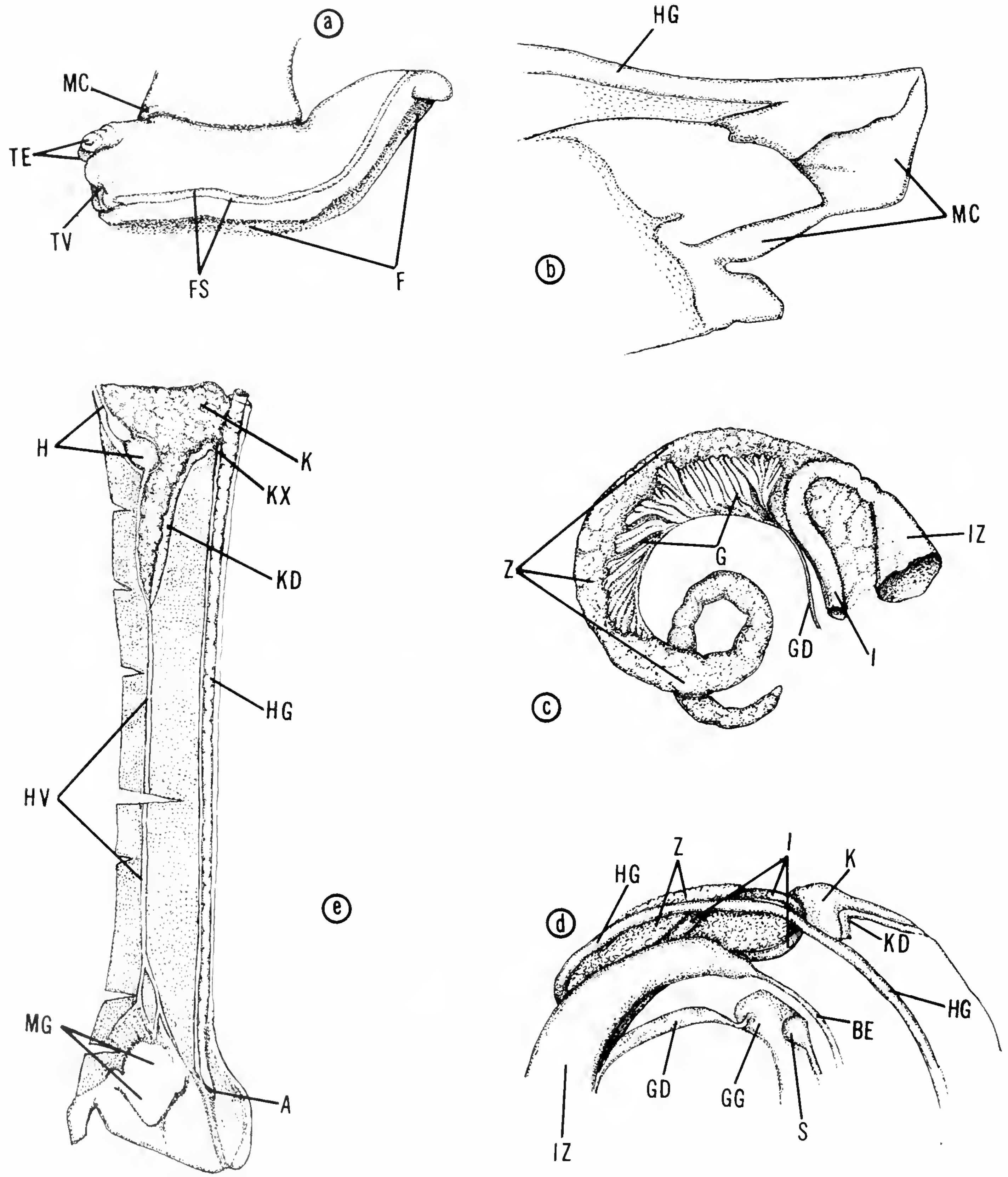

FIG. 163. Anatomy of *Endodonta fricki*. Waianae Mts., Oahu, Hawaii. BPBM 128063: **a**, Head and foot from left side, rhinophores fully retracted; **b**, detail of mantle collar in undissected specimen; **c**, apex of visceral mass showing relationship of ovotestis (G), digestive gland (Z), and intestine (I); **d**, relative position of organs at apex of pallial cavity, systems slightly separated; **e**, pallial region flattened and pinned out. (See Appendix for explanation of abbreviations.)

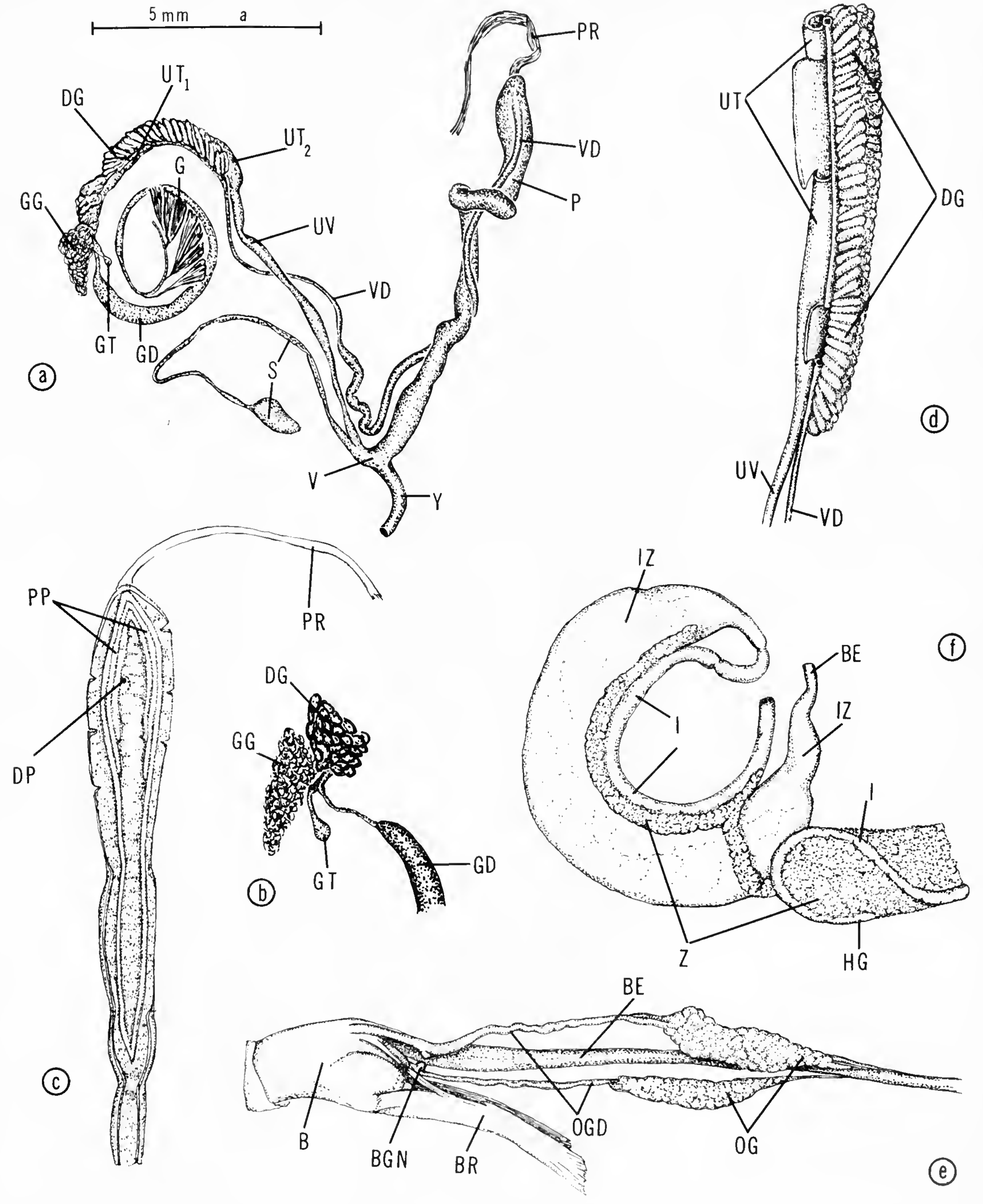

FIG. 164. Anatomy of *Endodonta fricki*. Waianae Mts., Oahu, Hawaii. BPBM 128063: **a**, genital system dissected out and uncoiled; **b**, detail of apical genitalia; **c**, interior of penis showing pilasters (PP) and opening of vas deferens (DP); **d**, organization of prostate-uterus; **e**, buccal mass and esophagus from right side; **f**, ventral view of stomach and loops of intestine prior to hindgut. (See Appendix for explanation of abbreviations.)

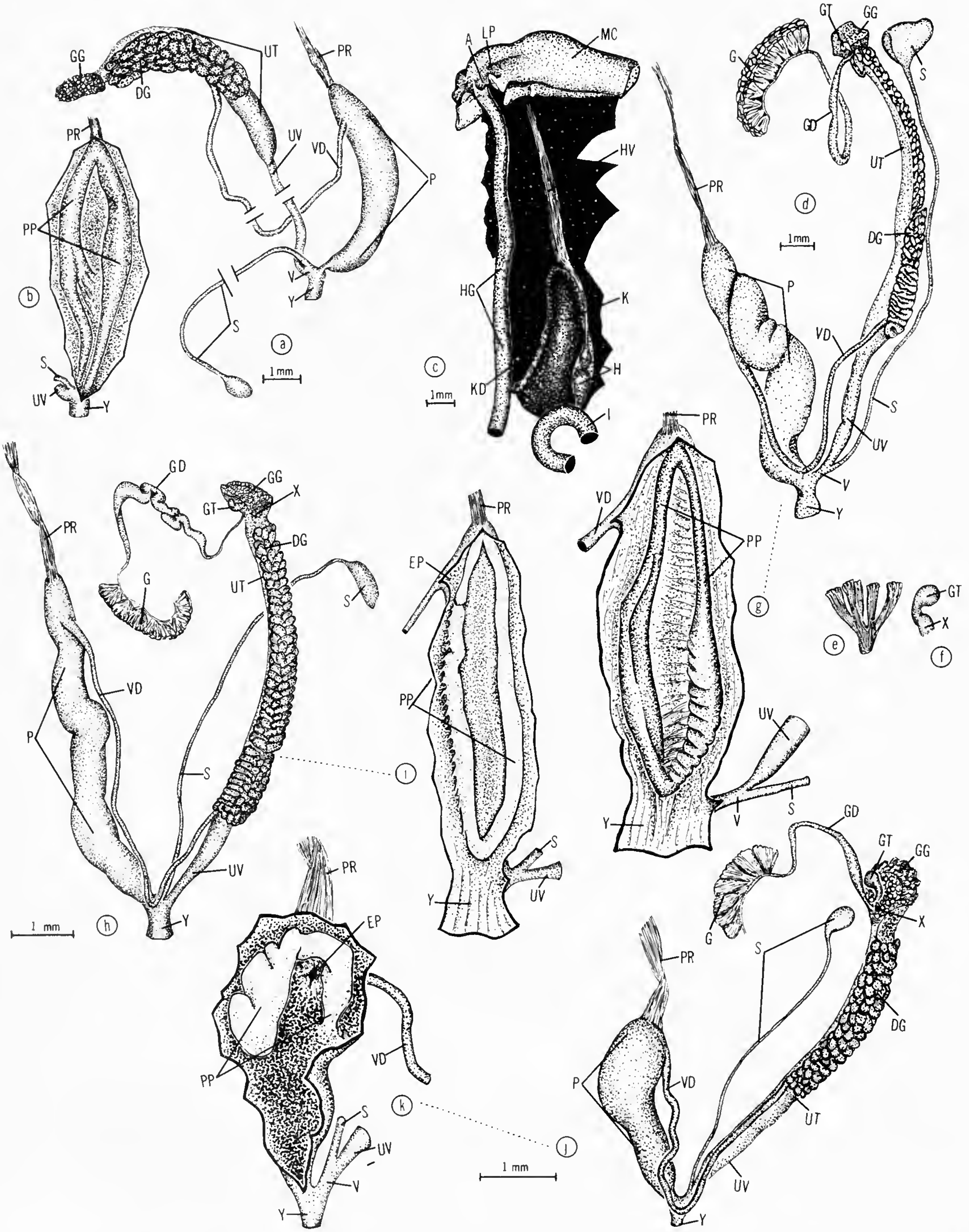

FIG. 165. Anatomy of: **a-b**, *Endodonta lamellosa* (Ferussac). Koolau Mts., Oahu. BPBM 16556. *a*, genitalia, *b*, interior of penis; **c-g**, *Nesophila tiara* (Mighels). Wailua, Kauai. BPBM 81310. *c*, pallial region, *d*, genitalia, *e*, structure of ovotestis clump, *f*, form of talon and juncture with carrefour, *g*, interior of penis; **h-i**, *Cookeconcha jugosus* (Mighels). Wailua, Kauai. BPBM 81197. *h*, genitalia; *i*, interior of penis; **j-k**, *Cookeconcha hystricellus* (Pfeiffer). Popowela, Waianae Mts., Oahu. BPBM 35421. *j*, genitalia, *k*, interior of penis. Scale lines equal 1 mm.

the shell. *E. lamellosa* has a short penis, 4.4-6.1 mm. long, with the vas deferens inserting well below the apex and the pilasters are thick and very large apically; *E. marsupialis* has a very large penis, 12-15 mm. long, with the vas deferens entering far (3.5 mm.) below the penis head; and *E. fricki* has a penis 9-10 mm. long, with the vas deferens inserting almost directly below the penis head and the pilasters much smaller and lower than in *E. lamellosa* (fig. 165a-b). Dissections of specimens from different populations in the Waianae Mountains might reveal a situation similar to that found in the Arizona-New Mexico *Sonorella*, where penial size is correlated with dryness of habitat. The many populations of *E. fricki* were ideally suited for undertaking such an investigation.

Endodonta ekahanuiensis, new species. Figure 166a-c.

Diagnosis. — Shell very small, diameter 2.73-2.81 mm. (mean 2.77 mm.), with 4¾ normally coiled whorls. Apex and spire moderately strongly elevated, rounded above, last whorl not descending more rapidly. H/D ratio 0.520-0.542 (mean 0.531). Umbilicus widely open, U-shaped, early whorls not decoiling, last whorl decoiling more rapidly, contained 3.32-3.64 times (mean 3.48) in the diameter. Apical whorl with prominent radial ribs and typical microribbing. Postnuclear whorls with broad, rounded, protractively sinuated radial ribs, 37-45 (mean 41) on the body whorl, whose interstices are less than twice their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of broad, low spiral cords present below periphery. Sutures shallow, whorls flatly rounded down to supraperipheral sulcus. Keel threadlike, protruded, lower palatal margin evenly rounded, basal margin more strongly rounded to obtusely rounded umbilical margin. Walls of umbilicus flatly rounded, retaining sculpture to apex. Aperture flatly rounded above and below protruded threadlike periphery, inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly one-quarter whorl: upper high and slender, with sharp anterior descension, becoming twisted upward posteriorly with a broadly expanded bifid lateral portion on posterior two-thirds, separation of main and bifid sections very indistinct to appearing deflected downwards; 2nd slightly lower posteriorly, broadly expanded above, with gradual descension to broadly threadlike anterior third that terminates slightly in front of upper parietal. Columellar barrier a high lamellar blade, broadly expanded and serrated above posteriorly, slightly twisted downwards from plane of coiling, with gradual anterior descension midway across columellar callus. Palatal barriers 4, extending posteriorly slightly more than one-eighth whorl, slightly recessed, with one supraperipheral accessory trace just below 4th palatal: lower 3 high and bladelike, with progressively more gradual anterior descension and with 1st and 3rd slightly smaller than 2nd, all broadly expanded above; 4th supraperipheral, longer, lower, less deeply recessed, with very gradual anterior descension. Palatal trace very deeply recessed, about half height of 4th palatal.

The very small size, retention of strong radial ribbing on the body whorl, very high spire, and broadly expanded palatal barriers separate *Endodonta ekahanuiensis* from the other described species. In having secondary spiral sculpture on the shell base, it resembles the Kauai Island *E. binaria* and *E. laminata,* both of which are much, much larger (mean diameters 4.26 and 6.22 mm., respectively), lack major ribs on the body whorl, and have two to six palatal traces. The protruded keel at once separates *E. ekahanuiensis* from all described *Cookeconcha*.

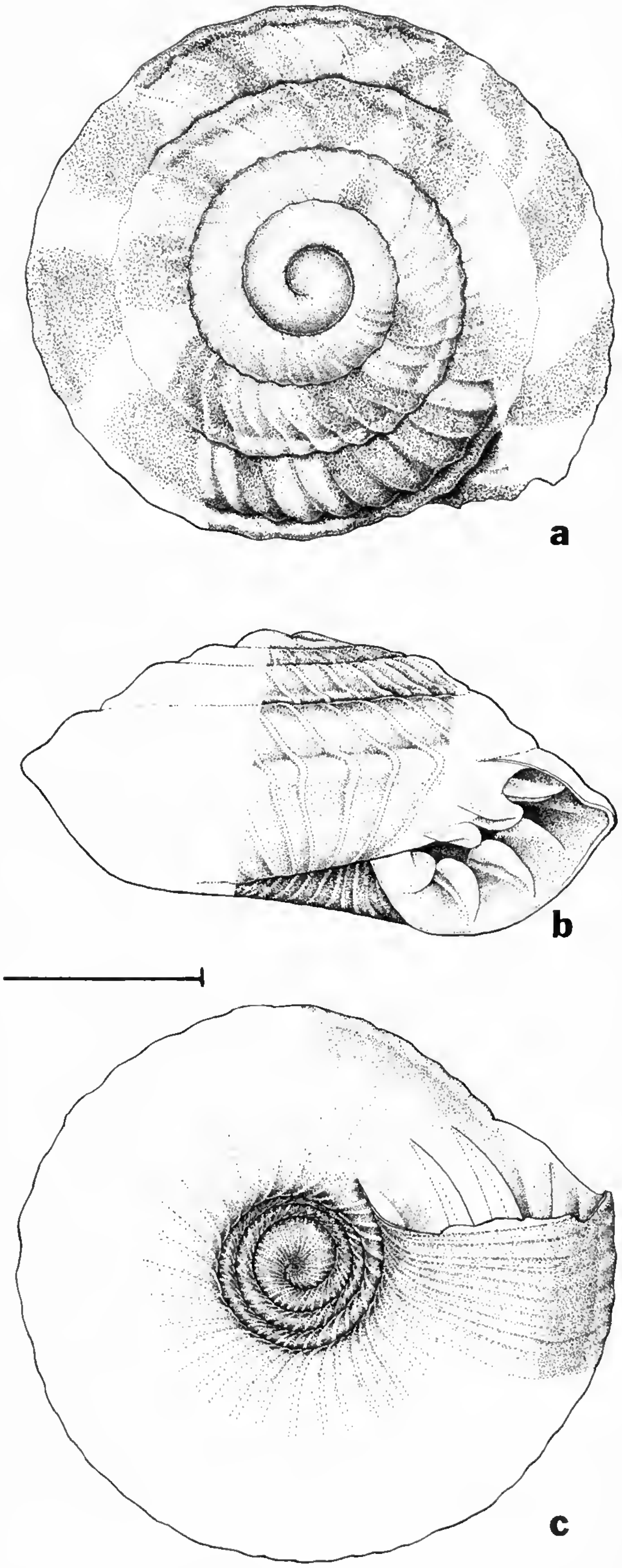

FIG. 166. **a-c**, *Endodonta ekahanuiensis,* new species. Holotype. FMNH 154483. Station W410C-6, Waianae Mts., Oahu, Hawaiian Islands. Scale line equals 1 mm. (MM).

Description. — Shell very small, with slightly less than 4¾ normally coiled whorls. Apex and spire moderately elevated, rounded above, last whorl not descending more rapidly, H/D ratio 0.520. Apical whorls 1½, sculpture partly eroded, visible in sutures as prominent, rather widely spaced radial ribs, broadly rounded, with one or two microradials in between and vague traces of microspiral ribbing. Postnuclear whorls with major and microribbing as in diagnosis, body whorl with 37 major ribs. Secondary spiral cording starting distinctly below periphery and stopping well before umbilical margin. Sutures shallow, whorls flatly rounded down to prominent supraperipheral sulcus. Keel threadlike, protruded, lower palatal wall evenly rounded down to obtusely rounded umbilical margin. Ground color leached from shell, lower spire, and body whorl with irregularly broad, dark reddish flammulations that become narrow and zigzagged on shell base. Umbilicus widely open, U-shaped, barely decoiling until last whorl, which decoils much more rapidly, contained 3.64 times in the diameter. Aperture subquadrangular, flatly rounded above and below rostrate periphery, inclined about 15° from shell axis. Apertural barriers as described in "*Diagnosis*" above. Height of holotype 1.46 mm., diameter 2.81 mm.

Holotype. — Loc. 3 (= W410C-6), north branch, south Ekahanui Gulch, Waianae Mountains, Oahu, Hawaiian Islands. FMNH 154483.

Range. — Known only from the type collection.

Paratype. — FMNH 154605.

Material. — Hawaiian Islands: Oahu, Waianae Mountains, north branch, south Ekahanui Gulch (2 specimens, FMNH 154483, FMNH 154605). Additional type lot material is BPBM 125254.

Remarks. — I had not intended to describe any Hawaiian taxa in this study, but naming of this species was necessary in order to avoid overemphasizing the differences between *Cookeconcha* and *Endodonta*. Without *E. ekahanuiensis, Endodonta* would have appeared as being separated in both size (compare tables LXXIV and XCVIII) and ribbing character; with *E. ekahanuiensis* included, the differences are bridged and recognition of *Endodonta* as a specialized offshoot from *Cookeconcha*-type ancestors becomes much easier.

The extent of this species' range on Oahu is unknown. A map showing the exact position of the type locality is given by Welch (1938, p. 105, map 13).

Endodonta binaria (Pfeiffer, 1856)

Helix binaria Pfeiffer, 1856, Proc. Zool. Soc. London, **1856**, p. 33 — Sandwich Islands; Pfeiffer, 1859, Mon. helic. viv., **4**, p. 156; Pfeiffer, 1868, Mon. helic. viv., **5**, p. 222; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 260; Tryon, 1887, Man. Conchol., (2), **3**, p. 61, pl. 11, figs. 87, 88.

Endodonta binaria (Pfeiffer), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474 — Kauai; Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 189; Pilsbry, 1893, Man. Conchol., (2), **9**, p. 25.

Patula (Endodonta) binaria (Pfeiffer), Clessin, 1881, Nomen. Helic. viv., p. 95.

Helix (Endodonta) binaria Pfeiffer, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 — Kauai.

Endodonta (Nesophila) binaria (Pfeiffer), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 289.

Diagnosis. — Shell small, diameter 4.11-4.41 mm. (mean 4.26 mm.), with 5¾-6⅛ normally coiled whorls. Apex and spire moderately and almost evenly elevated, somewhat rounded above, last whorl not descending more rapidly, H/D ratio 0.448-0.459 (mean 0.452). Umbilicus widely open, U-shaped, last whorl decoiling much more rapidly, contained 3.35-3.57 times (mean 3.46) in the diameter. Apical sculpture of major radials and fine microradials and spirals. Postnuclear whorls with thick, prominent radial ribs at first, becoming broadly rounded and somewhat indistinct after first postnuclear whorl, fading into irregular ridges well before start of body whorl, but retained on shell base and in umbilicus as relatively prominent ribs. Microsculpture of fine radial riblets, crossed by spiral riblets that are less than half the size of the radials and much more crowded. Secondary sculpture of several low, rounded spiral cords developed on shell base, but absent from above periphery. Sutures very shallow, whorls flatly rounded down to shallow supraperipheral sulcus. Strongly protruded threadlike keel followed by evenly rounded, compressed lower palatal margin that curves slightly more rapidly to right-angled umbilical shoulder. Walls of umbilicus distinctly flattened. Aperture subquadrangular, flattened laterally above and below rostrate periphery, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper very slender and sharply descending anteriorly, twisted upward and outward posteriorly with a broadly expanded lateral bifid section posteriorly; 2nd equal in size and shape to 1st posteriorly, anterior three-eighths a threadlike trace reaching to margin of upper parietal. Columellar barrier high and bladelike, expanded and serrated above posteriorly, parallel to plane of coiling, extending midway across columellar callus. Palatal barriers 4, extending posteriorly to line of vision, first 3 sub-, 4th supraperipheral, with two accessory traces: all palatals bifid posteriorly, 3rd and 4th lower than first 2, with gradual anterior descension, moderately recessed within aperture. Accessory traces high, threadlike ridges, both between 3rd and 4th palatals, one sub- and the other supraperipheral. Upper parietal and upper palatal nearly touching on elevated portions.

Range. — Kauai, Hawaiian Islands.

Material. — Hawaiian Islands (2 specimens, FMNH 46567 ex Webb, Geret).

Remarks. — Pfeiffer's original description overlooked the palatal barriers, hence Sykes (1900, p. 289) referred *E. binaria* to *Nesophila*. The smaller size and presence of two accessory palatal traces are the main features separating *E. binaria* from the description of *E. apiculata*. Study of the abundant Kauai material in the Bernice P. Bishop Museum will be required to determine their relationships.

In retaining rather widely spaced, low, and rounded major radial ribs on the shell spire and base, *E. binaria* departs from the pattern found in most *Endodonta*. The sculpture is very similar to that found in *Kondoconcha othnius* from Rapa, but the similarities are convergent. The extreme broadening and flattening of the barriers in *E. binaria* also is unusual. Many taxa have bifid parietals, but *E. binaria* is the only species known to date with bifid palatals.

Endodonta apiculata Ancey, 1889

Endodonta apiculata Ancey, 1889, Bull. Soc. Malacol. France, **6**, pp. 188-189 — Kauai, Hawaiian Islands; Pilsbry, 1892, Man. Conchol., (2), **8**, p. 95; Pilsbry, 1893, *op. cit.*, (2), **9**, p. 25; Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 287.

Helix (Endodonta) apiculata (Ancey), Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16.

Range. — Kauai, Hawaiian Islands.

Material. — No specimens examined.

Remarks. — The retention of some radial sculpture on the spire and presence of spiral sculpture on the shell base relate this to *E. binaria,* also described from Kauai. *Endodonta apiculata* differs in being distinctly larger (diameter 6 mm.), having more whorls (6½) and lacking (?) any accessory traces on the palatal wall.

Endodonta rugata (Pease, 1866)

Helix rugata Pease, 1866, Amer. Jour. Conchol., 2, p. 291 — Sandwich Islands; Pfeiffer, 1876, Mon. helic. viv., 7, p. 256; Tryon, 1887, Man. Conchol., (2), 3, p. 67.

Endodonta rugata (Pease), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474 — Maui, Hawaiian Islands; Ancey, 1889, Bull. Soc. Malac. France, **6**, p. 187; Pilsbry, 1893, Man. Conchol., (2), 9, p. 25.

Patula (Endodonta) rugata (Pease), Clessin, 1881, Nomen. helic. viv., p. 96.

Helix (Endodonta) rugata Pease, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16.

Endodonta (Thaumatodon) rugata (Pease), Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 289.

Range. — Maui, Hawaiian Islands.

Material. — None.

Remarks. — The carinated body whorl, wide umbilicus, large size (5 mm. diameter), and presence of secondary spiral sculpture suggest that *E. rugata* is a relative of *E. binaria* and *E. apiculata.*

Endodonta laminata (Pease, 1866)

Helix laminata Pease, 1866, Amer. Jour. Conchol., 2, p. 292 — Sandwich Islands; Pfeiffer, 1876, Mon. helic. viv., 7, p. 255.

Endodonta laminata (Pease), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474 — Kauai, Hawaiian Islands; Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 188; Pilsbry, 1893, Man. Conchol., (2), **9**, p. 25; Sykes, 1900, Fauna Hawaiiensis, Moll., 2, (4), p. 287 — Kahiliwi to Haena, Kauai, Hawaiian Islands; Cockerell, 1925, Nautilus, **38**, (3), p. 83 — Haena Caves, Kauai.

Patula (Endodonta) laminata (Pease), Clessin, 1881, Nomen. helic. viv., p. 96.

Helix (Endodonta) laminata Pease, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 — Kalihawai to Haena, Kauai.

Diagnosis. — Shell slightly larger than average, diameter 6.05-6.55 mm. (mean 6.22 mm.), with 6¼-6½ normally coiled whorls. Apex and spire moderately and evenly elevated, rarely slightly rounded above, last whorl not decoiling more rapidly, H/D ratio 0.377-0.436 (mean 0.411). Umbilicus widely open, U-shaped, regularly decoiling, contained 3.12-3.84 times (mean 3.50) in the diameter. Apical sculpture of low, rather broad, widely spaced radial ribs with typical microsculpture between, continuing onto first postnuclear whorls, fading into indistinct irregularity by antepenultimate whorl, absent from lower spire and body whorl which retains irregular traces of very fine microradial and slightly finer microspiral ribbing. Secondary sculpture of broad, low spiral cords present between subperipheral sulcus and umbilical shoulder. Sutures shallow, whorls flatly rounded down to shallow supraperipheral sulcus. Threadlike keel strongly protruded, followed by very shallow subperipheral sulcus, lower palatal wall flattened, basal margin evenly rounded to obtusely angled umbilical margin. Walls of umbilicus flatly rounded. Aperture subquadrangular, flattened laterally above and below strongly protruded periphery, inclined about 35° from shell axis. Parietal barriers 2, extending posteriorly less than one-quarter whorl: upper very high and thin with sharp anterior descension, twisted outward posteriorly but neither bifid nor strongly expanded; 2nd distinctly lower posteriorly, anterior third threadlike, terminating opposite end of upper parietal. Columellar barrier high and bladelike, weakly expanded above, with gradual anterior descension, extending midway across columellar callus, lying parallel to plane of coiling. Palatal barriers 4, lower extending less than one-eighth whorl posteriorly, with three to six accessory traces: lower 3 high and crescentic, progressively reduced in height, moderately recessed, with sharp anterior descension; 4th supraperipheral, much longer, with more gradual anterior descension, less deeply recessed within aperture. Traces normally between columellar and 1st palatal; 1st and 2nd; with two between 3rd and 4th. Additional traces may be between 2nd and 3rd, above 4th palatal.

Range. — Kahiliwi to Haena, Kauai, Hawaiian Islands.

Material. — Hawaiian Islands: Kauai (6 specimens, FMNH 46455, FMNH 117042).

Remarks. — Ancey (1904, p. 66, pl. 5, figs. 13, 14) reported an unknown species of *Cookeconcha* from Palihoukapapa, Hamakua slope of Mauna Kea, at 4,000 ft. elevation, Hawaii as *Endodonta laminata.* Probably it is a new species.

The widely open, V-shaped umbilicus with roundly shouldered margin, low spire, presence of weak, reduced major radials on the upper spire, and irregularly spaced spiral sculpture on the shell base serve both to identify *E. laminata* and relate it to the other Kauai taxa.

The upper parietal barrier is weakly bifid, and the upper palatal has its tip turned outward toward the periphery. All other barriers are simple crescents. Accessory palatal traces normally are between the columellar and 1st palatal; between 1st and 2nd palatals; above 3rd and below periphery; below 4th and above periphery. Additional traces are sometimes present between 2nd and 3rd palatal or above 4th palatal.

There is a weak supraperipheral sulcus.

Endodonta kamehameha Pilsbry & Vanatta, 1906. Figure 167c-d.

Endodonta kamehameha Pilsbry & Vanatta, 1906, Proc. Acad. Nat. Sci., Philadelphia, 57, pp. 784-785, pl. 43, figs. 3, 4 — Wailau Pali, Mapulehu, Molokai, Hawaiian Islands.

Diagnosis. — Shell large, diameter 6.38-7.30 mm. (mean 6.91 mm.), with 5⅞-6⅜ normally coiled whorls. Apex and spire very slightly and evenly elevated, last whorl decoiling slightly more rapidly, H/D ratio 0.432-0.485 (mean 0.453). Umbilicus open, U-shaped, slightly and regularly decoiling, contained 3.23-3.69 times (mean 3.42) in the diameter. Apical sculpture unknown, postnuclear whorls macroscopically smooth, with only irregular growth striae visible under high magnification. Sutures very shallow, whorls flat down to shallow supraperipheral sulcus. Knife-edge keel sharply protruded, whorls flatly rounded down to obtusely angled umbilical margin. Walls of umbilicus flatly rounded. Aperture subquadrangular, flattened above and below protruded knife-edge periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly three-sixteenths of a whorl: upper a high, thin blade, weakly expanded above on posterior half, descending abruptly to anterior third that is a low ridge; 2nd a broad, low, rounded ridge posteriorly, anterior half to five-eighths threadlike, terminating opposite end of upper parietal. Columellar barrier low and bladelike, weakly elevated above, lying parallel to plane of coiling, with gradual anterior descension to middle of columellar callus. Palatal barriers normally 4, supraperipheral often absent, rest relatively low and short, extending posteriorly about one-eighth whorl: lower 3 subperipheral, moderately recessed, low ridges not or weakly expanded above, 1st slightly smaller than 2nd and 3rd; 4th supraperipheral, when present, a very low ridge to threadlike trace, longer than lower palatals and not so deeply recessed.

Range. — Molokai, Hawaiian Islands.

Material. — Hawaiian Islands: Molokai, Wailau (3 specimens, FMNH 73198), Kamalo (1 specimen, FMNH 90629).

Remarks. — The widely open, narrowly U-shaped, regularly decoiling umbilicus, colorless shell, and great size reduction of all apertural barriers, with the upper parietal being a simple lamella rather than bifid, easily separate *Endodonta kamehameha* from the other described species.

There is no major radial sculpture, a barely perceptible supraperipheral sulcus and the umbilical walls are flat sided, but the umbilical margin is less sharply angled than in the Oahu species.

All other described *Endodonta* have the upper parietal bifid. I suspect its simplicity in *E. kamehameha* is correlated with the secondary size reduction of all apertural barriers. One specimen had the upper palatal absent.

Endodonta concentrata Pilsbry & Vanatta, 1906. Figure 167e-f.

Endodonta concentrata Pilsbry & Vanatta, 1906, Proc. Acad. Nat. Sci., Philadelphia, **57**, p. 785, pl. 43, figs. 5, 6 — Lanai, Hawaiian Islands.

Diagnosis. — Shell rather small, diameter 4.70-5.43 mm. (mean 5.06 mm.), with 5-5½ normally coiled whorls. Apex and spire moderately and evenly elevated, slightly rounded above, last whorl descending a little more rapidly, H/D ratio 0.458-0.487 (mean 0.471). Umbilicus rather narrow, U-shaped, early whorls barely decoiling, penultimate whorl narrowing slightly, body whorl decoiling a little more rapidly, contained 4.43-5.50 times (mean 4.90) in the diameter. Apical whorls and postnuclear whorls macroscopically smooth, lower spire with irregular growth wrinkles and occasional vague indications of a microreticulation visible under 96× magnification. Sutures not indented, whorls flat down to protruded knife-edge keel, compressed and flatly rounded to basal margin, then more sharply rounded to obtusely angled umbilical margin. Sides of umbilicus flattened. Aperture subquadrangular, flattened laterally above and below acutely angled periphery, inclined almost 45° from shell axis. Parietal barriers 2, extending posteriorly one-quarter whorl: upper very high and thin anteriorly with sharp descension, becoming broadly bifid and serrated above posteriorly; 2nd slightly lower, broadly expanded but not bifid posteriorly and gradually descending from middle to anterior end, which is even with termination of upper parietal. Columellar barrier high, broadly expanded and serrated above posteriorly, lying parallel to plane of coiling, sharply descending anteriorly to lip margin. Palatal barriers 4, extending three-sixteenths of a whorl posteriorly, with or without a single large recessed accessory subperipheral trace located above 3rd palatal: lower 3 coequal in height, broadly expanded above, subperipheral, with progressively more gradual anterior descension and deeper recession; 4th supraperipheral, lower, longer, with very gradual anterior descension, moderately expanded above. Palatal trace, when present, about one-third height and length of major barriers, only weakly expanded above.

Range. — Lanai, Hawaiian Islands.

Material. — Hawaiian Islands: Lanai (3 specimens, FMNH 73192, FMNH 90627), Lanaikale (4 specimens, FMNH 46613).

Remarks. — As in *Endodonta marsupialis,* the comparatively high spire and narrow umbilicus of *E. concentrata* are correlated and related to formation of a "brood chamber." In *E. concentrata,* however, there is little or no indication of actual umbilical narrowing and no trace of the sinus extension that characterizes *E. marsupialis.* The umbilical narrowing in *E. concentrata* has been achieved by a tightening of coiling and thus a cessation of widening from the third whorl. In form, the umbilicus is a perfect U-shaped, with sharply rounded margins.

The low mean whorl count, more than a half whorl less than in any other *Endodonta,* and small size combine with the above two characters to identify this species.

The apertural barriers are typical, with the upper parietal distinctly bifid, but the remaining barriers simple. The accessory palatal trace, which may be present or absent, is always between the 3rd palatal and the periphery.

There is no trace of major radial postnuclear sculpture and no supraperipheral sulcus.

Endodonta lamellosa (Ferussac, 1824). Figure 165a-b.

Helix (Helicodonta) lamellosa Ferussac, 1821, Tab. Syst. Animales Moll., Part **2**, p. 34 — Islands of South Seas (*nomen nudum*); Ferussac, *in* Quoy & Gaimard, 1824, Voy. "Uranie"... Freycinet, Zool., p. 469; Ferussac, 1832, Hist. Nat. Moll. terr. fluv., **3**, pl. 51a, fig. 3.

Helix lamellosa Ferussac, Pfeiffer, 1848, Mon. helic. viv., **1**, pp. 184-185 (partly) — Wahoo (= Oahu, Hawaiian Islands); Deshayes, 1851, Hist. Nat. Moll. terr. fluv., **1**, p. 369 (French not Latin description) — Sandwich Islands; Pfeiffer, 1853, Mon. helic. viv., **3**, p. 142 (partly); Reeve, 1854, Conchol., Icon., ***Helix***, pl. 111, fig. 630 — Sandwich Islands; Pfeiffer, 1859, Mon. Helic. viv., **4**, p. 154; Pfeiffer, 1868, Mon. helic. viv., **5**, p. 219; Pease, 1871, Jour. de Conchyl., **19**, p. 96 (partly) — Oahu, Hawaiian Islands; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 255.

Endodonta lamellosa (Ferussac), Albers, 1850, Die Heliceen, p. 89; Mörch, 1865, Jour. de Conchyl., **13**, pp. 395-396; Pease, 1871, Proc. Zool. Soc., London, **1871**, p. 474 — Oahu (partly); Ancey, 1889, Bull. Soc. Malacol. France, **6**, p. 186 (partly); Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 287 — Konahuanui, Oahu (partly); Cooke, 1928, Bull. B. P. Bishop Museum, **47**, pp. 14-21, figs. 3, 4, 5 (anatomy).

Pitys lamellosa H. & A. Adams, 1858, Genera Recent Moll., **2**, p. 113 and **3**, p. 71, fig. 5.

Patula (Endodonta) lamellosa Clessin, 1881, Nomen. helic. viv., p. 96 (partly).

Helix (Endodonta) lamellosa Ferussac, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16 — Waianae Mts. (error) and Konahuanui, Oahu, Hawaiian Islands.

Diagnosis. — Shell distinctly larger than average, diameter 5.86-7.37 mm. (mean 6.61 mm.), with 5⅜-6⅝ normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl not descending more rapidly, H/D ratio 0.402-0.472 (mean 0.439). Umbilicus rather narrow, U-shaped, barely decoiling at first, slightly narrowed at penultimate whorl, last whorl decoiling rather rapidly, contained 3.18-5.10 times (mean 4.21) in the diameter. Apical and postnuclear

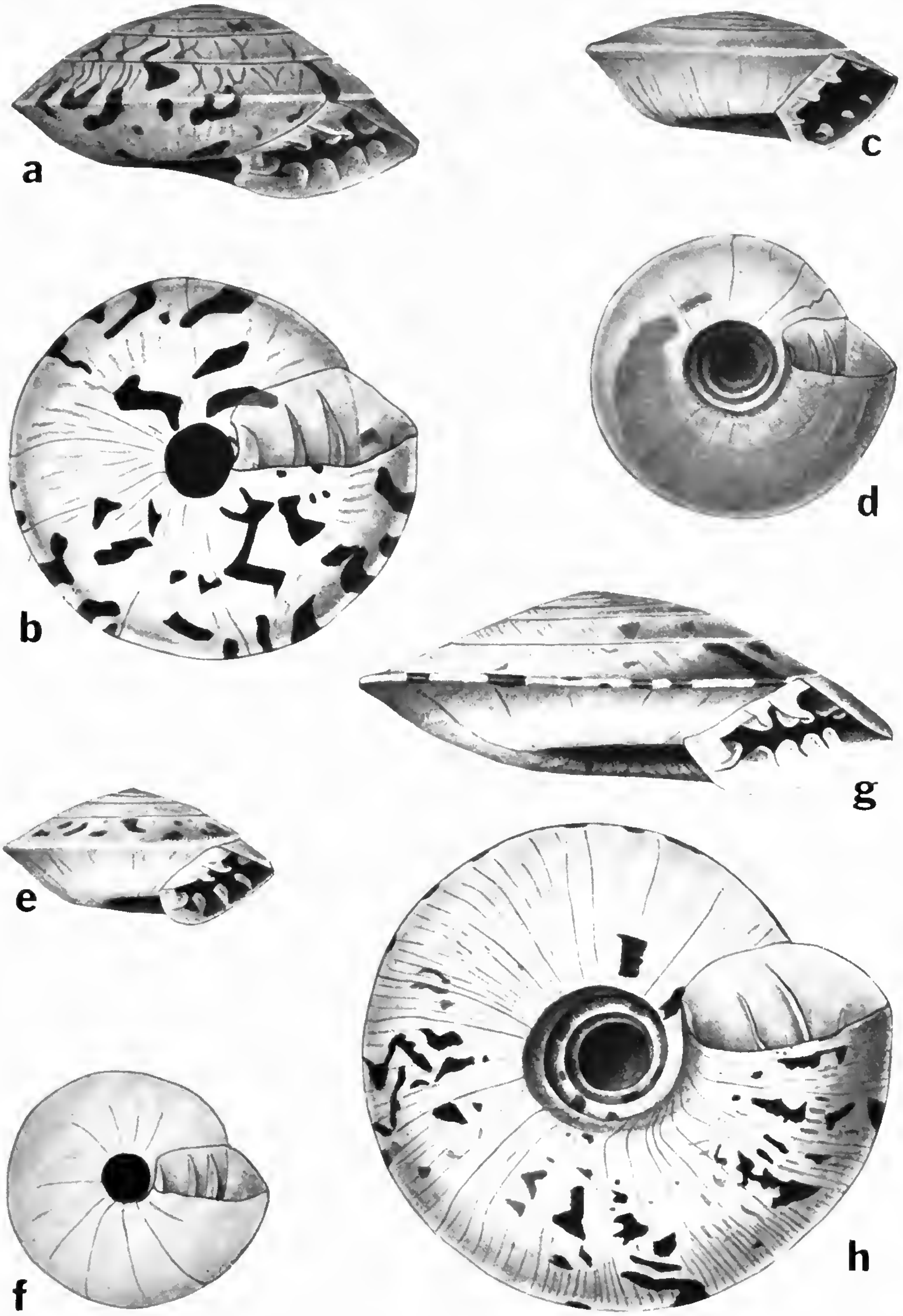

FIG. 167. **a-b**, *Endodonta marsupialis* Pilsbry & Vanatta. Oahu, Hawaiian Islands. Holotype. ANSP 58190; **c-d**, *Endodonta kamehameha* Pilsbry & Vanatta. Wailau Pali, Mapulehu, Molokai. Hawaiian Islands. Holotype. ANSP 90140; **e-f**, *Endodonta concentrata* Pilsbry & Vanatta. Lanai, Hawaiian Islands. Holotype. ANSP 89241; **g-h**, *Endodonta fricki* (Pfeiffer). "Kauai" (error for Waianae Mts., Oahu), Hawaiian Islands. ANSP. Copied from Pilsbry and Vanatta (1906, pl. 43) with permission of the Academy of Natural Sciences, Philadelphia. Relabelled for this use.

whorls macroscopically smooth, rarely with faint traces of microreticulations, often with faint and irregular growth lines. Sutures shallow, whorls flatly rounded down to moderate supraperipheral sulcus. Keel threadlike, strongly protruded, a shallower subperipheral sulcus, lower palatal wall compressed, evenly rounded down to right angled umbilical margin. Walls of umbilicus flat to slightly concave, last two whorls with a distinct keel. Aperture subquadrangular, flattened above, evenly rounded below strongly protruded threadlike keel, inclined about 35° from shell axis. Parietal barriers 2, extending posteriorly about three-sixteenths of a whorl: upper with sharp anterior descension, high and thin, twisted upwards and much elevated posteriorly with a broadly expanded and serrated bifid lateral extension on posterior half; 2nd with posterior third elevated, about two-thirds height of upper, moderately expanded above, anterior half threadlike, recessed or terminating opposite end of upper parietal. Columellar barrier high and bladelike, moderately expanded above posteriorly, with gradual anterior descension midway across callus, lying parallel to plane of coiling. Palatal barriers 5, extending posteriorly one-eighth whorl, almost always with two accessory traces: lower palatal high, weakly expanded above, only slightly recessed, with gradual anterior descension; 2nd, 3rd, and 4th progressively reduced in height, more deeply recessed, with more gradual anterior descension; 5th supraperipheral, equal in height to 4th posteriorly, much longer, with very gradual anterior descension, less deeply recessed within aperture. Accessory traces, small, crescentic, rather deeply recessed, situated between 4th and 5th palatals, one sub-, the other supraperipheral.

Range. — Mt. Konahuanui and Mt. Puu Kahuauli, Koolau Mts., Oahu, Hawaiian Islands.

Material. — Hawaiian Islands: Oahu (15 specimens, FMNH 73199, FMNH 91143, FMNH 91839, FMNH 154481), Mt. Konahuanui (4 specimens, FMNH 46275).

Remarks. — The identification of *Helix lamellosa* Ferussac, 1824 by Cooke (1928, pp. 14-19) is an elegant example of historical and biological investigation. The somewhat more detailed synonymy given above was possible only because of Cooke's efforts.

A more open umbilicus that markedly decoils on the last whorl, lower whorl count, smaller size, and distinctly lower spire easily separate *E. lamellosa* from the other Koolau species, *E. marsupialis*. *E. fricki* from the Waianae Range is much larger (mean diameter 8.99 mm.), with a lower spire, more widely open umbilicus, has only 4 major palatal barriers, and averages one-half whorl more than *E. lamellosa* (table XCVIII).

As in all the large Oahu species, *E. lamellosa* has no postnuclear major radial sculpture, the sides of the U-shaped umbilicus are flat and the umbilical margin sharply angled. The marked umbilical decoiling of the last whorl is shared with *E. fricki* (fig. 167h), but is not duplicated by any other Hawaiian species that has been named. There is no supraperipheral sulcus.

The upper parietal barrier is bifid, but the others are neither expanded nor twisted. Cooke (1928, p. 17) summarized barrier variation in 97 specimens from Mt. Konahuanui. One example had a 2nd columellar. All specimens had 5 major palatals, 4 subperipheral (= basal in Cooke's terminology), and 1 supraperipheral (erroneously referred to as "upper parietal" by Cooke, an obvious *lapsus calami*). All specimens had the supraperipheral accessory trace present and 75.8 per cent (72 of 95) had the subperipheral accessory trace present. The parietals extend less than three-sixteenths of a whorl, the palatals less than one-eighth whorl.

My dissections agree with those of Cooke (*loc. cit.*). The penis is much shorter than in either *E. fricki* or *E. marsupialis*, although variable in length. Cooke (1928, p. 19) measured three penes as 4.4, 5.3, and 6.1 mm. long, a normal range of variation within the family. My examples were 4.5-5.6 mm. long. No complete specimens were available to me and the attached anatomical description is based upon fragmentary examples.

Obvious differences from *E. fricki* involve the prostate with its much greater number of acini and the smaller penis with proportionately much larger pilasters.

Description of soft parts. — Foot and tail as in *E. fricki*, relatively short. Sole undivided. Pedal grooves typical, no caudal horn or middorsal groove. Slime network inconspicuous. Head projecting slightly in front of foot. Ommatophores with black eyespot. Gonopore as in *E. fricki.*

Body color yellow-white, without darker markings.

Mantle collar and glandular extension as in *E. fricki.*

Pallial region with anterior portion as in *E. fricki*, no specimens with basal portions seen. Lung roof clear, no granulations. Hindgut typical.

Ovotestis and hermaphroditic duct not seen. Albumen gland (fig. 165a) very small compared to prostate. Talon not seen. Prostate (DG) of several rows large acini opening into a small tube appressed to surface of uterus, individual acini and rows much more numerous than in *E. fricki.* Uterus (UT) bipartite, better preserved specimens with faint indications of accessory glandular patches seen in *Thaumatodon*, extending below base of prostate.

Vas deferens (VD) typical, recurved at penioviducal angle, entering penis laterally, about 0.67-1.0 mm. below apex, underneath edge of one pilaster. Penial retractor (PR) arising from columellar muscle just above origin of buccal retractor, inserting onto unexpanded head of penis. Penis (P) tapered anteriorly, rather broadly expanded just below apex, about 4.5-5.6 mm. long, very narrow at junction with atrium. Penis internally with two large, rather high and broad pilasters that unite apically (fig. 165b), taper abruptly in midsection down to atrium, one becoming weakly split in midsection, the other with a thick, lateral upward extension. Atrium (Y) up to 1 mm. long, much longer than in most Polynesian genera.

Free oviduct (UV) elongated, simple, equal in length to uterus. Spermatheca (S) with head appressed to base of albumen gland, shaft inserting just on oviducal side of penioviducal angle. Vagina (V) very short, almost absent in some examples.

Free muscle system as in *E. fricki.*

Anterior parts of digestive system as in *E. fricki.*

Jaw of narrow, partly fused, indistinct lamellar plates.

Radula with more than 88 rows, central tooth about 13μ square, 6 laterals with 12-14 marginals.

(Based on BPBM 16556, seven fragmentary examples.)

Endodonta marsupialis Pilsbry & Vanatta, 1906. Figure 167a-b.

Helix lamellosa Pfeiffer, 1845 (not Ferussac, 1824), Zeit. Malak., **2**, p. 85; Pfeiffer, 1848, Mon. helic. viv., 1, pp. 184-185 (partly); Deshayes, 1851, Hist. Nat. Moll. terr. fluv., **1**, p. 369 (Latin description) — Sandwich Islands; Pfeiffer, 1852, Syst. Conchyl. Cab., *Helix*, 1, **12**, (2), pp. 197-198, pl. 100, figs. 6-9 — Oahu (plate published in 1850); von Martens, 1860, Die Heliceen, p. 90; Tryon, 1887, Man. Conchol., (2),**3**, p. 67, pl. 12, figs. 32-34.

Patula (Endodonta) lamellosa Clessin, 1881 (not Ferussac, 1824), Nomen. Helic. viv., p. 96 — Oahu (partly).

Endodonta lamellosa Ancey, 1889 (not Ferussac, 1824), Bull. Soc. Malacol. France, **6**, p. 186 — Oahu (partly); Pilsbry, 1893, Man. Conchol., (2), **9**, p. 25; Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 287 (partly).

Endodonta marsupialis Pilsbry & Vanatta, 1906, Proc. Acad. Nat. Sci., Philadelphia, **57**, p. 784, pl. 43, figs. 1, 2 — Oahu, Hawaiian Islands; Cooke, 1928, Bull. B. P. Bishop Museum, **47**, pp. 21-24, fig. 6 (anatomy) — west slope of Mt. Tantalus, above Pauoa Valley, Oahu, Hawaiian Islands.

Diagnosis. — Shell large, diameter 6.64-7.76 mm. (mean 7.20 mm.), with 6¼ - 6½+ rather tightly coiled whorls. Apex and spire markedly elevated, rounded above, last whorl not descending more rapidly, H/D ratio 0.475-0.485 (mean 0.480). Umbilicus secondarily narrowed to form brood chamber, early whorls U-shaped, not decoiling, narrowed by a combination of tighter coiling and inward columellar-umbilical margin extension during last two whorls, contained 4.59-5.62 times (mean 5.11) in the diameter. Apical and postnuclear whorls macroscopically smooth, rarely with a faint trace of microribbing and often with irregular growth wrinkles. Sutures weakly indented, whorls flatly rounded down to shallow supraperipheral sulcus. Threadlike keel strongly protruded, lower palatal margin flat or gently rounded after very shallow subperipheral sulcus, baso-umbilical margin acutely angled with distinct keel. Walls of umbilicus flattened. Aperture subquadrangular, flattened above, weakly rounded below protruded threadlike keel, inclined about 35° from shell axis. Parietal barriers 2, extending posteriorly slightly less than one-quarter whorl: upper quite high and very slender with rather sharp anterior descension, main arm not expanded, twisting upward posteriorly with a broad, moderately expanded lateral bifid portion posteriorly; 2nd distinctly lower, moderately expanded and serrated posteriorly, with gradual descension to anterior threadlike third that terminates opposite end of upper parietal. Columellar barrier high and bladelike, weakly expanded above posteriorly, slightly twisted downwards from plane of coiling, with gradual anterior descension almost to lip edge. Palatal barriers 5, extending posteriorly a little more than one-eighth whorl, with (59.3 per cent) or without (40.7 per cent) a supraperipheral trace, only rarely (2.3 per cent) with a subperipheral trace: first 3 palatals high, bladelike, moderately recessed, coequal in height, with progressively more gradual anterior descension; 4th subperipheral, reduced in height and length, identical to 3rd in shape; 5th supraperipheral, posterior expanded portion equal in height to 3rd, with very gradual anterior descension to threadlike portion, much less recessed anteriorly.

Range. — Known only from Mount Tantalus, directly above Pauoa Valley, Koolau Mountains, Oahu, Hawaiian Islands.

Material. — Hawaiian Islands: Oahu, Mount Tantalus, above Pauoa Valley (2 specimens, FMNH 116902).

Remarks. — The relatively high spire, narrow umbilicus with the last two whorls developing a basal sinus that narrows the umbilicus, and large size easily separate *E. marsupialis* from *E. lamellosa.*

Major radial sculpture is absent and there is only a weak supraperipheral sulcus. As usual, the upper parietal is bifid, but the other barriers are simple. Of the 86 specimens examined by Cooke (1928, p. 22), 59.3 per cent had one supraperipheral trace and 40.7 per cent lacked a supraperipheral trace. Only 2 of 86 examples (2.3 per cent) had a subperipheral trace. As in *E. lamellosa*, all individuals had 5 major palatals.

Umbilical narrowing to form a brood chamber is accomplished differently than in *Libera, Gambiodonta,* or *Pseudolibera* (see pp. 28, 384, 431, respectively). Two whorls before the aperture, the basocolumellar margin starts to grow inward, forming a distinct sinus (fig. 167a). The upper parietal margin does not follow the inwardly extended sinus of the preceeding whorl (as it does in *Libera*), giving an "overlapping" effect to last whorl growth. The extent of this narrowing is comparatively minor, since the early whorls do not decoil nearly to the extent seen in *Libera* or *Gambiodonta.*

Cooke (1928, pp. 22-23) indicated that *E. marsupialis* was characterized by having the oviduct and penis "distinctly twisted or kinked" and "folded two or three times." These differences are artifacts produced through partial contraction of the animal into the shell and should be given no systematic weight. Size differences in the albumen gland and spermatheca may be seasonal. There is an important difference in penial length. Three dissected individuals of *E. marsupialis* had penes 12.0, 14.0, and 15.0 mm. long. The insertion of the vas deferens into the penis was proportionately lower down than in either *E. lamellosa* or *E. fricki.* No material was dissected during this study.

Endodonta fricki (Pfeiffer, 1858). Figures 163; 164; 167g-h.

Helix fricki Pfeiffer, 1858, Proc. Zool. Soc., London, **1858**, pp. 21-22 — Sandwich Islands; Pfeiffer, 1859, Malak. Blatt., **6**, p. 11 — Sandwich Islands; Pfeiffer, 1868, Mon helic. viv., **5**, p. 219; Pfeiffer, 1876, Mon. helic. viv., **7**, p. 255; Tryon, 1887, Man. Conchol., (2), **3**, p. 67, pl. 12, figs. 35, 36.

Helix lamellosa Pease, 1871 (not Ferussac, 1824), Jour. de Conchyl., **19**, p. 96 (partly) — Oahu, Hawaiian Islands.

Endodonta lamellosa Pease, 1871 (not Ferussac, 1824), Proc. Zool. Soc., London, **1871**, p. 474 — Oahu (partly); Pilsbry, 1893, Man. Conchol., (2), **9**, p. 25, pl. 4, figs. 40 and 41; Sykes, 1900, Fauna Hawaiiensis, Moll., **2**, (4), p. 287 (partly) — Waianae Mts., Oahu; Pilsbry & Vanatta, 1905, Proc. Acad. Nat. Sci., Philadelphia, **57**, pp. 783-784, pl. 43, figs. 7, 8 (partly).

Endodonta fricki (Pfeiffer), Ancey, 1889, Bull. Soc. Malacol. France, **6**, pp. 186-187; Pilsbry, 1893, Man. Conchol., (2), **9**, p. 25; Cooke, 1928, Bull. B. P. Bishop Museum, **47**, pp. 24-27, fig. 7 (anatomy).

Helix (Endodonta) fricki Pfeiffer, Baldwin, 1893, Catalogue Land and Fresh Water Shells, p. 16.

Diagnosis. — Shell very large, diameter 8.03-10.1 mm. (mean 8.99 mm.), with 6-7 rather loosely coiled whorls. Apex almost flat, spire slightly elevated, last whorl not descending more rapidly, H/D ratio 0.329-0.476 (mean 0.407). Umbilicus rather widely open, U-shaped, last whorl or whorl and a half decoiling rapidly, contained 3.17-4.17 times (mean 3.66) in the diameter. Apex smooth, postnuclear whorls without visible microsculpture, growth wrinkles relatively regularly spaced. Sutures not indented, whorls flat down to shallow supraperipheral sulcus. Knife-edge keel moderately protruded, lower palatal and basal margins evenly and flatly rounded to almost right-angled umbilical margin, which may be slightly keeled. Walls of umbilicus flat. Aperture subquadrangular, flattened above and below slightly protruded knife-edge periphery, inclined about 40° from shell axis. Parietal barriers 2, extending posteriorly three-sixteenths of a whorl: upper a high slender blade with gradual descension from the middle, posteriorly twisted upwards with a short, broadly expanded lateral bifid portion on posterior third; 2nd distinctly lower, anterior third threadlike, posterior portion often distinctly bifid, but never as strongly as 1st parietal. Columellar barrier a high lamella, lying parallel to plane of coiling, with gradual anterior descension midway across columellar callus. Palatal barriers 4, extending posteriorly slightly more than one-eighth whorl, usually with two, but sometimes with one or three accessory traces: lower 3 subperipheral, high, moderately to deeply recessed, with progressively more gradual anterior descension, 1st lower than 2nd and 3rd; 4th supraperipheral, posterior elevated portion hooked outward, with very gradual anterior descension, much longer and less deeply recessed. Palatal traces normally between 3rd and 4th, a larger subperipheral and a smaller supraperipheral, occasionally with a second subperipheral trace present.

Description. — Shell very large, with 6¾ normally coiled whorls. Apex and spire moderately elevated, rounded above, last three-quarters of body whorl deflected slightly below periphery, H/D ratio 0.443. Apical whorls 1½, sculpture eroded. Remaining whorls with low, irregular, protractively sinuated growth wrinkles, without major ribbing or microsculpture. Sutures very shallow, whorls flat with a slight supraperipheral sulcus, somewhat flattened on base of whorl. Periphery acutely keeled, very slightly protruding into a carina, becoming more rounded near aperture. Color light yellow-white with irregular reddish-brown flecks and small maculations. Umbilicus U-shaped, barely decoiling, contained 3.48 times in the diameter, whorls flattened internally with moderately indented sutures, outer margin of umbilicus somewhat shouldered. Aperture subquadrangular, flat above periphery, somewhat flattened directly below with strongly rounded basal margin, inclined about 30° from shell axis. Parietal barriers 2: upper slightly more than one-eighth whorl, narrow, strongly elevated, with sharp anterior descension, becoming broadly expanded and sinuately twisted upward posteriorly with a lateral lower bifid extension on posterior third; lower parietal moderately recessed within aperture, simple and crescentic, slightly lower than the upper and only weakly expanded above. Columellar barrier located at basal margin, a high, V-shaped ridge with gradual anterior descension, slanting across heavy columellar callus almost to lip edge. Palatal barriers 4, with two accessory traces: lower 3 palatals moderately elevated, short, crescentic, progressively further recessed within aperture, gradually decreasing in size with 3rd flattened above; 4th palatal elongated, only moderately recessed, with narrow, high, V-shaped anterior portion, posterior half becoming twisted laterally toward the periphery at a 90° angle, extending more than one-eighth whorl. Accessory traces located between 3rd and 4th palatals, lower subperipheral, a very short, low ridgelike knob situated just below peripheral margin and deeply recessed within aperture; upper palatal trace even lower, with more gradual anterior descension, equally recessed, situated just above periphery. Columellar wall and most of outer palatal wall with a heavy callus gradually decreasing in prominence. Height of lectotype 3.33 mm., diameter 7.52 mm.

Lectotype. — Hawaiian Islands. BMNH 1962716/1, ex Hugh Cuming collection.

Range. — Widely distributed in Waianae Mts., Oahu, Hawaiian Islands.

Paratype. — BMNH 1962716/2.

Material. — Hawaiian Islands (4 specimens, BMNH 1962716/2, FMNH 81972): Oahu (2 specimens, FMNH 154482), Kawaiiloa Valley (6 specimens, FMNH 53041); Makalea (24 specimens, FMNH 53042, FMNH 111526); Puu Paua (1 specimen, FMNH 90621); Nanakuli Valley (2 specimens, BPBM 127996); Lualualei, Halona, below Pohakea Pass (5 specimens, BPBM 128063).

Remarks. — The very large size, relatively low spire, outward extension of the upper palatal, and presence of only 4 major palatals are diagnostic. The outward deflection of the upper palatal is shared with *E. laminata* and not found in any other described species.

Major radial sculpture is absent from the postnuclear whorls and there is only a weak supraperipheral sulcus. Umbilical decoiling is marked on the last whorl, with the earlier whorls flatsided and barely decoiling to perfectly U-shaped. The umbilical margin is sharply angled. Cooke (1928, p. 25) demonstrated significant interpopulational differences in umbilical width (and probably rate of decoiling). The close similarity of umbilical width in measured material used for this study (table XCVIII) should not mislead future workers.

The apertural barriers differ from the other Oahu species in having only 4 major palatals, with the top of the upper deflected outwards. The upper parietal is markedly bifid and often the lower weakly bifid. Number and position of palatal traces seems to be variable. In 40 specimens I examined, 35 had two traces, one just above and the other just below the periphery; three had only the single supraperipheral trace; and two had a third trace present below the periphery in addition to the normal two. In colonies studied by Cooke (*loc. cit.*), the percentage with two subperipheral traces ranged from 18-41 per cent.

Material dissected by Cooke (1928, pp. 25-26) from Lualualei, Halona, below Pohakea Pass, Waianae Mountains (BPBM 128063) also was used in this study. Since only partial specimens of *E. lamellosa* were available, detailed studies were made of *E. fricki* (figs. 163, 164) to fix the name Endodontidae. Differences from *E. lamellosa* are discussed under that species.

Differences between the three dissected species of *Endodonta* have been discussed above. Of general interest was the presence of three eggs fastened inside the umbilicus of one dissected example. Flatly ovoid, the eggs were 0.79-0.82 mm. in length, 0.59-0.64 mm. in greater diameter, and 0.49-0.54 mm. in lesser diameter. Apparently, they were cemented in by a mucoid secretion (turned white and flaky in the preservative). All were partially coated with grains of red dirt. None of the eggs contained a formed shell, although in one embryo the foot could be distinguished.

Description of soft parts. — Foot long and slender (fig. 163a), not tapering posteriorly, bluntly rounded behind, truncated anteriorly with head projecting slightly in front of foot. Pedal grooves rather low on foot, suprapedal much weaker than pedal, both grooves uniting over tail. Sole undivided longitudinally, smooth, without transverse corrugations. Tail without middorsal groove, caudal foss or caudal horn, bell-shaped in cross-section. Slime network very finely textured, rectangular, more prominent on tail than head region. Ommatophores very long. Gonopore a short slit located below right ommatophore, above and slightly behind right rhinophore.

Color in preservative very light yellow-white, no darker markings. Tip of ommatophores black, muscular portion brownish.

Mantle collar (MC, fig. 163b) short, thick, with bluntly rounded anterior edge. Pneumostome in parietal-palatal angle, masked by thickened edges of mantle collar, but without development of distinct lobes. Anus and pneumostome share common opening. Anus (A) opening just inside mantle collar with a distinct groove continuing through mantle collar in pneumostomal opening. Mantle glands (MG) extending very far onto lung roof. Entire area of mantle collar and mantle glands strongly indented by apertural lamellae in preserved material.

Pallial cavity (fig. 163e) extending apically for about one whorl, very narrow. Lung roof clear, without any traces of color patches or speckling. Kidney (K) slightly more than one-quarter length of pallial cavity, slender, with its base abutting on loop of intestine and reaching up to hindgut on upper margin. Ureter (KD) sigmurethrous, incomplete, opening at anterior edge of rectal kidney arm, without any groove to pneumostomal area. Heart (H) fairly large, angled in relation to hindgut, less than half length of kidney. Principal pulmonary vein (HV) long, unbranched until nearly reaching mantle glands, which are liberally supplied with venation.

Ovotestis (G, figs. 163c; 164a) composed of palmately clavate alveoli in numerous clumps strung along single collecting tubule, imbedded in digestive gland (Z) above intestine-stomach apical margin, but stopping far short of soft part apex (fig. 163c). Hermaphroditic duct (GD) exceedingly slender and thin in region of ovotestis, becoming a slim muscular tube just below stomach apex. Near lower margin of stomach, hermaphroditic duct enlarges greatly, runs past base of stomach to middle of albumen gland (GG), narrows abruptly, then reflexes inward to albumen gland, joining shaft of talon (GT). Albumen gland finely textured, elongated, lying above pallial cavity, with head of spermatheca pressed into outer side. Talon (fig. 164b) with slender duct and moderately expanded, tapering head, opening directly into prostate-uterus. Just before joining talon, last part of hermaphroditic duct weakly iridescent. Prostate (DG) rather short, composed of comparatively few large acini entering a separate very slender tube partly masked by walls of uterus (fig. 164d), with shaft of spermatheca (S) lying along upper prostate-uterus margin for lower two-thirds of length, crossing during apical third to top of prostate with head of spermatheca starting its expansion at upper end. Top of prostate large, partly enfolding uterine section, base of prostate narrow, partly enfolded in lower uterine chambers. Uterus (UT) bipartite: upper section (UT_1, fig. 164a) a very thin tube occupying more than half the length; lower chamber (UT_2) rather broadly expanded, weakly pustulose internally, opening into free oviduct (UV).

Vas deferens (VD) continuing from tube of prostate, equal in width to spermathecal shaft, lightly bound to penioviducal angle and rather firmly anchored to penis (P). No differentiated epiphallus. Vas deferens entering (DP, fig. 164a, c) laterally, slightly below apex of penis (P), just to one side of a large pilaster (PP). Penis very long, extending well into visceral hump, cylindrical, with thin smooth muscular walls. Internally (fig. 164c) with two sets of longitudinal pilasters (PP), smoothly muscular and split apically, uniting where penial retractor (PR) inserts, becoming single about one-quarter of way down, running parallel to near base where they unite. Edges of pilasters free and slightly extended upward. Below junction of pilasters is a weak constriction of the wall, followed by entrance to atrium (Y). Latter a distinctly separate, but short tube. Walls of penis and atrium with very weak glandular pustulations.

Free oviduct (UV), very long, thin-walled, much broader than vas deferens apically, tapering basally. Spermatheca (S) long, stalk a thin tube, lying along free oviduct and prostate, expanded head lying above pallial cavity, imbedded in albumen gland and head of prostate. Vagina (V) scarcely separable from atrium. Walls of free oviduct, spermatheca and vagina with a few longitudinal pilasters.

Buccal mass (fig. 164e) elongated, not elevated posteriorly, with very small generative sac. Buccal retractor attaching in U-shaped fan slightly behind midpoint of buccal mass, not split. Esophagus (E) entering buccal mass at midpoint of upper surface, a slender but solid tube with longitudinal pilasters, extending past apex of pallial cavity along inner margin. Just past apex of pallial cavity (fig. 164f), esophagus expands rather rapidly to form stomach (IZ). For first section above pallial cavity, hindgut follows parietal-palatal margin with stomach occupying parietal wall. A slender strip of digestive gland separates stomach and hindgut. Latter angles gradually outward onto palatal wall. About one-quarter whorl past pallial cavity, stomach reaches parietal-palatal margin, thus occupying entire parietal and palatal walls, intestine, digestive gland and hermaphroditic duct being restricted to basal-umbilical walls. Total apical extension of stomach one whorl. About one-eighth whorl from apex of stomach, it narrows slightly, then tapers and loops downward to a sharply constricted stomach-intestine junction (fig. 164f). Stomach walls very thin, junction point and recurved section thicker. First part of intestine (I) following basal-columellar margin forward to base of kidney, then looping upward along outer margin to just below hindgut (HG), turning apically and downward to just above initial intestinal part, then looping upward just below parietal-palatal margin and running forward as hindgut. Latter soon reaching parietal-palatal margin and continuing forward to anus (A).

Salivary glands (OG, fig. 164e) white, flanking esophagus and touching but not united above. Ducts (OGD) of salivary gland straight, passing into buccal mass at sides of esophagus.

Digestive gland extending from apex of soft parts to pallial cavity, much darker in color than ovotestis, consisting of narrow fingerlike lobes in region of stomach and intestinal looping.

Free muscle system simple and elongated. Right ommatophoral retractor passing between penioviducal angle. Right rhinophoral retractor passing outside penioviducal angle, uniting with ommatophoral retractor about one-quarter whorl into visceral hump. Left ommatophoral and rhinophoral retractors uniting in same area. Both tentacular retractors merge laterally with tail fan about midway from tip of insertion of tail fan on foot to apex of columellar retractor. Buccal retractors split well behind buccal mass, inserting in U-shaped fan (fig. 164e) less than one-quarter of distance from posterior margin of buccal mass; very slender posteriorly and merging with columellar retractor just above apex of pallial cavity. Tail fan fragmented into many strands radiating to sides of foot and base of visceral hump. Penial retractor (PR, fig. 164a) long, stout, merging with columellar retractor slightly above point of origin for buccal retractor. Apex of columellar retractor situated about one-half whorl above apex of pallial cavity.

Jaw of very fine, narrow, partly fused lamellar plates.

Radula only mounted in fragments. Central tooth about 11μ wide and 13μ long, usually with 6 laterals and 18-19 marginals.

(Based on BPBM 128063, five adult individuals.)

Genus **Pseudolibera**, new genus

Large Endodontidae in which the umbilicus is modified to form a brood chamber by inward growth of the last 1½ whorls. Apical sculpture consisting of prominent, rather narrow radial ribs, interspersed with finer riblets. Postnuclear sculpture of prominent, rounded, somewhat protractively sinuated radial ribs, too worn for counting in the only adult specimen, that are reduced on shell base. Strong secondary spiral cording visible on base of adult shell. Whorls about 5½, spire moderately and almost evenly elevated, slightly rounded above. Periphery strongly protruded into a rather sharp keel. Parietal wall with single, medially placed, high, bladelike barrier, extending for more than one-half whorl posteriorly, apparently with gradual anterior descension. No columellar or palatal barriers present. Anatomy unknown.

Type species. — *Pseudolibera lillianae,* new species.

Formation of an umbilical brood chamber produced similarities to both *Libera* and *Gambiodonta. Pseudolibera*'s method of brood chamber closure is more like that of *Libera,* but the general shape and protruded keel resemble *Gambiodonta.* The latter has many more apertural barriers, a more dome-shaped appearance and apical sculpture of quite heavy radial ribs. *Libera* has more apertural barriers than *Pseudolibera* (but fewer than *Gambiodonta*), lacks a protruded keel, and has very similar apical sculpture. In having only a single parietal barrier of great length, *Pseudolibera* recalls the Society Islands *Nesodiscus.* The genus has a broadly open umbilicus in which eggs are deposited and sometimes sealed in by a mucus membrane (fig. 151).

The characters of apical sculpture, single parietal barrier, very narrow keel, and gradual umbilical closure effectively separate *Pseudolibera lillianae* from both *Gambiodonta* and *Libera.* As its name suggests, the resemblance is closer to *Libera* than to *Gambiodonta.*

Only two specimens were available, a large and badly worn adult that Cooke (1934, pp. 5-6) listed as "*Libera* sp.," and a very small juvenile specimen that Aubert de la Rüe and Soyer (1958, p. 365) identified as *Endodonta obolus.* Apical and early post-apical sculpture is well preserved on the juvenile, while the adult gives evidence of the pattern used in umbilical closure. Despite this limited material, *Pseudolibera* is obviously generically distinct.

Umbilical closure is achieved essentially as in *Libera.* After the umbilicus reaches maximum diameter, growth stabilizes for about one whorl, then a gradual inward growth of the lower whorl edge commences. One whorl before cessation of growth, the rate of inward movement of the columellar-basal margin accelerates for slightly more than one-half whorl, stabilizing there for the last one-quarter whorl of basal-columellar margin growth. The leading edge of the columellar wall occupies the last portion of the final whorl of growth.

The presence of two endemic genera, *Pseudolibera* and *Kleokyphus,* on Makatea is quite surprising.

Pseudolibera lillianae, new species (Cooke & Solem). Figure 168a-b.

Libera sp., Cooke, 1934, Occ. Pap. B. P. Bishop Mus., **10,** (11), pp. 5-6 — Makatea, Tuamotu Islands.

Endodonta obolus Aubert de la Rüe and Soyer, 1958 (not Gould, 1846), Bull, Mus. Nat. d'hist. nat., (2), **30,** (4) pp. 356-357 — Makatea, Tuamotu Islands.

Diagnosis. — Shell large, diameter 6.42 mm., with 5½ normally coiled whorls. Apex and spire moderately and almost evenly elevated, slightly rounded above, last whorl not descending more rapidly. H/D ratio 0.487. Umbilicus constricted to form a brood chamber by growth of last 1½ whorls. Apical sculpture not clearly differentiated from post-apical. Postnuclear whorls with prominent, rounded, rather closely spaced, strongly protractively sinuated radial ribs, whose interstices are less than twice their width. Radial sculpture greatly reduced on shell base. Microsculpture a lattice of very fine radial riblets crossed by slightly finer and more crowded spiral riblets, with strong secondary spiral cording developed particularly on base of shell. Sutures shallow, whorls somewhat flattened laterally above strongly protruded, very narrow keel, with distinct sub- and suprasutural sulci. Shell base flatly rounded. Aperture subquadrangular, periphery strongly rostrate, inclined about 20° from shell axis. Parietal wall with a single medially placed barrier, extending more than one-half whorl posteriorly, relatively thin and not expanded above, with gradual anterior descension. No columellar or palatal barriers present.

The presence of only a single parietal and the absence of palatal and columellar barriers at once separates *Pseudolibera lillianae* from any species of *Gambiodonta* or *Libera,* the other Polynesian genera with an umbilical brood chamber. *Nesodiscus* from the Society Islands is similar in the structure of the parietal barrier, but differs most obviously in the character of its ribbing and the widely open umbilicus.

Description. — Shell large, with 5½ normally coiled whorls. Apex and spire moderately and evenly elevated, slightly rounded above, last whorl not descending, H/D ratio 0.487. Embryonic whorls 1⅜, sculpture mainly eroded, but traces of very large, broadly rounded radial ribs remain in sutures. Postnuclear whorls with remnants of protractive, broadly rounded radial ribs whose interstices are about equal to their width, with faint traces of close set spiral cords about one-half the diameter of the radial ribs. Base of shell with co-equal radial and spiral cords. Sutures shallow, whorls flattened above with slight supraperipheral sulcus. Periphery of body whorl an irregularly protruded knife-edge carina with a slight sulcus above and below. Base of shell gently rounded. Umbilicus constricted into brood chamber by the gradual protrusion of the basal lip of the last whorl and a half. Umbilical opening ovate, 1.32 mm. by 1.09 mm. in size. All color leached from shell. Aperture subquadrangular with rostrate outer margin. Parietal wall with single, long, very high bladelike barrier, extending beyond line of vision despite a three-sixteenths of a whorl break in outer lip of aperture. Columellar wall with heavy white callus. Remains of palatal wall without barriers. Height of holotype 3.13 mm., diameter 6.42 mm.

Holotype. — Tuamotu Islands: Makatea, 1 mile inland at 250 ft. elevation. Collected on a hillside around roots of a plant by Mrs. G. P. Wilder on October 24, 1932. BPBM 115805.

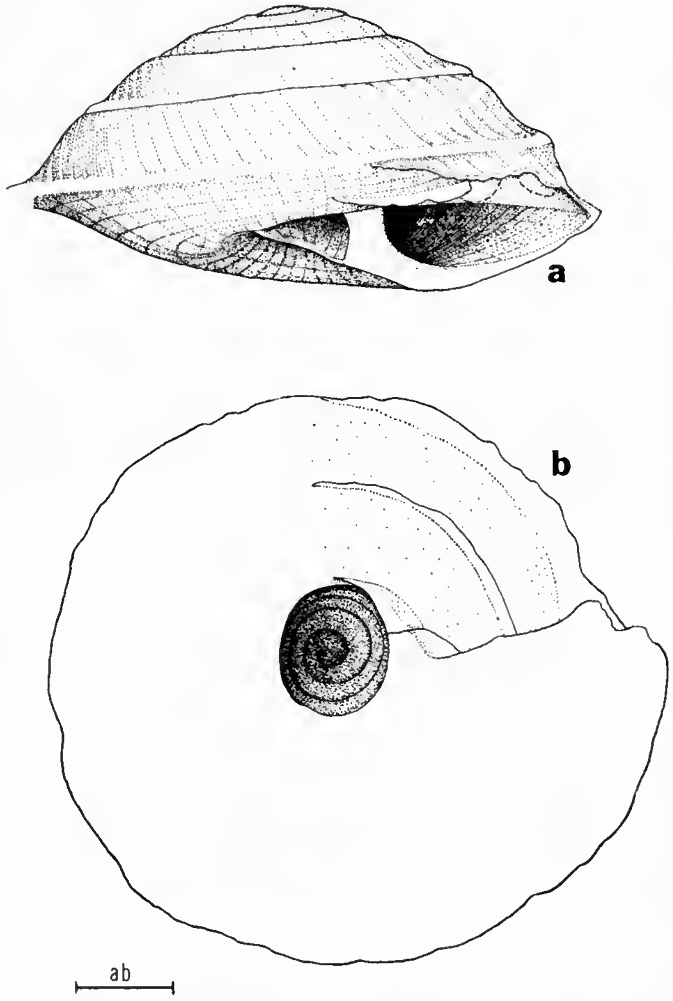

FIG. 168. **a-b,** *Pseudolibera lillianae,* new species. Makatea, Tuamotu Islands. Holotype. BPBM 115805. **a,** side view; **b,** basal view. Scale line equals 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Range. — Makatea, Tuamotu Islands.

Paratype. — Paris.

Material. — Makatea, 1 mile inland at 750 ft. elevation (1 specimen, BPBM 115805); Makatea (1 specimen, Paris Museum).

Remarks. — The single juvenile paratype shows details of the apical and early postnuclear sculpture in the shell umbilicus. Although too badly broken for measuring, it reveals that the parietal barrier extends posteriorly for over one-half whorl. The adult specimen shows that, as in *Gambiodonta grandis,* the major radial ribs are greatly reduced on the shell base.

The specific name *lillianae* is in honor of its collector, the late Mrs. G. P. Wilder. It was the intention of Dr. Cooke to use this name and I have accepted it here.

Genus **Libera** Garrett, 1881

(= *Garrettia* Cossman, 1910 not Paetel, 1873 and *Garrettina* Thiele, 1931)

Jour. Acad. Nat. Sci., Philadelphia, **9,** (1), p. 33.

Medium to very large-sized Endodontidae in which the umbilicus is secondarily narrowed to form a brood chamber by gradual inward growth during the last two whorls of growth. Apical sculpture typical, not enlarged. Postnuclear whorls with normal (*bursatella, cookeana, micrasoma, recedens, gregaria*), very widely spaced (*umbilicata, retunsa, streptaxon*), reduced (*dubiosa, spuria, tumuloides*), coarsened (*incognata, jacquinoti, fratercula, subcavernula*) or no (*heynemanni, garrettiana*) major radial sculpture. Secondary spiral cording present in those with normal (except *cookeana*) or widely spaced major radial ribbing, absent in those with coarsened sculpture, intensified in the *spuria-dubiosa-garrettiana* complex. Apex and spire markedly elevated (flattened in *streptaxon, recedens, gregaria*), often rounded above. Body whorl normally with weakly to strongly protruded keel, rounded in *retunsa*, only angulated in *micrasoma, cookeana*, and some *bursatella*. Supraperipheral and subperipheral sulci prominence correlated with degree of peripheral protrusion. Whorls 6⅜ - 8, rather tightly coiled, lower counts in smaller species. Parietal barriers normally 2 (only 1 in *retunsa* and *tumuloides*), extending posteriorly to line of vision or beyond, shorter in *bursatella, cookeana, retunsa;* normally equal only in *umbilicata* and *micrasoma;* all other species with lower reduced, either having a threadlike anterior extension or deeply recessed. Columellar barrier normally absent in *micrasoma, bursatella, incognata, fratercula fratercula*, and *tumuloides;* present or absent in *retunsa* and *fratercula rarotongensis;* medium-sized to large and usually deeply recessed in remaining species. Palatal barriers normally 3, frequently (*bursatella, micrasoma, incognata, subcavernula, fratercula rarotongensis*) reduced to 2, absent in *retunsa*, normally 1 in *tumuloides*, the typical endodontid number of 4 in *jacquinoti, fratercula fratercula, dubiosa, spuria, garrettiana.* Pallial region elongated, sometimes with kidney laterally compressed. Genitalia typical. Penis short to long, internally with two moderately to greatly elevated pilasters of varying prominence and folding. Vas deferens entering penis slightly to moderately below penial apex. Penial retractor originating on diaphragm, inserting directly onto penis head. Spermathecal shaft inserting directly onto peniovidual angle. Jaw and radula typical in dissected species.

Type species. — *Pitys cavernula* Garrett, 1872 (= *Helix subcavernula* Tryon, 1887) by subsequent designation of Pilsbry (1893-1895, p. 23).

Considerable confusion and uncertainty has existed concerning both the proper generic name and the identity of species described during the middle 19th century. *Garrettia* Cossman, 1900, and *Garrettina* Thiele, 1931, were proposed as replacement names for *Libera* Garrett, 1881, under the mistaken impression that *Libera* was preoccupied by a vaguely proposed suprageneric grouping of De Haan (see Pilsbry, 1893-1895, p. 23 for a discussion of this problem). *Libera* Garrett, 1881 is available.

The confusion over specific names is traceable to several factors. *Helix bursatella* Gould, 1846, was a mixture of several species and has not been restricted previously. It has been interpreted differently by every author. Pfeiffer's names *heynemanni* and *coarctata* were misidentified by Garrett (1884). Pfeiffer himself seemed totally confused by *bursatella, coarctata, jacquinoti, cavernula* (of Hombron and Jacquinot, not Garrett), and *turricula*. Every paper he published during the 1850's listed a different combination of synonyms. Ponsonby (1910) did an excellent job in sorting out literature references, but he did not know that Garrett's concepts of *bursatella, heynemanni,* and *coarctata* were different from Pfeiffer's, and included them under their nomenclatural citations. For any interested historian, Ponsonby's list of mid-19th century references is exhaustive. Most of these are catalog or checklist citations that had occasional varieties designated only by letters and not by valid nomenclatural units. I felt no qualms in omitting them from the present monograph. Many of these references are unrecognizable in view of the numerous species delineated below, are based on secondary literature citations, and have no scientific importance. References cited below are restricted to original descriptions, figures in monographs, and reports upon new field collections.

In order to stabilize the nomenclature, I have selected lectotypes or neotypes for the old names. Unfortunately, it usually was necessary to work with vaguely localized sets from old collections. We still have no exact localities for *L. streptaxon, L. heynemanni, L. jacquinoti, L. spuria,* and *L. incognata.* For *L. bursatella* I have selected a neotype from recently collected, well-localized materials. It is intended to fix and stabilize the nomenclature and thus allow work on field collections unencumbered by nomenclatural quibbling.

Available material of *Libera* came from five distinct periods of collecting. Each produced its own set of biases. The initial collecting was during exploratory voyages and resulted in the description of *L. bursatella* (Gould, 1846) (which was rediscovered by the Mangarevan Expedition), *L. jacquinoti* (Pfeiffer, 1850), *L. streptaxon* (Reeve, 1852), *L. heynemanni* (Pfeiffer, 1862), and *L. incognata,* new species. None of the last four have been collected subsequently. Possibly *L. dubiosa* Ancey, 1889, and *L. spuria* Ancey, 1889, date from the same period. Material probably originating from the U. S. Exploring Expedition (MCZ

216751) contained *L. micrasoma,* new species and *L. garrettiana,* new species. Both the latter were obtained subsequently, but the other species are represented in museum collections only by scattered individuals. The probable extent of specimen disappearance can be judged by the fact that although "over 300 individuals" of *Libera tumuloides* Garrett, 1872, were collected in 1869, only 72 of these could be located in the 1960's. To what extent the few examples seen of *L. jacquinoti, L. heynemanni, L. streptaxon,* and *L. incognata* represent size-biased selections is unknown.

Most material dated from the activities of Garrett between 1860 and 1884. *Libera retunsa* (Pease, 1864), *L. fratercula* (Pease, 1867), *L. tumuloides* (Garrett, 1872), *L. subcavernula* (Tryon, 1887), *L. recedens* Garrett, 1884, *L. gregaria* Garrett, 1884, and *L. garrettiana,* are new species that were first taken during this period. Only *L. fratercula* has been collected subsequently. Material from both Garrett and Pease has been distributed widely, traded and retraded by collectors, with distinct bias resulting. In Tables CIII and CVI there is clear indication that Garrett retained large specimens in his collection and that the Australian Museum, Sydney, eventually received very small to subadult examples of his species (see *L. subcavernula, L. tumuloides, L. dubiosa, L. garrettiana*). All measurements of material from these early periods can be used only with caution in view of this factor. Such size bias in older museum collections is common (Solem, 1966b, p. 16).

The other important collection was made by the Mangarevan Expedition from the B. P. Bishop Museum in 1934. Besides rediscovering *Libera bursatella,* they found *L. micrasoma, L. umbilicata, L. cookeana,* and *L. bursatella orofenensis,* all previously undescribed taxa. A detailed analysis of this material and its bias is presented below.

Extensive material of *Libera fratercula,* which occupies a narrow zone near the sea shore on the various Cook Islands, was collected by Dr. and Mrs. Peter Buck in 1929 and 1930, then again by Mr. Laurie Price in 1964 and 1965.

Only single specimens come from other sources.

The limited overlap of species obtained during different collecting periods suggests that even by 1860 significant portions of the Society Islands land snail fauna were extinct and that the process accelerated between 1860 and the mid-1930's. No attempt at collecting on the upper levels of Moorean and Tahitian mountains has been made recently. From data available on Rarotonga, I suspect that additional species may be collected at high altitudes, but that material taken during the Mangarevan Expedition in 1934 mostly will be extinct.

The documented extent of size and shape bias in the Garrett material makes use of comparative measurements somewhat hazardous. Hence statistical comparisons have been kept to a minimum.

Secondary narrowing of the umbilicus to form a brood chamber is shared with the genera *Gambiodonta* and *Pseudolibera.* The same phenomenon occurs in *Endodonta marsupialis* and *Taipidon semimarsupialis.* Some other species of *Endodonta,* the Rapan *Kondoconcha othnius,* and the Tongan *Thaumatodon euaensis* show partial development of this character. A full discussion of this phenomenon is given on pp. 27-30. *Libera* and *Gambiodonta* are separated by numerous characters. *Gambiodonta* (figs. 22a, d, 185) has the apical sculpture consisting of coarse, broadly rounded ribs; *Libera* (figs. 31a, 169) has the typical very fine apical sculpture. *Gambiodonta* narrows the umbilicus during about one-quarter to one-third whorl of growth, subsequent growth for the remainder of the full whorl serving only to maintain the relative position of the baso-columellar margin to the center axis; *Libera* narrows the umbilicus gradually over about two whorls of growth, the pattern altering only in depressed species such as *L. gregaria, L. recedens,* and *L. streptaxon,* where partial detachment of the parietal wall initiates closure. *Gambiodonta* has many accessory apertural traces, generally 4-5 parietals, and normally 4 palatals; *Libera* has no accessory apertural traces (except rarely in *L. micrasoma* and *L. incognata*), generally only 2 parietals and only 2-3 palatals (except the *dubiosa* group which has 4). *Pseudolibera* and *Libera* show much greater similarities in sculpture and pattern of umbilical closure, but *Pseudolibera* has only a single very large and long parietal extending posteriorly for one-half whorl; there are no columellar or palatal barriers; the periphery is protruded into a very sharp keel, and the whorl count of 5½ is very low for a large (diameter 6.42 mm.) shell. While *Libera retunsa* and *L. tumuloides* have only 1 parietal, the average pattern of *Libera* is very different from that of *Pseudolibera.* The gap between *Libera* and *Pseudolibera* in structural patterns is at least equal to the gap between *Mautodontha* and *Kleokyphus.*

Derivation of the Society Islands *Libera* from the *Garrettoconcha* group of *Mautodontha* would present fewest problems. While *Mautodontha* (*Garrettoconcha*) *parvidens* from Huahine, Moorea, and Tahiti normally has only 2 parietals and thus agrees with the barriers of *Libera,* the forms of *M. consobrina* from Huahine and *M. saintjohni* from Borabora provide better examples of shell shapes that can precede the formation of an umbilical brood chamber. None of the above species are suggested in any sense as ancestral to *Libera* itself, but they do indicate the pattern of change needed for *Mautodontha* to make the shift – loss of the 1st and 4th parietals; increase in spire elevation, whorl count and size; retention and/or widening of the umbilical opening into a U-shaped instead of a V-shaped pattern; then, much as in *Endodonta,* flattening of the umbilical walls and gradual narrowing of the umbilical opening during the last portion of shell growth. The smaller species of

Libera, such as *L. umbilicata* and *L. micrasoma,* have the parietals of equal length as in most *Mautodontha,* and have relatively slight umbilical narrowing, probably a function of their small size. They both show specializations in teeth and sculpture. There are no indications of secondary size reduction and thus probably they are the closest to the ancestral species in size and umbilical characters. The other small species, *Libera retunsa,* is quite specialized in barrier reduction, sculpture, extreme deflection of the body whorl, and is generalized only in respect to the comparatively minor umbilical narrowing and the rounded body whorl.

Additional evidence for the derivation of Society Islands *Libera* from *Mautodontha* (*Garrettoconcha*) comes from the pattern of sculpture. The high mean rib counts of those *Libera* with generalized sculpture (107-178, *micrasoma, bursatella, dubiosa, recedens, gregaria*) agree well with the pattern in the more generalized *Mautodontha* (123-153, *consobrina, saint-johni, punctiperforata, parvidens, daedalea*) and greatly exceeds the average counts in other genera from Eastern Polynesia.

There is sufficient variation within the Society Islands *Libera* to suggest that the genus may be polyphyletic in the sense of having been derived from two related species groups of *Mautodontha.* The series of species *Libera dubiosa, L. spuria,* and *L. garrettiana* differ radically in character of sculpture and general appearance from the most typical series. There is no qualitative difference in umbilical formation and I have no hesitation in classifying them in the same genus. So little anatomical material of both *Libera* and *Mautodontha* was available for study, that it is impossible to suggest exact phylogenies in view of the confusing shell variations.

Derivation of the three Cook Islands species, *L. fratercula* and its two derivatives, *L. subcavernula* and *L. tumuloides*, could have been from a Cook Islands stock of *Mautodontha* for which we have no record, or could be a secondary dispersal from the Society Islands. None of the recently extant Cook Islands *Mautodontha* show characters tending toward the brood-chamber pattern. Without study of anatomical structures in many more *Mautodontha* and *Libera* it will be impossible to eliminate the possibility that *Libera* is of polyphyletic origin from different groups of *Mautodontha.* Habitat destruction in both the Cook and Society Islands has proceeded to such an extent that collection of needed material is very unlikely. Shell characters are insufficient to allow resolution of this problem. While *Libera* may be a grade of structure that is composed of several parallel lines of evolution, the separate lines would be very close phyletically. Inclusion of the derived species within one genus requires no hesitation.

Within *Libera* there are no obvious unitary trends of variation. Instead there are diverse patterns of change that show few correlations. The normal endodontid sculpture of fine radial ribs with three to eight microradials between each pair of major ribs is present in most species. The same microradial spacing holds for species with broadened radial ribs (*fratercula, subcavernula,* and to a lesser extent in the very large *jacquinoti*). The situation in *L. incognata* is unknown because no unworn material was available. Dramatic increase in rib spacing is seen in *L. umbilicata, L. retunsa,* and *L. streptaxon,* with only *L. retunsa* having the microradial spacing increased. In *L. umbilicata* and *L. streptaxon* the number of microradials rises to about 30 and from 12 to 20, respectively. Reduction and loss of major ribbing has happened at least twice. In the Cook Islands, there is some reduction in *L. subcavernula* followed by loss of major ribbing in *L. tumuloides.* In the Society Islands, there is a graded series in three closely related species, *L. dubiosa* having normal sculpture, loss on the body whorl and lower spire in *L. spuria,* followed by complete loss of major radial ribbing in *L. garrettiana.* Possibly the much larger and macroscopically smooth *L. heynemanni* is part of the same series. Secondary spiral cording is absent from those species with broadened major radial ribs and varies from weak or only on shell base (*recedens, gregaria, micrasoma*) to very prominent (*streptaxon, retunsa, dubiosa, spuria, garrettiana*). Spacing frequency of the secondary spiral cording is least in *garrettiana* (fig. 177c) and greatest in *L. retunsa* (fig. 178d).

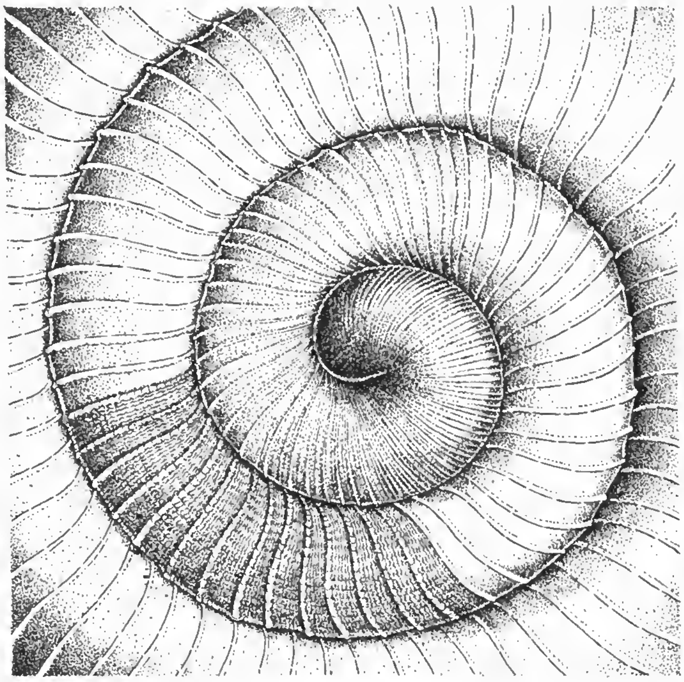

FIG. 169. Apical sculpture of *Libera bursatella bursatella* (Gould). (MM).

The above variation in ribbing character is only partly reflected in the rib spacing variation (table XCIX). Both increased spacing and broadening of the ribs can alter the ribs/mm. drastically. Those with secondarily widely spaced sculpture, *umbilicata, re-*

TABLE XCIX. - RIBS AND RIB SPACING IN LIBERA

Name	Ribs	Ribs/mm.
micrasoma	107.2±2.49 (103-117)	7.64±0.150 (7.30-8.39)
b. bursatella	119.0±2.76 (98-161)	7.14±0.175 (6.12-8.95)
b. orofenensis	171.8±6.21 (158-185)	10.44±0.585 (8.68-12.02)
cookeana	91.4±2.06 (85-95)	3.72±0.051 (3.52-3.84)
gregaria	177.8±4.51 (155-198)	8.16±0.201 (7.28-8.98)
recedens	178.2±7.12 (152-198)	9.57±0.425 (8.17-10.53)
dubiosa	125.2±4.68 (111-138)	7.43±0.486 (5.64-8.51)
umbilicata	29.3±1.77 (26-32)	2.50±0.127 (2.26-2.69)
retunsa	51.2±2.15 (43-55)	3.94±0.252 (2.97-4.43)
streptaxon	46.4±1.31 (36-55)	2.44±0.078 (1.81-2.91)
incognata	49.8±1.31 (43-55)	2.18±0.042 (2.00-2.34)
jacquinoti	55.0±1.58 (47-67)	1.94±0.136 (1.66-2.47)
fratercula		
Mangaia	83.5±1.22 (74-112)	4.86±0.068 (3.81-6.13)
Mauke	78.9±2.18 (66-93)	4.53±0.158 (3.65-5.60)
Atiu	80.0±1.81 (66-93)	5.01±0.100 (4.23-5.77)
rarotongensis	83.0±2.84 (66-105)	4.22±0.135 (3.31-5.44)

tunsa, and *streptaxon* have between 2.4 and 4.0 ribs/mm., while those with broadened ribs, *incognata*, *fratercula*, and *jacquinoti*, range between 1.9 and 5.0 ribs/mm. This range undoubtedly is extended on the lower side by the size correlated rib spacing increment in *jacquinoti*, but is a duplicated spacing effect for the other species. Only in *L. recedens*, as a secondary result of extreme body whorl deflection, and *L. bursatella orofenensis*, as a result of sharp increase in rib number, is there a large ribs/mm. average (9.6 - 10.4).

Most species have a typically domed spire, but in *L. streptaxon* (fig. 179a) and, to a lesser extent, both *L. recedens* and *L. gregaria* (fig. 175a, e), the spire is flat or only weakly elevated. In these species the umbilical closing is altered. Closure is not as gradual and involves partial detachment of the parietal wall followed by strong deflection of the body whorl in *L. recedens* (fig. 170) and *L. streptaxon*. This change allows maintainence of an adequate internal cavity for egg deposition and the increased deflection permits adequate closure. While effective in the end result, I suspect this was a secondary development within *Libera* correlated with spire depression, since use of a thin parietal wall plate provides minimal strength to the umbilical closure.

Whorl contours depend upon the degree of peripheral keel protrusion. Only *L. retunsa* has the periphery rounded and only *L. bursatella, L. cookeana,* and *L. micrasoma* have weak peripheral angulation. The remaining taxa have slight to extremely strong peripheral protrusion. As would be expected, this is roughly correlated with size increase, the larger species having greater protrusion of the keel. In all species with prominent keel development, it is a threadlike rounded protrusion, not sharply narrowed and angled as in *Pseudolibera,* and there are prominent supraperipheral and subperipheral sulci.

While mean whorl count ranges from 6⅜ - 8+, there is no single correlation with size. Two large species, *L. incognata* and *L. jacquinoti,* do have high whorl counts, but *L. cookeana* is of equal size and has a lower count. A comparatively small species, *L. streptaxon,* has a high count. Of the smallest *Libera,* only *L. retunsa* has a low whorl count, while the others reach the median range for the genus.

Barrier variation is equally uncorrelated with size (table C). In *L. bursatella, L. cookeana,* and *L. retunsa* the parietals are only one-quarter whorl long, in the remaining species they extend essentially to or slightly beyond the line of vision. Normal reduction to only one parietal is found in *L. retunsa,* the second smallest species, and *L. tumuloides,* which is larger than average but does not reach the upper quartile of size range. Both of these also are the only species with normal reduction to less than 2 palatals. In contrast, the largest species, *L. cookeana, L. incognata,* and *L. jacquinoti,* retain essentially a full complement of apertural barriers. This is quite different from the pattern in *Nesodiscus,* where barrier reduction and increased size are directly correlated. Columellar barrier size ranges from very large in *L. recedens* and *L. gregaria* (fig. 175a, e); reduced or absent in *L. retunsa* and *L. fratercula rarotongensis*; to always absent in *L. micrasoma, L. bursatella,* and *L. fratercula fratercula.* When present, the columellar barrier normally is deeply recessed.

Variation in anatomy was concentrated in the pallial region and penial complex. In *L. bursatella* (fig. 171d) there is significant lateral compression of the kidney resulting in a "pocket" arrangement at the posterior margin. In other examined species, the pallial region followed normal endodontid pattern. Within the penial complex, the origin of the penial retractor from the diaphragm was unexpected and the generally only slightly subapical insertion of the vas deferens into the penis was slightly unusual. Penial variation concerned primarily length and pilaster pattern. On Mt. Aorai, where *L. bursatella, L. micrasoma,* and *L. cookeana* were partly sympatric — *L. micrasoma* has two equal-sized, low pilasters; *L. bursatella,* subequal pilasters, one of which is higher and rather complexly folded; and *L. cookeana* has very unequal pilasters, one of which is very high and simple (fig. 172a-b), with the other greatly reduced to absent in the upper half. Size relationships of the penes are: *L. micrasoma,* 3.9-4.1 mm. long; *L. bursatella* 4.3-4.5 mm. long; and *L.*

cookeana, 5.9 mm. long. There is thus both penial size and pilaster differences between the three sympatric species on Mt. Aorai. The other species dissected, *L. bursatella orofenensis* and both races of *L. fratercula,* had penial pilaster patterns that essentially agreed with those of *L. bursatella bursatella,* having slight inequality in pilaster height and the higher one modestly folded.

The anatomical features of *Libera* are relatively conservative. Absence of a fleshy extension to the penis head and high insertion of the vas deferens agree with the more generalized taxa. The penioviducal angle insertion of the spermatheca, moderately elevated pilasters, and very long talon differentiate *Libera* from both *Nesodiscus* and *Endodonta.* The complexly folded or elevated penis in *Libera* approaches that of *Australdonta,* but is more similar to the type seen in *Opanara.*

While certain species are obviously more closely related to each other than to the remaining, no clear hierarchy can be recognized. *Libera dubiosa, L. spuria,* and *L. garrettiana* form one series; *L. recedens* and *L. gregaria* are closely related; *L. tumuloides* and *L. subcavernula* are derived from *L. fratercula; L. bursatella, L. micrasoma,* and *L. cookeana* probably are closely related. The other species seem relatively isolated in position, and none of the groups listed above are obviously related. Either the *dubiosa* or *bursatella* series could be near the ancestral type for *Libera.*

Distributional data on *Libera* are comparatively sparse and quite unsatisfactory in comparison with other genera. For five species known only from material taken prior to Garrett's collections of 1860-1863, *L. streptaxon, L. incognata, L. jacquinoti, L. spuria,* and *L. heynemanni,* even the island of origin is unknown or uncertain. For species collected by Garrett, either between 1860 and 1863 or from 1870 to 1883, there are general island quadrant references that indicate geographical isolation. From impressions gained by comparing *Partula* data in Crampton (1916) with Garrett's *Partula* data, I suspect that all his collections were from relatively low elevations. None of the *Libera* species he described or first collected during this period were obtained by the Mangarevan Expedition in 1934. On Tahiti, *L. retunsa* was found "on the south side" and *L. garrettiana* (reported by Garrett, 1884, p. 35 as *L. heynemanni)* "in several valleys on the northwest part." On Moorea, *L. dubiosa* (recorded by Garrett, 1884, p. 34 as *L. coarctata)* was "diffused throughout several valleys on the north and east side of Moorea," *L. gregaria* "in two valleys on the southwest part," and *L. recedens* was found on the "lower part of one valley on the west side." While *L.*

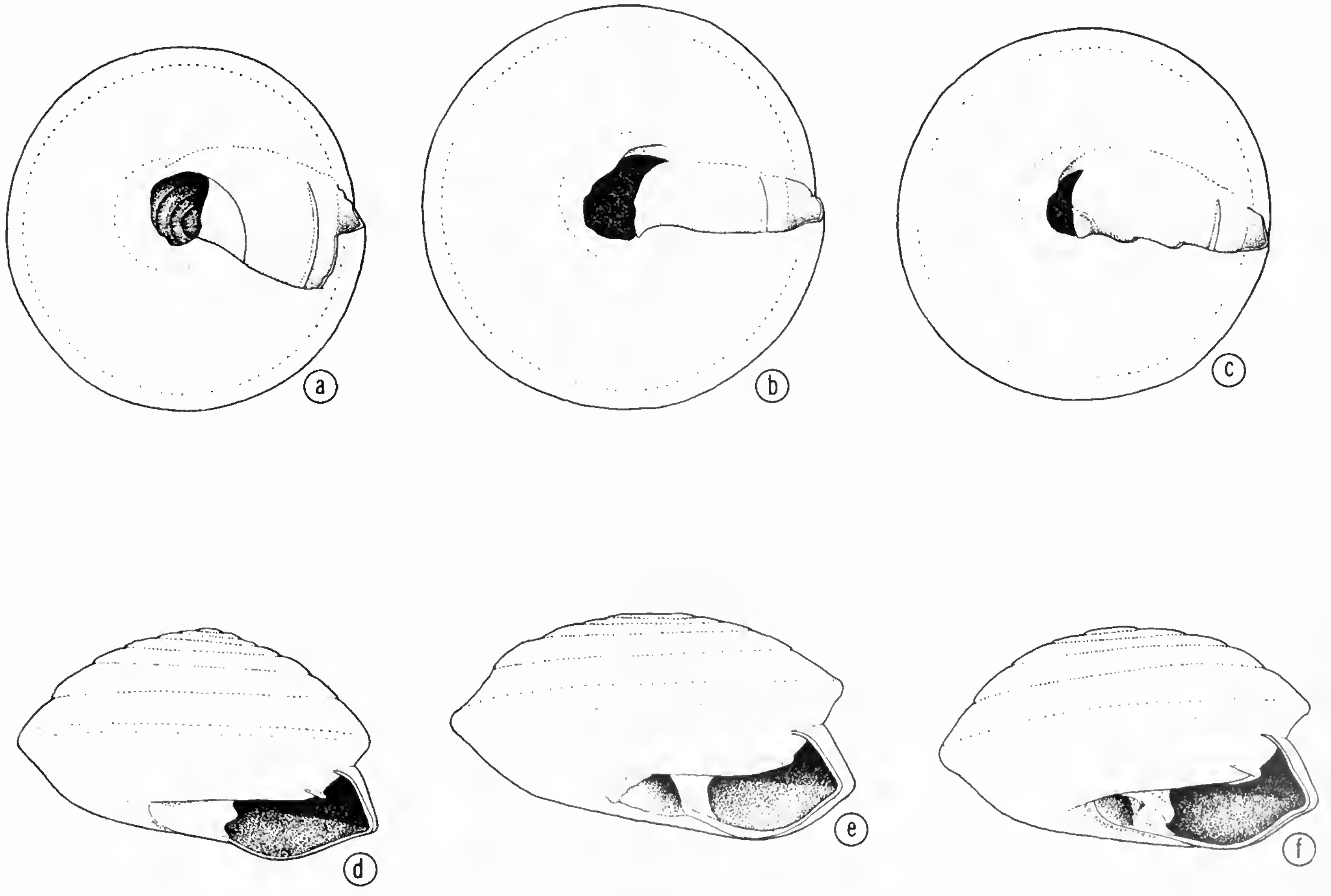

FIG. 170. Body whorl deflection and form of umbilical closure in *Libera recedens.* FMNH 156777. Scale line equals 1 mm. (SG).

recedens was stated to be low in a valley and thus can be presumed extinct, it is possible that populations of the others are extant. Only *L. recedens* and *L. gregaria* of the above species could be considered very closely related and possibly subspecies. The morphologic gap between the two is so large that I have accepted Garrett's specific separation. *L. dubiosa* from Moorea and *L. garrettiana* from Tahiti are members of a monophyletic assemblage, but have a much greater morphologic gap than in the prior case. I have no hesitation in considering them distinct species.

All *Libera* collected during the Mangarevan Expedition were taken above 4,000 ft. elevation. These involved two partial transects, one by botanists on Mt. Orofena, the other by malacological assistants and an entomologist on Mt. Aorai. On Mt. Orofena, *Libera bursatella orofenensis* and *L. umbilicata,* both previously undescribed taxa, were taken at the same place (Station 949). Since the latter was found only at that station, the wider occurrence of *L. b. orofenensis* does not alter their sympatry. On Mt. Aorai, *L. bursatella bursatella, L. micrasoma,* and *L. cookeana* were found at Station 865, and two of the three species at Stations 863, 864, and 866. In each case, *L. b. bursatella* was overwhelmingly predominant in numbers, and *L. cookeana* was most sparsely represented. The penial differences at these stations are discussed above.

Both sympatric and allopatric distribution patterns are present in the Society Islands *Libera.* Unfortunately, it is probably too late for field investigations of these patterns.

In the Cook Islands, one species, *Libera fratercula,* is widely distributed near the seashore and there were two inland derivatives of this species, *L. subcavernula* and *L. tumuloides,* on Rarotonga. The latter was restricted to "a small area of about one-half an acre, and nearly two miles inland," while the former was "Found plentifully in the mountain ravines." Neither was collected during 1964 or 1965. Quite probably they are extinct.

With two exceptions, the ecological occurrence of *Libera* is characteristic of the family. Garrett's references to habitat are repetitious for "on the ground in forests," "beneath rotten wood," "beneath loose stones and decaying wood," "congregating in immense numbers on the under side of loose stones," and "beneath decaying vegetation." They are restricted to the ground stratum in heavy forest, generally under stones or rotting wood. *Libera fratercula* is found in coastal forests on several of the Cook Islands and apparently has become adapted to life in the comparatively exposed and dry zone of coral boulders that extends from just above the storm high tide mark to a little more than 150 yd. inland. They are found under the coral boulders, but this habitat is relatively open and thus subject to periodic drying. Hence there is considerable phenotypic variation even over 200 yd. intervals within a continuously distributed colony. This is quite different from the situation seen in wet forest litter endodontids, where variation between populations was either at the subspecific level or virtually absent because of habitat stability.

Libera bursatella bursatella was found to be abundant "in the axils of ie'ie" (*Freycinetia arborea*) at Station 863 on Mt. Aorai. The only other nonterrestrial records for endodontids are of some *Cookeconcha* found in moss on tree trunks, while *Priceconcha tuvuthaensis* Solem (1973d) was taken on tree trunks in Lau. Thus the semiarboreal occurrence of *Libera* is quite unusual.

Since *Libera fratercula* occupies a zone with superabundance of lime, the exceptionally thick shell and unique method of the young exiting from the brood chamber (see pp. 418-419 and Solem, 1970) could evolve quite easily. For other species at inland and elevated localities where volcanic rocks are far more prevalent than coralline, lime is much less abundant and the more conservative pattern of thin shell and the young exiting through the basocolumellar margin at the narrowed umbilical opening is followed.

Inevitably there were a few specimens and references that were not referable to named taxa, yet were not present in sufficient quantity for naming. These are listed as *Libera* sp. after the species discussion. Garrett's material from Aitutaki undoubtedly was distinct, but all these specimens were destroyed during World War II. A very unusual form is represented by a single specimen (RSM 1961.61.40) from Moorea. The shell is subadult, 5.43 mm. in diameter, 2.63 mm. high, with 6⅜ whorls. There are 2 parietals, lower with anterior two-thirds threadlike, a large columellar and 4 palatals, with the 1st greatly reduced in size. It is obviously related to the *dubiosa-spuria-garrettiana* series, but differs in the strongly protruded cordlike periphery, low spire (H/D ratio 0.484), and relatively strong radial ribbing. The peripheral protrusion starts after 4⅛ whorls near a repaired break in the shell and may be a simple abnormality. Possibly this shell should be referred to *L. dubiosa.*

KEY TO THE GENUS *Libera*

1. Prominent major radial sculpture present on body whorl or at least penultimate whorl 5
No major radial sculpture on body whorl, or penultimate whorl. 2
2. Parietal barriers 2; Society Islands 3
Parietal barrier 1; Rarotonga. *Libera tumuloides* (Garrett, 1872)
3. Surface with prominent microribbing and secondary spiral sculpture 4
Surface macroscopically smooth. *Libera heynemanni* (Pfeiffer, 1862)
4. Major radial ribs present on upper spire. *Libera spuria* Ancey, 1889
No major radial ribs present ....*Libera garrettiana*, new species
5. Normally 2 or more parietals; 2 - 4 palatals; body whorl angulated or keeled 6

Normally 1 parietal; no palatals; body whorl evenly rounded. *Libera retunsa* (Pease, 1864)

6. Major radial sculpture narrow, not broadened; generally secondary spiral cording prominent 11
   Major radial ribs broadened and much thicker; no secondary spiral cording 7
7. Major ribs persisting over entire body whorl 8
   Major ribs becoming very irregular on body whorl and part of penultimate whorl .... *Libera subcavernala* (Tryon, 1887)
8. Mean ribs on body whorl less than 60 9
   Mean ribs on body whorl more than 75 10
9. Mean H/D ratio about 0.650; spire rounded above; keel weakly protruded; normally 2 palatals; mean diameter about 7.30 mm. .... *Libera incognata*, new species
   Mean H/D ratio about 0.540; spire not strongly rounded above; keel strongly protruded; normally 4 palatals; mean diameter about 8.50 mm. .... *Libera jacquinoti* (Pfeiffer, 1850)
10. Mean diameter about 6.60 mm.; only 2 palatals. *Libera fratercula rarotongensis*, new subspecies
    Mean diameter about 5.60 mm.; normally 4 palatals. *Libera fratercula fratercula* (Pease, 1867)
11. Fewer than 70 ribs on body whorl 18
    More than 80 ribs on body whorl 12
12. Palatals normally 2 or 3 13
    Palatals normally 4 .... *Libera dubiosa* Ancey, 1889
13. Mean rib counts about 170 - 180 16
    Mean rib counts less than 130 14
14. Adult size less than 6.25 mm.; no columellar; 2 palatals 15
    Adult size more than 7.00 mm.; 1 columellar; 3 palatals. *Libera cookeana*, new species
15. Parietals equal in length .... *Libera micrasoma*, new species
    Lower parietal deeply recessed. *Libera bursatella bursatella* (Gould, 1846)
16. Prominent columellar barrier present 17
    No columellar barrier. *Libera bursatella orofenensis*, new subspecies
17. Body whorl strongly deflected beneath penultimate whorl. *Libera recedens* Garrett, 1884
    Body whorl not strongly deflected. *Libera gregaria* Garrett, 1884
18. Adult diameter less than 4 mm.; spire strongly elevated. *Libera umbilicata*, new species
    Adult diameter more than 5 mm.; spire flat or depressed. *Libera streptaxon* (Reeve, 1852)

Libera micrasoma, new species. Figures 171f-h; 173c-e.

Diagnosis. — Shell very small, diameter 4.12-4.71 mm. (mean 4.46 mm.), with 6¼ - 7½ normally coiled whorls. Apex slightly protruding or less frequently flat, whorls of spire descending progressively more rapidly, body whorl not or only slightly deflected, H/D ratio 0.550-0.686 (mean 0.612). Umbilicus secondarily narrowed to form brood chamber by only moderate inward growth of baso-columellar margin, opening circular, contained 2.96-4.80 times (mean 3.66) in the diameter. Postnuclear sculpture of relatively narrow, high and prominent, protractively sinuated radial ribs, 103-117 (mean 107.2) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are visible only under 96× magnification. Base of shell with traces of very few and indistinct spiral cords, absent from upper surface. Sutures deep, whorls strongly rounded above, flattened laterally down to very weakly angled periphery, lower palatal and basal margins gently and evenly rounded down to marked sulcus above acutely angled baso-columellar margin, columellar wall flat or slightly concave inside umbilicus. Aperture ovate, compressed laterally above and below very weakly and obtusely angled periphery, inclined about 20° from shell axis. Parietal barriers normally 2, occasionally with a 3rd (6.3 per cent) or with two small traces (6.3 per cent), extending posteriorly to line of vision: upper parietal high and bladelike, more expanded and elevated on posterior third, with gradual anterior descension; 2nd equally high on posterior three-eighths, anterior half moderately raised, bladelike, with gradual anterior descension that terminates slightly in front of upper parietal end. Columellar wall flat or weakly convex, with a moderately developed callus, no barriers. Palatal barriers 2, both subperipheral, extending posteriorly more than one-eighth whorl, not so deeply recessed as in most *Libera:* lower basal in position, a weakly elevated threadlike ridge with gradual anterior descension; 2nd slightly higher posteriorly, longer, with more gradual anterior descension.

Libera micrasoma has 2 parietals of equal length that extend posteriorly to the line of vision and is much smaller (table C) than the sympatric *Libera bursatella bursatella. L. umbilicata* from Mt. Orofena agrees in the parietal barriers, but is even smaller, with 3 palatals, has comparatively weak and very widely spaced radial ribs (mean rib count 29.3). The other species of equal size, *L. retunsa,* has very strong secondary spiral cording, a strongly deflected body whorl, and a deeply recessed lower parietal.

Description. — Shell very small, with 7 tightly coiled whorls. Apex and early spire almost flat, lower whorls descending sharply, H/D ratio 0.633. Apical whorls 1¼, sculpture of widely spaced major radial ribs with two or three minor riblets between and crossed by closely spaced, very fine spiral riblets. Postnuclear whorls with high, prominent, roundly lamellate, protractively sinuated radial ribs, 117 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of low, rounded radial riblets, five to eight between each pair of major ribs, that completely overshadow very closely spaced and extremely fine spiral riblets. Sutures deep, whorls strongly rounded above, compressed laterally down to faint and obtuse angulation, evenly and gently rounded on base to sulcus. Umbilicus modified into a brood chamber by the broad and gradual constriction of the last two whorls, opening relatively wide, nearly circular, contained 3.78 times in the diameter. Color yellow horn, with broad, reddish flammulations that become zigzagged on shell base. Aperture subquadrangular, rounded above and below the obtusely angled periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper lamellate for its entire length, higher on posterior third; lower with threadlike anterior half becoming equally elevated posteriorly, extending slightly beyond end of upper parietal. Columellar wall flat with a heavy white callus, barriers absent. Palatal wall with 2 moderately deeply recessed, short ridgelike barriers that extend more than one-eighth whorl: upper longer and with more gradual anterior descension than lower, both subperipheral. Height of holotype 2.81 mm., diameter 4.44 mm.

Holotype. — Society Islands: Tahiti, Station 865, Mt. Aorai trail at 5,600-6,300 ft. elevation. Collected by E. Zimmerman, Y. Kondo, and D. Anderson on September 15, 1934. BPBM 145287.

Range. — Mt. Aorai, 5,600-6,300 ft. elevation, Tahiti, Society Islands.

Paratypes. — Same as list of material.

Material. — Tahiti: Mt. Aorai trail (Station 865) at 5,600-6,300 ft. elevation (13 specimens, BPBM 145287-8); valley west of Aorai trail (Station 866) at 6,000 ft. elevation (6 specimens, BPBM 145293).

Remarks. — At first glance *Libera micrasoma* seems to be only a small form of *L. bursatella bursatella*, but the greater length and equal size of the parietal barriers, much smaller size, and stronger sculpture separate the two sympatric species. The

TABLE C. - RANGE OF VARIATION IN LIBERA

	Number of specimens	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
micrasoma	19	107.2(103-117)	2.72(2.41-3.20)	4.46(4.12-4.71)	0.612(0.550-0.686)	6 3/4+(6 1/4-7 1/2)	3.66(2.96-4.80)	2-3+0-2	0	2
bursatella bursatella (Gould)	384	119.0(98-161)	3.10(2.61-3.86)	5.39(4.64-5.88)	0.576(0.482-0.694)	6 3/4-(6-8)	4.57(3.38-6.16)	2	0	0-1-2
bursatella orofenensis	40	171.8(158-185)	3.09(2.75-3.60)	5.17(4.71-5.56)	0.599(0.512-0.688)	6 7/8+(6 3/8-7 3/4)	4.15(3.30-5.33)	1-2	0	0-1-2-3
cookeana	6	91.4(85-95)	4.01(3.53-4.51)	7.60(7.19-8.17)	0.528(0.467-0.577)	7 1/4-(6 3/4-7 1/2)	3.92(3.03-5.00)	2	1	3
gregaria (Garrett)	101	177.8(155-198)	3.35(2.76-3.99)	6.72(6.27-7.26)	0.498(0.437-0.577)	7 1/8+(6 3/4-7 1/2)	Irregular	2-3	1	2-3
recedens (Garrett)	61	178.2(152-198)	3.12(2.61-3.59)	5.66(5.36-6.67)	0.553(0.464-0.627)	7+(6 5/8-7 1/2)	Irregular	2	1	3
dubiosa (Ancey)	62	125.2(111-138)	3.22(2.57-3.92)	5.42(4.84-5.88)	0.594(0.525-0.697)	7 1/4-(6 1/2-8)	5.49(3.85-7.00)	2	1	4
spuria (Ancey)	100	ABSENT ON LOWER WHORLS	2.88(2.22-3.49)	4.83(4.18-5.49)	0.595(0.500-0.697)	6 1/2+(6-7 1/2)	5.34(4.00-7.80)	2	1	2-3-4
garrettiana	113	ONLY MICROSCULPTURE	2.71(2.48-3.07)	4.85(4.51-5.29)	0.559(0.503-0.607)	6 3/8+(5 5/8-7)	4.91(3.81-5.57)	2	1	3-4
umbilicata	4	29.3(26-32)	2.50(2.29-2.75)	3.71(3.66-3.79)	0.673(0.625-0.736)	7-(6 1/2-7 1/2)	3.16(2.94-3.41)	2	1	3
retunsa (Pease)	11	51.2(43-55)	2.76(2.29-3.14)	4.30(3.86-4.64)	0.644(0.567-0.758)	6 3/8-(5 7/8-7)	4.08(3.28-5.00)	1-2	0-1	0-2
streptaxon (Reeve)	26	46.4(36-55)	3.25(2.55-3.53)	6.06(5.23-6.67)	0.542(0.434-0.616)	7 5/8(6 5/8-8)	6.45(3.75-8.06)	2	0-1	3
heynemanni (Pfeiffer)	15	ABSENT	3.60(2.94-5.49)	6.52(5.23-8.43)	0.538(0.484-0.578)	6 7/8+(6 1/4-8 3/8)	5.05(4.00-6.78)	2-3	1	3-4
incognata	17	49.8(43-55)	4.75(3.99-5.43)	7.30(6.80-7.97)	0.650(0.571-0.761)	8+(7 1/2-8 7/8)	5.62(3.80-7.27)	2+0-1	0-1	2-3-4
jacquinoti (Pfeiffer)	29	55.0(47-67)	4.56(3.79-5.49)	8.46(7.45-9.28)	0.539(0.446-0.617)	7 5/8+(6 7/8-9)	6.49(3.78-8.93)	2	1	3-4
fratercula fratercula (Pease)	1,475	81.5(65-112)	2.79(2.48-4.44)	5.60(4.84-6.54)	0.570(0.475-0.696)	6 1/2+(5 1/2-7 3/4)	7.40(5.20-13.0)	2	0	2-3-4
fratercula rarotongensis	1,424	83.0(66-105)	4.32(3.13-6.18)	6.59(5.43-8.15)	0.656(0.519-0.844)	7 3/8+(6-8 3/4)	7.55(4.26-13.4)	2	0-1	2
subcavernula (Tryon)	73	REDUCED TO IRREGULARITY	3.89(3.07-5.00)	6.29(5.29-7.63)	0.618(0.548-0.711)	6 1/2+(5 1/2-7 1/4)	5.68(3.58-8.09)	1-2	1	2-3
tumuloides (Garrett)	72	ABSENT	4.37(3.55-5.13)	6.51(6.18-7.17)	0.671(0.553-0.812)	6 5/8-(6 1/8-7 1/2)	5.08(3.62-6.93)	1	0-1	1-2

apical whorls are of the same size as *L. b. orofenensis* (table CI), and thus significantly smaller than those of *L. b. bursatella*. Apparently penial sizes and pilaster patterns differ.

L. micrasoma is quite generalized in structure and sculpture, with the relatively open umbilicus correlating with the smaller size. The relatively small palatals and loss of the 3rd correspond well with the features of *L. bursatella*.

Sixteen of 19 examples (84.2 per cent) were adult. While the diameters of the two populations sampled did not overlap (table CII), those from Station 865 were adult to gerontic, and those from Station 866 were barely adult. The statistically significant difference (for diameters, "*t*" = 4.031) is based on age differential in this case.

Description of soft parts. — Foot and tail squashed in only whole example.

Body color yellow-white, without darker markings.

Mantle collar thin and rather narrow, a prominent glandular extension onto pallial roof.

Pallial region extending one-and-one-quarter whorls apically. Lung roof clear, without granulations. Kidney about 2.6 mm. long, rectal arm about 1.2 mm. long, kidney much less compacted than in *L. bursatella*. Ureter typical. Heart about 1 mm. long, slightly angled from hindgut. Principal pulmonary vein unbranched, extending to edge of pallial mantle collar extension. Hindgut extending one-eighth whorl above pallial cavity apex, not angling downward from margin.

Ovotestis not examined because of disintegration in apical viscera. Hermaphroditic duct (fig. 171f, g, GD) very long and slender, anterior half slightly swollen, then tapering down to union with carrefour after a sharply angled turn. Albumen gland (GG) very flat and narrow, elongated, only one or two acinal layers thick. Talon (GT) long, with slender shaft and gradually swollen head that is grossly expanded at tip. Carrefour (X) moderately expanded, receiving hermaphroditic duct laterally, expanding to enter prostate-uterus. Prostate (DG) of two or three rows of acini that are about one-third as wide as they are long, opening into a narrow tube. Uterus (UT) bipartite, lower chamber two-thirds length of upper with much thicker and more glandularized walls.

Vas deferens (VD) typical, entering penis about 0.5 mm. below apex. Penial retractor (PR) originating from diaphragm, inserting directly on head of penis. Penis (fig. 171h, P) about 3.9-4.1 mm. long, quite slender, very slightly tapering apically, internally with two pilasters (PP), both higher than wide, tending to weakly split or be very slender apically, generally fading out near atrium. Atrium (Y) short, not so wide as in other dissected *Libera*.

Free oviduct distinctly longer than prostate, tapering gradually until at midpoint no wider than vas deferens, no further narrowing. Spermatheca with typical head, shaft inserting directly on peni-oviducal angle.

Free muscle system without unusual features.

(Based on BPBM 145287, one whole adult 4.08 mm. in diameter, with 6⅝ whorls and 107 ribs on the body whorl, plus several extracted fragmentary specimens.)

Libera bursatella (Gould, 1846)

Abundant material of this species was obtained by the Mangarevan Expedition on both Mt. Aorai and Mt. Orofena above 4,000 ft. elevation. On Mt. Aorai it was associated with *L. cookeana* and *L. micrasoma*; on Mt. Orofena with *L. umbilicata*. *L. bursatella* was overwhelmingly dominant, with 417 specimens to only 29 of the other three. *L. umbilicata* is recognizable by its minute size (mean diameter 3.71 mm.), few ribs (26-32) and in having the parietals of equal length. *L. micrasoma* has the 2 parietals of equal length, much more prominent sculpture, and generally is 0.5 mm. less in diameter at similar whorl counts (table CI). *L. cookeana* is much larger (mean diameter 7.60 mm.), with more widely spaced radial ribs (ribs/mm. 3.72), and has a third palatal trace. In contrast, *L. bursatella* has the 2nd parietal deeply recessed, possesses rather low sculpture that is more closely spaced, 6.12-12.02 ribs/mm., and is of intermediate size (adult diameter 4.64-5.88 mm.) (table C). Only the Moorean *L. recedens* and *L. gregaria* appear similar in sculpture, but these species have a large columellar and 3 palatal barriers, while *L. bursatella* lacks the columellar and normally has only 2 palatals.

Differences between the Mt. Aorai and Mt. Orofena populations are confined to ribbing, with the former having 98-161 (mean 119.0) ribs on the body whorl and a spacing of 6.12-8.95 (mean 7.14) ribs/mm. and the latter 158-185 (mean 171.8) ribs on the body whorl with a spacing of 8.68-12.02 (mean 10.44) ribs/mm., and also early whorl diameter (table CI). In the Mt. Aorai shells there are generally three to six microradial riblets between each major pair; in the Mt. Orofena shells two to four microradials (fig. 174c, d). The disparity in quantities collected, 40 from Mt. Orofena and 378 from Mt. Aorai, is sufficient to make the small mean size difference (0.22) probably an artifact of sampling rather than having any biological significance. The slight mean difference in H/D ratio (0.023) is equally insignificant, particularly when compared with the large differences between populations of the Mt. Aorai *bursatella* (table CII).

Unlike the situation in the Mangarevan *Anceyodonta obesa* (p. 203), where rib counts remain constant despite significant size changes, or in the Rapan *Opanara areaensis, Orangia cookei, Rhysoconcha,* and *Ruatara oparica,* where changes in both size and

TABLE CI. - EARLY WHORL DIAMETER IN LIBERA

Name	Number of Specimens Examined	3WD	4WD	5WD
microsoma	6	1.23±0.013 (1.19-1.26)	1.62±0.013 (1.59-1.66)	2.03±0.022 (1.92-2.05)
bursatella orofenensis	6	1.21±0.022 (1.13-1.29)	1.61±0.031 (1.49-1.72)	2.04±0.033 (1.92-2.15)
bursatella bursatella	6	1.41±0.041 (1.32-1.52)	1.88±0.052 (1.76-2.02)	2.37±0.065 (2.19-2.58)
cookeana	6	1.42±0.013 (1.39-1.46)	1.96±0.018 (1.92-2.02)	2.59±0.035 (2.48-2.72)
recedens	6	1.14±0.011 (1.12-1.18)	1.56±0.014 (1.51-1.61)	2.07±0.017 (2.01-2.11)
gregaria	6	1.22±0.015 (1.18-1.28)	1.70±0.024 (1.64-1.81)	2.36±0.024 (2.30-2.47)

rib count are correlated, *Libera bursatella* shows a change in rib count and spacing that is independent of size and shape. This is recognized as a subspecific difference, with the nominate race, *L. bursatella bursatella,* restricted to Mt. Aorai, and a new race, *L. b. orofenensis,* found on Mt. Orofena. No intermediate examples were seen. Since localized collections of each form were taken from single transects on each mountain, the possibility of clinal variation remains to be investigated. I would not be at all surprised to find that sampling of spatially intermediate areas would provide morphologically intermediate populations. This is suggested by the rib counts and rib spacing found in the unlocalized BMNH set (table CII), which contained specimens with 117, 117, 135, and 161 ribs. It has been classified as typical *bursatella* on the basis of rib spacing (ribs/mm. 6.63, 6.78, 7.55, and 8.91, respectively). The specimens are large (mean diameter 5.64 mm.) and this is the only material that came close to spanning the gap in rib counts between the Mangarevan Expedition *L. b. bursatella* (98-137) and *L. b. orofenensis* (158-185).

Libera bursatella bursatella (Gould, 1846). Figures 171a-e; 174a-c.

Helix bursatella Gould, 1846, Proc. Boston Soc. Nat. Hist., **2**, p. 175 — Tahiti and Eimeo (= Moorea), Society Islands (partly); Gould, 1852, U. S. Explor. Exped. Wilkes, **12**, pp. 51-53 — "2,000-5,000 ft. elevation," Tahiti and Eimeo (partly); Gould, 1860, Atlas of Shells, U. S. Explor. Exped., Wilkes, pl. 4, figs. 52f, g, h, i — not other cited figures except possibly k, l, m (juvenile).

Libera bursatella (Gould), Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), pp. 39-40 (partly).

Diagnosis. — Shell slightly smaller than average, diameter 4.64-5.88 mm. (mean 5.39 mm.), with 6-8 normally coiled whorls. Apex usually slightly elevated, occasionally flat, whorls of spire descending progressively more rapidly, body whorl usually descending slightly more rapidly, H/D ratio 0.482-0.694 (mean 0.576). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of baso-columellar margin, which becomes acutely angled at adulthood, opening generally circular to subcircular, at adult size contained 3.38-6.16 times (mean 4.57) in the diameter. Postnuclear whorls with prominent, crowded, strongly protractively sinuated radial ribs, 98-161 (mean 119.0) on the body whorl, whose interstices are 1-3 times their width. Microsculpture of fine radial riblets, three to six between each pair of major ribs, with exceedingly fine and crowded spiral riblets, visible only under 96× magnification. Secondary sculpture of low and broadly rounded, quite crowded spiral cords that are most prominent on shell base and generally absent near periphery. Sutures impressed, whorls flatly rounded down to periphery, which varies from obtusely rounded to obtusely angulated or even slightly protruded (rarely), lower palatal margin evenly rounded, basal margin generally flatly rounded to a weak to prominent sulcus just before a sharply angled baso-columellar margin. Aperture ovate, flatly rounded above and below variable periphery, columellar walls strongly sinuated, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly slightly less than one-quarter whorl: upper moderately elevated, bladelike, slightly expanded and serrated above on posterior third, with very gradual anterior descension; 2nd equal in height to upper posteriorly, deeply recessed, with gradual anterior descension, only one-half length of upper parietal. Columellar wall with broad callus, more strongly rounded and convex posteriorly, but without a barrier. Palatal barriers normally 2, sometimes only 1 (5.1 per cent) or absent (5.1 per cent), subperipheral, extending posteriorly about one-eighth whorl, deeply recessed: lower smaller and shorter than upper, elevated and bladelike, with gradual anterior descension; 2nd slightly higher, longer, with more gradual anterior descension, more clearly expanded above.

The nominate race of *Libera bursatella* differs from the subspecies *orofenensis* primarily in its more widely spaced radial ribbing, with *L. bursatella bursatella* averaging about 119 ribs and *L. bursatella orofenensis* about 172 ribs. Specimens of *L. cookeana* are quite similar in general effect, but are immediately separable by their much larger size (mean diameter 7.60 mm.), possession of a supraperipheral palatal trace, and much more widely spaced radial ribbing. *L. micrasoma* has the parietal barriers of equal length and is much smaller (mean diameter 4.46 mm.). The two Moorean species with relatively regular and normal ribbing, *L. recedens* and *L. gregaria,* differ immediately in having a prominent columellar barrier, very fine radial ribbing (mean rib count about 178), and a prominent 3rd palatal.

Description. — Shell of less than average size, with slightly more than 7 moderately tightly coiled whorls. Apex and early spire flattened, lower whorls descending progressively more rapidly, last whorl only slightly deflected, H/D ratio 0.602. Embryonic whorls 1⅜, sculpture partially eroded, remnants consisting of fairly small, broadly rounded radial ribs with one or two riblets between. Remaining whorls with moderately low and broadly V-shaped, protractively sinuated radial ribs, 98 on the body whorl, whose interstices are 1-3 times their width. Microsculpture (fig. 174c) of numerous fine radial riblets, very fine spiral riblets, and low secondary spiral cords that become more prominent on shell base. Sutures shallow, whorls slightly rounded above weak supraperipheral sulcus, periphery obtusely angulated, more strongly rounded below periphery, somewhat flattened with a slight sulcus at umbilical margin. Umbilicus secondarily constricted by inward growth of baso-columellar margin, opening nearly circular, contained 4.50 times in the diameter. Color yellowish-white with zigzag flammulations on spire and body whorl, becoming weaker below periphery. Aperture subquadrangular, with flat columellar margin and gently rounded palatal margins, inclined about 25° from shell axis. Parietal barriers 2, extending about one-quarter whorl: upper lamellate for entire length, higher posteriorly; lower recessed and only half length of upper, slightly more elevated at posterior end. Columellar wall with slight callus, but no barriers. Palatal wall with 2 deeply recessed, short, low, lamellate ridges, situated below periphery. Height of neotype 3.07 mm., diameter 5.10 mm.

Neotype. — Society Islands: Tahiti, Station 863, Mt. Aorai trail at 4,700-5,500 ft. elevation. Collected by E. Zimmerman, Y. Kondo, and D. Anderson on September 14, 1934. BPBM 142059.

Range. — Slopes of Mt. Aorai from 4,700 ft. probably to summit, Tahiti, Society Islands.

Material. — Tahiti (6 specimens, BMNH 84.11.20.3-8): Aorai trail (Station 863) at 4,700-5,500 ft. elevation (169 specimens, BPBM 142058-70, BPBM 145911); Aorai trail (Station 864) at 5,500-5,600 ft. elevation (35 specimens, BPBM 145219-24); Aorai trail (Station 865) at 5,600-6,300 ft. elevation (62 specimens, BPBM 145280-6, BPBM 145290-2, BPBM 145926); valley west of Aorai trail (Station 866) at 6,000 ft. elevation (90 specimens, BPBM 145293-300); Aorai

TABLE CII. - LOCAL VARIATION IN MANGAREVAN EXPEDITION LIBERA

	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
bursatella bursatella						
BMNH 84.11.20.3-8	4	3.01±0.096 (2.81-3.27)	5.64±0.056 (5.49-5.75)	0.533±0.0125 (0.512-0.568)	6 1/2- (6 1/4-6 1/2)	6.18±0.210 (5.80-6.77)
BPBM 142059 (adult) Sta. 863 (4700-5500')	24	2.98±0.034 (2.61-3.27)	5.43±0.030 (5.10-5.69)	0.548±0.0063 (0.494-0.602)	6 1/2 (6 1/4-6 5/8)	4.69±0.086 (3.65-5.60)
BPBM 142058-9, BPBM 142066-7 (gerontic) Sta. 863 (4700-5500')	11	3.24±0.099 (2.88-3.86)	5.60±0.074 (4.97-5.88)	0.578±0.0172 (0.500-0.678)	6 3/4+ (6 1/4-7 5/8)	4.83±0.088 (3.62-5.87)
BPBM 145219 (adult) Sta. 864 (5500-5600')	6	2.97±0.043 (2.89-3.16)	5.49±0.056 (5.39-5.72)	0.541±0.0093 (0.518-0.585)	6 1/4+ (6-6 1/2)	4.89±0.153 (4.56-5.53)
BPBM 145290 (light color phase) Sta. 865 (5600-6300')	5	2.83±0.093 (2.63-2.96)	5.53±0.075 (5.33-5.79)	0.505±0.0091 (0.482-0.536)	6 1/8+ (6-6 1/2)	4.46±0.332 (3.68-5.60)
BPBM 145280-1 (adults) Sta. 865 (5600-6300')	16	3.19±0.071 (2.75-3.53)	5.10±0.080 (4.64-5.75)	0.624±0.0090 (0.557-0.694)	7 3/8- (6 5/8-8)	4.07±0.133 (3.38-5.00)
BPBM 145392 (gerontic) Sta. 866 (6000')	7	3.37±0.089 (3.01-3.66)	5.42±0.030 (5.29-5.49)	0.622±0.0147 (0.561-0.666)	7 1/2- (7 1/8-8)	4.11±0.144 (3.56-4.67)
bursatella orofenensis						
BPBM 145587 Sta. 946 (5500-5700')	5	3.26±0.103 (3.03-3.62)	5.11±0.068 (4.93-5.26)	0.639±0.0023 (0.588-0.688)	7 1/8- (6 3/4-7 3/4)	3.74±0.136 (3.30-4.00)
BPBM 145811, -6-8 Sta. 949 (4500')	6	2.97±0.091 (2.76-3.36)	5.37±0.091 (5.00-5.59)	0.553±0.0147 (0.512-0.600)	6 5/8 (6 3/8-7)	4.72±0.297 (3.30-5.33)
micrasoma						
BPBM 145287-8 Sta. 865 (5600-6300')	10	2.76±0.061 (2.56-3.22)	4.57±0.033 (4.47-4.74)	0.605±0.0120 (0.550-0.681)	6 7/8 (6 1/2-7 1/2)	3.62±0.176 (2.96-4.80)
BPBM 145393 Sta. 866 (6000')	6	2.71±0.089 (2.43-3.03)	4.34±0.045 (4.14-4.41)	0.624±0.0181 (0.570-0.686)	6 1/2+ (6 1/4-7)	3.73±0.166 (3.42-4.47)
umbilicata						
BPBM 145820 Sta. 949 (4500')	4	2.50±0.108 (2.29-2.75)	3.71±0.031 (3.66-3.79)	0.673±0.0250 (0.625-0.736)	6 7/8+ (6 1/2-7 1/2)	3.16±0.125 (2.94-3.41)
cookeana						
Sta. 863-65 (4700-6300')	6	4.01±0.161 (3.53-4.51)	7.60±0.146 (7.19-8.17)	0.528±0.0208 (0.467-0.600)	7 1/4- (6 3/4-7 1/2)	3.92±0.339 (3.03-5.00)

trail (Stations 869, 870) at 5,000 ft. elevation (10 specimens, BPBM 145490, BPBM 145532-5); Aorai trail (Station 867) at 4,700-6,300 ft. elevation (11 specimens, BPBM 145694-700); Mt. Aorai at 2,235 (?) m. (=7,360 ft.) elevation[1]. (1 specimen, FMNH 41007 collected by John N. Dixon on June 19, 1946).

Remarks. — The name *Helix bursatella* Gould, 1846, has been interpreted differently by each subsequent writer. The story of how the Wilkes shells became mixed is well known (see Johnson, 1964, pp. 10-11). Gould's description and figures represent several species. The Wilkes' collections were made between 2,000 and 5,000 ft. elevation (Gould, 1852, p. 53). Material studied by Garrett (1884) and other authors presumably came from the same or lower zones. Several specimens in museum collections (USNM 5452, USNM 20913-20919, MCZ 169066, MCZ 216751) are labelled as *Helix bursatella* and are presumed to be part of the Wilkes material. None of the specimens exactly match the type figures. The sets contain a mixture of at least four species, mostly represented by worn, partially fungus-eaten examples. Under these circumstances it was thought best to select a neotype that matches Gould's figures of the typical form and at the same time fix a precise type locality. Gould (1860, pl. 4, figs. 52, a-m) figured, under the name *Helix bursatella*, specimens of the form discussed here (figs. f-i, and probably k-m), *L. streptaxon* (figs. b-e) and *L. incognata* (fig. 52, a). Figures 52, f-i, which Gould stated in the plate explanations to be the "typical form," compare exactly with some of the material collected on Mt. Aorai. Gould's figured shell shows 94 ribs on the body whorl. This is so near the range shown by Mt. Aorai shells that I have no hesitation in designating Gould's figures f-i as representing *bursatella*, and in selecting a neotype (BPBM 142059 from Station 863, Mt. Aorai trail between 4,700 and 5,500 ft. elevation) to match these figures.

The possibility exists that two species are confused under this name. Dissection of material from Station 866 (the whole specimens had a much sharper peripheral angulation than in the type), produced a penis length of 4.3-4.5 mm. Dissection of specimens from Station 863 (BPBM 142059) showed three whole specimens that agreed with the type in peripheral angulation had penial lengths of 5.0-6.7 mm.; two of three fragmentary extracted specimens had penial

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[1] Since the elevation of Mt. Aorai is given as 7,321 ft., I doubt the accuracy of this elevation.

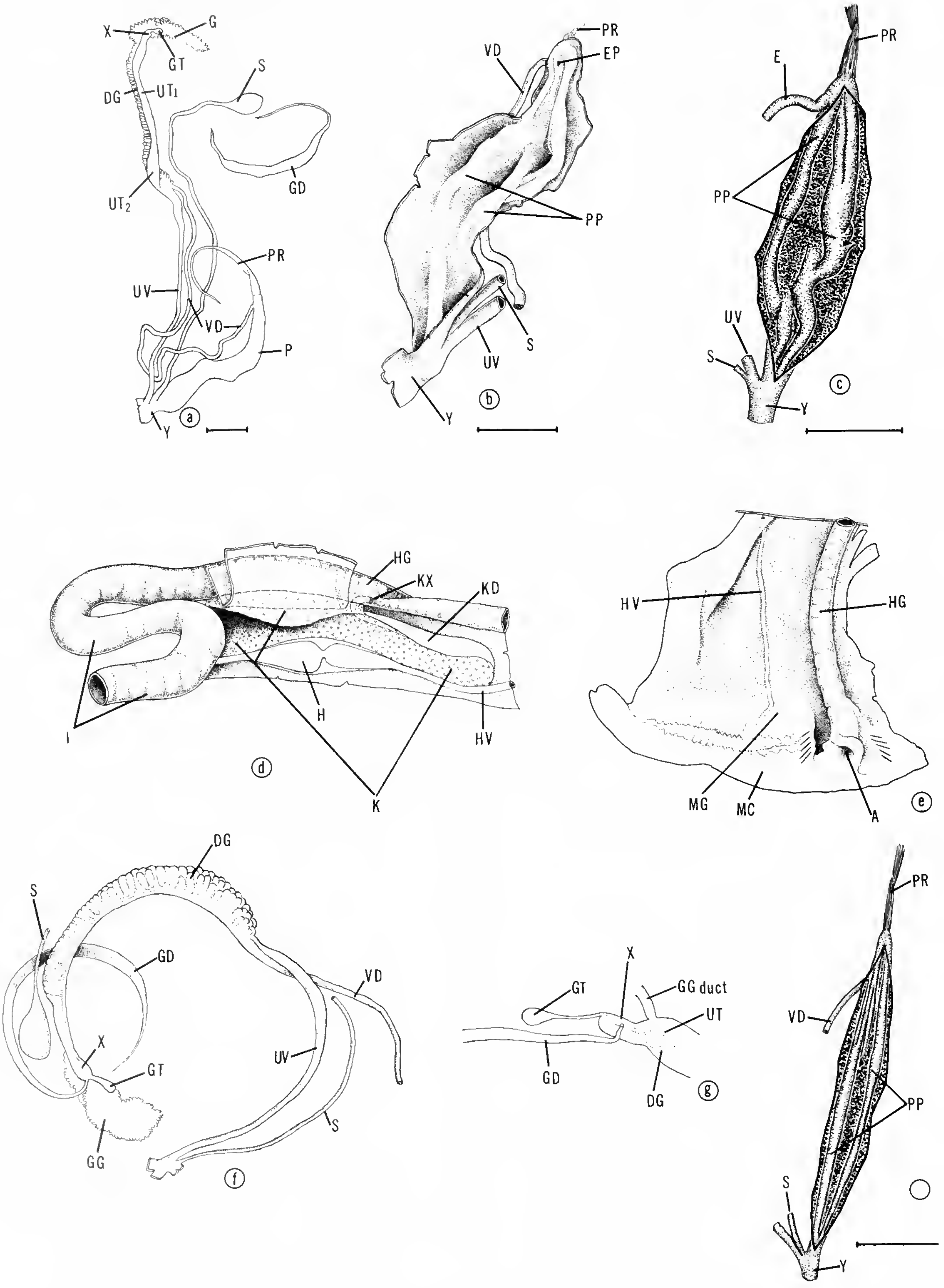

FIG. 171. Anatomy of *Libera;* **a-e**, *Libera bursatella bursatella.* Station 866, Mt. Aorai, Tahiti, Society Islands. BPBM 145394. *a,* genitalia, *b,* interior of penis, *c,* interior of penis, *d,* apical portion of pallial region, *e,* anterior portion of pallial region; **f-h**, *Libera micrasoma.* Station 865, Mt. Aorai, Tahiti, Society Islands. BPBM 145287. *f,* genitalia without penial region, *g,* detail of carrefour region, *h,* interior of penis. Scale lines equal 1 mm.

lengths of 5.1 and 7.0 mm.; and a third fragmentary example had a penis length of only 3.4 mm. (fig. 171c). No basic pilaster differences were noted.

Review of synoptic shell material indicated a partial dimorphism, with one form having an obtusely angulated periphery, the other being much more sharply angulated and occasionally acutely angulated at the periphery. Measurements of shells from the Mangarevan Expedition also produced discordant data. Specimens from Station 865 (BPBM 145392) that had been sorted out as "gerontic" at the Bishop Museum and "adult" examples from Station 865 (BPBM 145280-1) were proportionately much higher and with larger whorl counts (table CII) than the "light color phase" adults from Station 865 (BPBM 145290) or material from Stations 863 and 864. Since pill box capacity is limited and there were many specimens from the stations involved — Station 863 (169 specimens), Station 864 (35 specimens), Station 865 (62 specimens), and Station 866 (90 specimens) — these differences may partly reflect size bias introduced during sorting activities in the middle 1930's. I did not have enough material on loan or sufficient unextracted soft parts to see whether the penial and peripheral variations are correlated. Possibly there is sufficient material in the Bishop Museum to determine whether variation or sibling species are involved, but this will have to be investigated by others. Tentatively, I am treating the Mt. Aorai populations as one species. A similar dimorphism appears to be present in the Mt. Orofena populations (see below).

Some confusion of very young *Libera b. bursatella* and *Mautodontha aoraiensis* existed, since at least one specimen of the latter was located in a set (BPBM 142065) of "ananeanic" *Libera bursatella*. The two species are readily distinguished by the smaller nuclear whorls, narrower umbilicus, more ovate whorl contour, absence of palatal dentition, and absence of secondary spiral cording in the *Mautodontha*. The juvenile *Libera* have the body whorl laterally compressed, there is at least one palatal trace and the 2 parietals are more widely spaced and proportionately much lower.

Description of soft parts. — Foot truncated anteriorly, slightly tapering to tail, which is bluntly rounded behind. Sole undivided. Pedal grooves relatively low on foot, pedal much more prominent than suprapedal. Slime network prominent on sides of body and above tail. Head projecting in front of foot. Ommatophores partly retracted in all material, typical in eyespot size and color. Gonopore located just above foot margin, behind right rhinophore and just below right ommatophore.

Body color yellow-white, without darker markings.

Mantle collar (MC) very narrow, a prominent glandular extension onto mantle roof (fig. 171e). Pneumostomal opening narrow, without any mantle lobes or laps. Anus (A) with typical slanted opening just inside pneumostome.

Pallial region (fig. 171d, e) extending 1¼ - 1½ whorls apically. Lung roof clear, without granulations. Kidney (K) about 3.6 mm. long, rectal arm about 2.04 mm. long, laterally compressed with a slight turnover producing a narrow pocket in which the ureter opens. Ureter (KD) starting at apex of kidney, reflexed along rectal arm of kidney, opening next to hindgut just inside kidney foldover. Heart (H) about 1.45 mm. long, lying parallel to hindgut. Principal pulmonary vein (HV) slender, fusing with heavy glandular extension of mantle collar. Hindgut (HG) typical, extending slightly less than one-quarter whorl above apex of pallial cavity before deflecting into intestinal loops.

Ovotestis of palmately clavate alveoli, occupying one-half whorl above stomach apex, buried in albumen gland and angled as in *Endodonta* (fig. 163c). Hermaphroditic duct (fig. 171a, GD) very long, slender apically, medially swollen, continuing to about 0.67 mm. before junction with carrefour (X) where it narrows and becomes transparent. Albumen gland (GG) long and slender, broader basally. Talon (GT) elongated and slender with gradually bulbous head, carrefour (X) only slightly swollen, hidden by acini of albumen gland. Prostate (DG) with two or three rows of short acini opening into a narrow duct that continues past end of prostate as vas deferens. Uterus (UT) bipartite, upper half slenderer and with less glandular walls than in lower half, which extends beyond end of prostate.

Vas deferens (VD) lightly bound to peniovidual angle, passing up along penis, entering penis laterally about 0.2 mm. below apex between pilasters. Penial retractor (PR) arising from diaphragm at apex of pallial cavity, inserting directly onto head of penis. Penis (P) about 4.3-4.5 mm. long, slightly tapered at apex, irregularly swollen medially and near base, internally with two pilasters, high and complexly folded (fig. 171b, PP), one larger than other, not extending into atrium. Atrium (Y) short and rather wide.

Free oviduct (UV) much longer than prostate, very slender, no larger in diameter than vas deferens. Spermatheca (S) with ovately expanded head lying above pallial cavity along surface of albumen gland, slender shaft narrower than vas deferens and free oviduct, inserting directly onto peniovidual angle. Vagina absent.

Free muscle system very elongated, but without structural peculiarities. Right ommatophoral retractor passing through peniovidual angle, uniting with right rhinophoral retractor just posteriorly of buccal mass. Tentacular retractors unite with tail fan slightly more than one-third of way to apex of columellar muscle.

Buccal mass elongately oval, with very slender generative sac. Buccal retractors not split, inserting on posterior margin of buccal mass, joining tail fan laterally about 5 mm. below columellar muscle apex. Stomach extending from one-quarter whorl above apex of pallial cavity for 1¼ whorls, early expansion occupying one-eighth whorl. Intestinal looping typical, occupying one-quarter whorl.

Digestive glands extending four whorls above ovotestis to nuclear whorls in preserved adults. Salivary glands lying lateral to esophagus, weakly joined posteriorly above.

(Based on BPBM 145394, whole individual 5.26 mm. in diameter with 7⅜+ whorls and several extracted examples.)

Libera bursatella orofenensis, new subspecies. Figure 174d-f.

Diagnosis. — Shell smaller than average, diameter 4.71-5.56 mm. (mean 5.17 mm.), with 6⅜-7¾ normally coiled whorls. Apex barely protruding or rarely flat, whorls of spire descending progressively more rapidly, last whorl not descending more rapidly, H/D ratio 0.512-0.688 (mean 0.599). Umbilicus secondarily narrowed to form brood chamber by regular and gradual inward extension of basocolumellar margin, opening in adult circular to subcircular, contained 3.30-5.33 times (mean 4.15) in the diameter. Postnuclear whorls with prominent, crowded, somewhat finer than in nominate subspecies, strongly protractively sinuated radial ribs, 158-185 (mean 171.8) on the body whorl, whose interstices are 1-2 times their width. Microsculpture of rather prominent radial riblets, two to four between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification. Secondary sculpture of low and broadly rounded, quite crowded spiral cords, that are most prominent on shell base. Sutures impressed, whorls flatly rounded down to obtusely rounded or angulated periphery, lower palatal and basal margins flatly rounded down to acutely angled and strongly protruded baso-columellar margin, with a distinct sulcus outside the angulation. Aperture subovate, flatly rounded above and below obtusely rounded or angulated periphery, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly slightly less than one-quarter whorl, sometimes (6.3 per cent) with lower one absent: upper low and bladelike, very weakly expanded above on posterior third, with very gradual anterior descension; 2nd equal in height to upper posteriorly, deeply recessed, equal to about half the length of upper. Columellar wall flatly rounded and convex internally, without barriers. Palatal wall normally with 2 barriers, frequently (25 per cent) with only 1 present, occasionally with a 3rd palatal (6.3 per cent) or with all palatals absent (6.3 per cent): both palatals subperipheral, low and bladelike, very weakly expanded above, with gradual anterior descension, moderately deeply recessed within aperture.

The more numerous radial ribs (158-185) of *Libera bursatella orofenensis* immediately separate it from *Libera bursatella bursatella* with only 98-161 major radial ribs. The Moorean species, *L. recedens* and *L. gregaria,* have similar ribbing counts, but both have a prominent columellar barrier. The very small *Libera umbilicata* from Mt. Orofena has the parietals of equal length and less than 35 major ribs, whose interstices are 6-9 times their width.

Description. — Shell of less than average size, with 7¼ normally coiled whorls. Apex and early spire somewhat flattened, lower whorls descending progressively more rapidly, H/D ratio 0.608. Embryonic whorls 1⅜, sculpture of larger radials with two fine riblets between each pair, and extremely close-set and very faint microspirals. Postnuclear whorls with prominent, narrow, relatively crowded, strongly protractively sinuated radial ribs, 158 on the body whorl, whose interstices are less than twice their width. Microsculpture of relatively prominent radial riblets, two to four between each pair of major ribs, with barely visible and extremely crowded microspirals. Secondary microsculpture of low, broadly rounded spiral cords that are most prominent on shell base. Sutures impressed, whorls evenly and gently rounded down to obtusely angled periphery, with lower palatal and basal margin gently and evenly rounded to inwardly protruded and sharply angled baso-columellar margin. Color light yellow horn, with prominent, broad, somewhat irregular, reddish flammulations. Umbilicus typically narrowed to form brood chamber, opening circular, contained 3.95 times in the diameter. Aperture subovate, gently rounded above and below obtusely angled periphery, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly almost one-quarter whorl: upper moderately elevated, very slender, weakly expanded on posterior third, with gradual anterior descension; 2nd equal in height posteriorly to upper, slightly more than half length of upper, deeply recessed within aperture. Columellar wall convex internally with a moderate callus, without barriers. Palatal barriers 2, rather deeply recessed, extending posteriorly about one-eighth whorl: both elevated and bladelike with gradual anterior descension. Height of holotype 3.14 mm., diameter 5.17 mm.

Holotype. — Society Islands: Tahiti, Station 945, south ridge of Mt. Orofena at 5,700-6,600 ft. elevation. Collected by Harold St. John and Raymond Fosberg on September 25, 1934. BPBM 145574.

Range. — Upper Papenoo Valley and Mt. Orofena at 4,000-6,000 ft. elevation, Tahiti, Society Islands.

Paratypes. — Same as list of material.

Material. — Tahiti: east end of south ridge, Mt. Orofena (Stations 949, 956) at 4,500 ft. elevation (19 specimens, BPBM 145653, BPBM 145811-9); south ridge of Mt. Orofena (Stations 944-6) at 5,000-6,600 ft. elevation (17 specimens, BPBM 142351-2, BPBM 145574-5, BPBM 145587-90); Papenoo Valley (Station 952) at 4,000 ft. elevation (1 specimen, BPBM 145625); ridge of Papenoo Valley (Station 954) at 5,200-5,500 ft. elevation (3 specimens, BPBM 145844-6).

Remarks. — The figured paratype of *Libera bursatella orofenensis* is exceptionally elevated and has the periphery less angulated than usual. It does illustrate the sculptural difference from the nominate race very well. Mean size and shape differences (table C) from *L. b. bursatella* are insignificant, particularly when the large interpopulational variation (table CII) is noted. Only in regard to early whorl diameter is there a distinct difference (table CI), with the nominate race being larger.

Only 40 *orofenensis* (16 adult) were collected, compared with 384 *bursatella* (74 adult). The shift in quantity and percentage of adults results from collecting bias. The Mangarevan Expedition botanists, H. St. John and R. Fosberg, who made the collections of *L. b. orofenensis,* could be expected to collect fewer juveniles and a smaller total quantity than would the malacological assistants, Anderson and Kondo, who collected *L. b. bursatella.* Hence the 40 per cent adult ratio in *orofenensis* probably is considerably inflated by collecting bias and the 19.3 per cent ratio in *L. b. bursatella* would be more accurate.

Differences between the two populations with several adults, (table CII), Stations 946 and 949, are marked and statistically significant. With 9 df, "*t*" = 2.1520 for height, 2.260 for diameter, and 3.8075 for H/D ratio. The differences are the same order of magnitude as those found between the nominate race populations discussed above. The differences probably are not age connected. The specimens with lower whorl count have a distinctly narrower umbilicus and hence are nearer to full adulthood, while the specimens with higher whorl count have a wider umbilicus and were less adult in their growth characters. The smaller diameter of the latter is caused by their greater height and change in coiling pattern.

The only sympatric species, *L. umbilicata,* is immediately separable by its very widely spaced radial sculpture, much smaller size (mean diameter 3.71 mm.), and in having the 2 parietal barriers equal in length. The Moorean *Libera recedens* and *L. gregaria* have very similar sculpture, but are much larger, more depressed, have a prominent columellar barrier and 3 palatals.

Description of soft parts. — Only broken extracted specimens were available for study. Preservation was poor and no illustrations were prepared. The penis was short, 2.5-3.3 mm. long in three examples, but had the same pilaster pattern seen in the nominate subspecies. Whether the size difference is a factor of age or systematically important is uncertain.

(Based on BPBM 145584, four partial examples.)

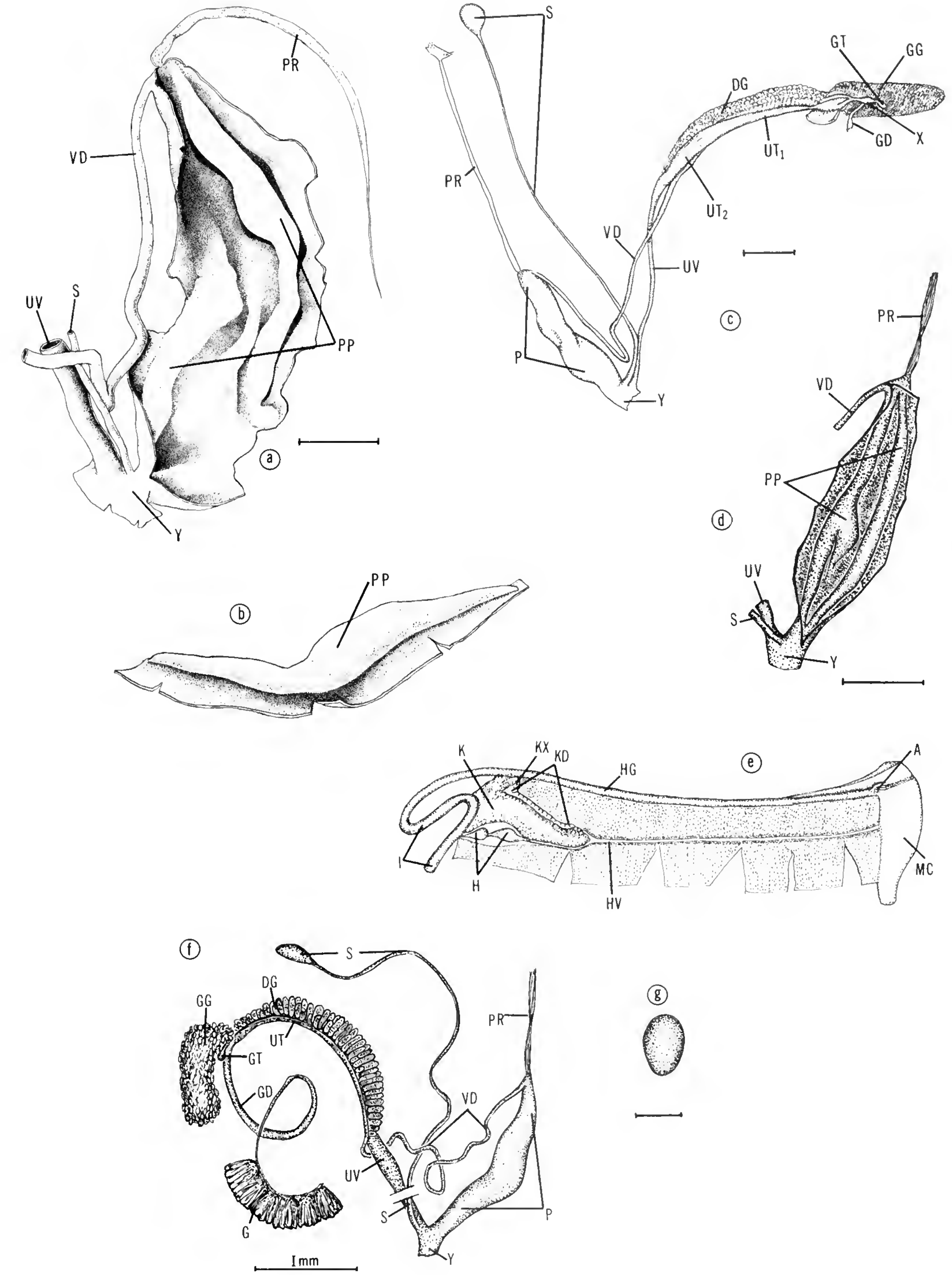

FIG. 172. Anatomy of *Libera:* **a-b**, *Libera cookeana.* Station 865, Mt. Aorai, Tahiti, Society Islands. BPBM 145289. *a,* interior of penis, *b,* lateral view of raised pilaster; **c-g**, *Libera fratercula rarotongensis.* Station 6, 2 miles east of Avarua, Rarotonga, Cook Islands. FMNH 144556. *c, f,* genitalia (angle of ovotestis incorrect), *d,* interior of penis, *e,* pallial region, *g,* egg. Scale lines equal 1 mm.

Libera cookeana, new species. Figures 172a, b; 173a, b.

Diagnosis. — Shell very large, diameter 7.19-8.17 mm. (mean 7.60 mm.), with 6¾-7½ normally coiled whorls. Apex and early spire slightly elevated, whorls of lower spire descending progressively more rapidly, body whorl distinctly deflected below periphery of penultimate whorl, H/D ratio 0.467-0.577 (mean 0.528). Umbilicus secondarily narrowed to form brood chamber by gradual inward expansion of sharply angled baso-columellar margin, opening in adult subcircular, contained 3.03-5.00 times (mean 3.92) in the diameter. Postnuclear whorls with rather low, prominent, strongly protractively sinuated radial ribs, 85-95 (mean 91.4) on the body whorl, whose interstices are 2-3 times their width. Occasional traces of typical microradial ribbing remaining, but all specimens with sculpture worn and only slight traces of any sculpture below periphery of body whorl. Sutures deep, whorls rather strongly rounded down to very obtusely angulated periphery, lower palatal and basal margins more gently and evenly rounded down to distinct sulcus before baso-columellar angulation. Aperture subovate, more strongly rounded above than below periphery, inclined about 30 - 35° from shell axis. Parietal barriers 2, extending posteriorly almost one-quarter whorl: upper rather sharply elevated and weakly expanded on posterior quarter, moderately abrupt descension to raised ridge-like anterior two-thirds; lower with posterior portion equal in height and length to upper, anterior segment absent or retained (one of six specimens) as a vague threadlike trace. Columellar wall with a low, deeply recessed, very broad and rounded barrier, visible only by extreme tilting of aperture. Palatal barriers 3, moderately deeply recessed, extending posteriorly less than one-eighth whorl: lower 2 subperipheral, quite elevated, thin and slender, only weakly expanded above, upper less flattened above and with more gradual anterior descension; 3rd supraperipheral, a short, low inconspicuous threadlike trace.

The much larger adult size without any increase in whorl count, more widely spaced radial ribbing, distinct columellar barrier, and presence of a 3rd palatal immediately separate *Libera cookeana* from the sympatric *L. bursatella bursatella*. The only other Society Islands species of similar size, *L. incognata,* differs in its greatly reduced ribbing (43-55 major ribs), proportionately higher spire (mean H/D ratio 0.650), and generally higher whorl count.

Description. — Shell very large, with 7½ normally coiled whorls. Apex slightly protruding, lower whorls of spire descending progressively more rapidly, body whorl deflected below level of penultimate whorl periphery, H/D ratio 0.577. Apical sculpture and sculpture on early spire completely eroded, sculpture visible in umbilicus as typical radial ribbing. Postnuclear whorls with prominent, broadly rounded, rather widely spaced radial ribs, 91 on the body whorl, whose interstices are 2-4 times their width. Surface worn, but microsculpture occasionally visible as five to eight relatively large riblets between each pair of major ribs, with very occasional traces of secondary spiral cording. Surface too worn to detect status of any spiral microsculpture. All traces of color leached from shell. Umbilicus secondarily narrowed to form brood chamber by inward growth of baso-columellar margin, last whorl at aperture showing evidence of parietal wall detachment, opening subcircular except for detachment area, contained 3.87 times in the diameter. Aperture subovate, gently rounded above and below obtusely angled periphery, inclined about 30° from shell axis. Parietal barriers 2, extending posteriorly almost one-quarter whorl: upper high and bladelike, distinctly more highly elevated on posterior quarter, anterior half a low, raised lamellar ridge; 2nd parietal deeply recessed, equal in height and with same shape as elevated posterior portion of upper parietal, about half the length of upper parietal. Columellar wall with single low and broadly rounded lamellar trace, visible clearly only by extreme tilting of aperture. Palatal barriers 3, deeply recessed within aperture, extending posteriorly more than one-eighth whorl: lower 2 subperipheral, high and bladelike, 2nd slightly higher, flattened on top, with progressively more gradual anterior descension; 3rd a weak, supraperipheral, short, very deeply recessed threadlike trace. Height of holotype 4.38 mm., diameter 7.68 mm.

Holotype. — Society Islands: Tahiti, Station 865, Mt. Aorai, near top of trail at 5,600-6,300 ft. elevation. Collected by E. Zimmerman, Y. Kondo, and D. Anderson on September 15, 1934. BPBM 145289.

Range. — Mt. Aorai at 4,700-6,300 ft. elevation, Tahiti, Society Islands.

Paratypes. — Same as list of material.

Material. — Tahiti: near top of Mt. Aorai trail (Station 865) at 5,600-6,300 ft. elevation (3 specimens, BPBM 145289, BPBM 145924-5); Mt. Aorai (Station 863) at 4,700-5,500 ft. elevation (1 specimen, BPBM 145912); Mt. Aorai (Station 864) at 5,500-5,600 ft. elevation (2 specimens, BPBM 145922).

Remarks. — Scattered individuals of this species were taken at stations where *Libera bursatella bursatella* was common to abundant. At first glance, *L. cookeana* would be taken for a gerontic specimen of that species. The gap between the largest *L. bursatella* (diameter 5.88 mm.) and the smallest *L. cookeana* (diameter 7.19 mm.) is substantial. In addition, *L. cookeana* has a distinct columellar barrier, a 3rd palatal, with less frequent and much more widely spaced radial ribs (ribs/mm. 3.52-3.84 in *cookeana*; 6.12-8.95 in *bursatella*). The early whorl diameter in *L. cookeana* (table CI) is identical at three whorls, but diverges rapidly at five whorls and beyond. Juvenile specimens of the two species might be difficult to separate except by rib counts and spacing. No juveniles of *L. cookeana* were available, but a few juvenile *L. bursatella* had a 3rd palatal present so that this character cannot be relied upon for separation.

Species with occasional huge gerontic individuals, such as *Minidonta simulata* (fig. 70d), have the larger shells with greatly reduced apertural barriers; hence, the presence of a columellar and one additional palatal in these specimens, compared with *L. bursatella,* greatly lowers the possibility that they are gerontic shells. In addition, the penial pilaster of *L. cookeana* (fig. 172a, b) is quite different from that found in *L. bursatella* (fig. 171b, c), its grossly unequal pilasters contrasting strongly with the subequal pilasters in the latter.

Description of soft parts. — Foot and tail typical, slightly tapering and bluntly rounded posteriorly. Sole undivided. Pedal grooves prominent, rather high on foot. Head and ommatophores typical. Gonopore in normal position.

Body color yellow-white, without darker markings.

Mantle collar thicker than in *L. bursatella,* without glandular extension onto pallial roof.

Pallial region about 14 mm. long. Lung roof clear, without granulations. Kidney with very vague outline, poorly preserved. Ureter typical. Heart very small, proportionately. Principal pulmonary vein a narrow tube fading out shortly before mantle collar. Hindgut typical.

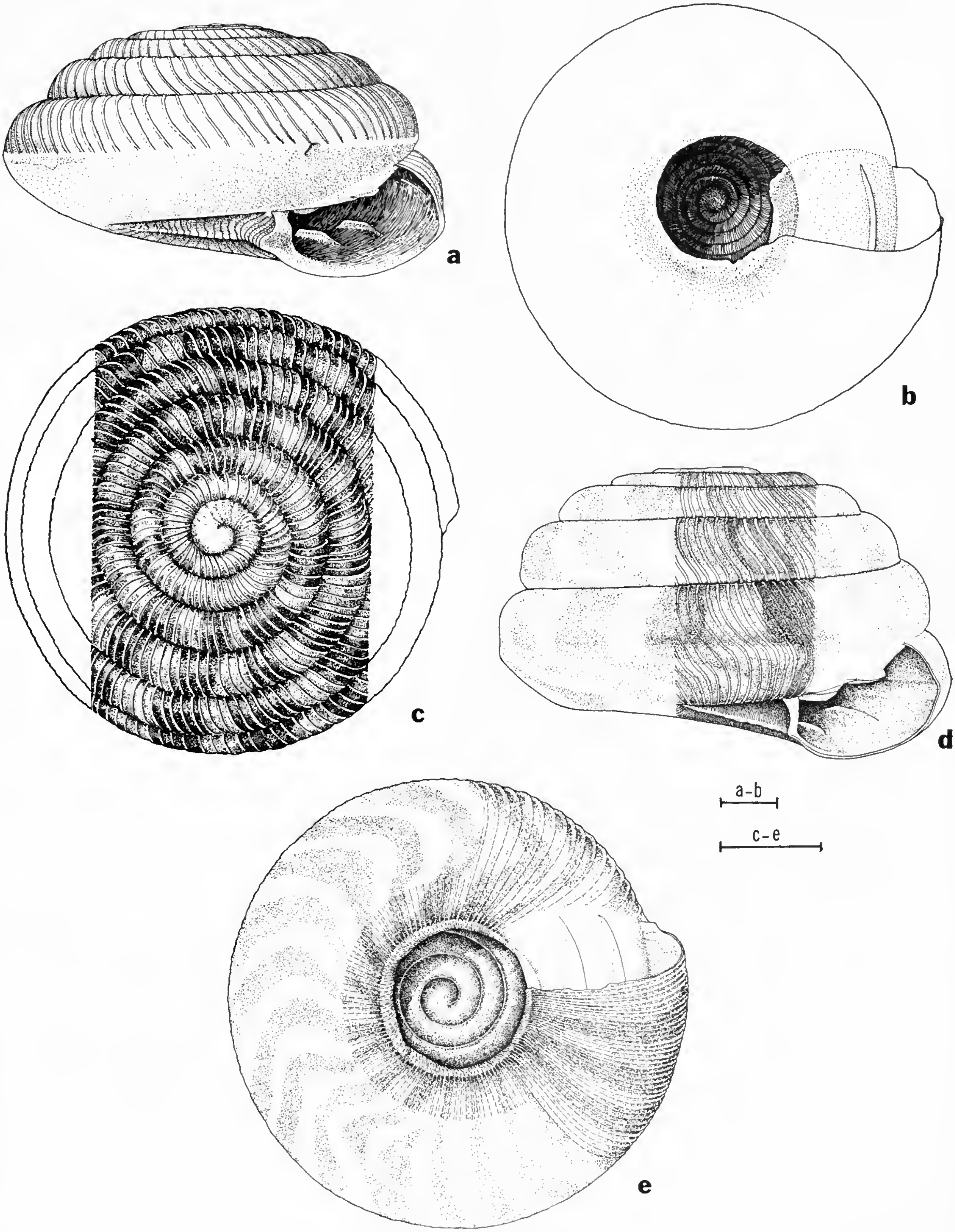

FIG. 173. **a-b**, *Libera cookeana*, new species. Station 865, Mt. Aorai, 5,600-6,300 ft. elevation, Tahiti, Society Islands. Holotype. BPBM 145289; **c-e**, *Libera micrasoma*, new species. Station 865, Mt. Aorai, 5,600-6,300 ft. elevation, Tahiti, Society Islands. Holotype BPBM 145287. Scale lines equal 1 mm. Figure *d* shows microradial ribbing on part of last two whorls. Figures *a-b* by YK reproduced through the courtesy of Bernice P. Bishop Museum; *c-e* (MM).

Ovotestis could not be located in apical liver mass. Hermaphroditic duct as in *L. bursatella*. Albumen gland, talon, and carrefour not differentiated from simple S-loop connecting head of prostate-uterus to hermaphroditic duct. Prostate proportionately of very small acini, opening into narrow tube. Uterus bipartite, proportionately larger than prostate, normal in size.

Vas deferens entering penis about 0.25 mm. below apex, lightly attached to penioviducal angle. Penial retractor arising from diaphragm, inserting directly on head of penis. Penis (fig. 172a, P) about 5.9 mm. long, tapering apically, sharply constricted at base, evenly expanded medially. Internally with a single high pilaster extending from atrium to apex, lower and broadly rounded on basal quarter, with a second much lower and more broadly rounded pilaster on lower half of penis. Atrium short, relatively broad.

Free oviduct equal in length to prostate, same diameter as vas deferens. Spermatheca with very small oval head, shaft much slenderer than free oviduct, inserting directly onto penioviducal angle.

Free muscle system as in *Libera bursatella*.

Buccal mass slender and elongated, with small generative sac.

(Based on BPBM 145289, two fragmentary examples.)

Libera gregaria Garrett, 1884. Figure 175a-c.

Libera gregaria Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 36, pl. 2, figs. 6, a, b – southwest part of Moorea, Society Islands; Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), p. 42.

Helix (*Libera*) *gregaria* (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 72, pl. 13, figs. 83-84.

Endodonta (*Libera*) *gregaria* (Garrett), Pilsbry, 1893, *op. cit.*, (2), 9, p. 24.

Diagnosis. – Shell quite large, diameter 6.27-7.26 mm. (mean 6.72 mm.), with 6¾-7½ normally coiled whorls. Apex and early spire flat or barely elevated, whorls of spire descending slightly more rapidly, body whorl usually deflected slightly below periphery of penultimate whorl, rarely deflected markedly, H/D ratio 0.437-0.577 (mean 0.498). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of baso-columellar margin during last whorl and one-half, near aperture closure speeded by partial detachment of parietal wall, opening highly irregular in shape and size. Postnuclear sculpture of narrow, broadly V-shaped, protractively sinuated, rather crowded radial ribs, 155-198 (mean 177.8) on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, four to six between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets, occasionally with traces of narrow, rather widely spaced secondary spiral cording. Sutures shallow, whorls flatly rounded down to distinct supraperipheral sulcus, periphery weakly protruded into a threadlike keel, lower palatal wall with a distinct subperipheral sulcus, evenly and more strongly rounded down to very prominent sulcus before baso-columellar margin. Columellar wall deeply concave and U-shaped due to extreme umbilical narrowing. Aperture subquadrangular, more strongly rounded below than above protruded periphery, inclined about 25° from shell axis. Parietal barriers 2, rarely (2 per cent) a 3rd present, extending posteriorly to line of vision: upper parietal slightly more elevated and expanded above on posterior third, with very gradual anterior descension; 2nd parietal equal in height posteriorly, anterior half threadlike, extending slightly beyond end of upper parietal. Columellar wall deeply concave, surmounted by prominent, crescentic, broad barrier, that twists distinctly upward from plane of coiling during its descent across top of columellar callus. Palatal barriers 3, rarely 2, moderately deeply recessed, extending posteriorly about one-eighth whorl: lower basal in position, high and slender, flattened above on posterior half, with rather gradual anterior descension; 2nd palatal usually slightly reduced in height, more flattened above, with more gradual anterior descension, situated midway between lower palatal and periphery; 3rd palatal, when present, supraperipheral, greatly reduced in height, a raised threadlike trace more deeply situated within aperture.

The large size, threadlike anterior termination of the 2nd parietal and generally only slight deflection of the body whorl combine to separate *Libera gregaria* from the otherwise extremely similar *L. recedens,* in which the periphery is normally markedly deflected, there is no threadlike anterior half to the 2nd parietal, and the mean diameter is more than a millimeter less (5.69 mm.). Juvenile examples can be separated on the basis of five whorl diameter, which is 2.1 mm. or less in *L. recedens* and generally 2.3 mm. or more in *L. gregaria.*

Description. – Shell large, with slightly more than 7½ relatively loosely coiled whorls. Apex and early spire flat, later whorls descending moderately, body whorl slightly deflected, depressed-helicoidal in form, H/D ratio 0.524. Apical whorls and upper spire with sculpture eroded. Lower spire and body whorl with fine, protractively sinuated radial ribs, about 170 on the body whorl, whose interstices are about twice their width. Microsculpture eroded. Sutures shallow, whorls flatly rounded above acutely angulated periphery, evenly rounded on basal margin. Color mainly leached from shell with traces of reddish maculations remaining. Umbilicus strongly constricted to form brood chamber by growth of last whorl and a half. Partial parietal wall detachment produced a thin plate that covered much of the umbilicus and sealed several embryos inside the brood chamber. Aperture subcrescentic, flattened laterally above protruded periphery, inclined about 20° from shell axis. Parietal barriers 2, extending slightly more than one-quarter whorl: upper high and lamellate, elevated on posterior third, with very gradual anterior descension; lower parietal equally high posteriorly but with anterior half low and threadlike. Columellar wall with heavy callus surmounted by a high, broadly rounded barrier, with gradual anterior descension, extending up onto shell lobe that constricts umbilicus. Palatal barriers 3, moderately recessed, about one-eighth whorl long: lower 2 subperipheral, high, crescentic, bladelike, with gradual anterior descension; 3rd palatal V-shaped, shorter, supraperipheral, threadlike. Height of lectotype 3.59 mm., diameter 6.86 mm.

Lectotype. – Society Islands: southwest part of Moorea. Collected by Andrew Garrett. ANSP 47825.

Range. – Two valleys on southwest part of Moorea, Society Islands (Garrett, 1884, p. 36).

Paratypes. – BPBM 4881, ANSP 290106.

Material. – Moorea (74 specimens, BPBM 4881, BPBM 167412, FMNH 156776, RSM 1961.61.56). Unlocalized and Society Islands (27 specimens, BPBM 8597-8, BPBM 87517, FMNH 46359, ANSP 47825, ANSP 290106).

Remarks. – Typical adults of *Libera recedens* and *L. gregaria* are readily separable by the smaller size (table C) and much greater whorl deflection of the former. Juveniles and specimens of *L. gregaria* with abnormally large body whorl deflection can be separated by the distinct differences in early whorl diameter (table CI). Although Garrett's figures suggest that *L. recedens* is much more sharply keeled, this is not a reliable character for separation. The differences cited above should be relied on for identification.

Available material was not dimorphic in any character measured, so that there is no evidence of

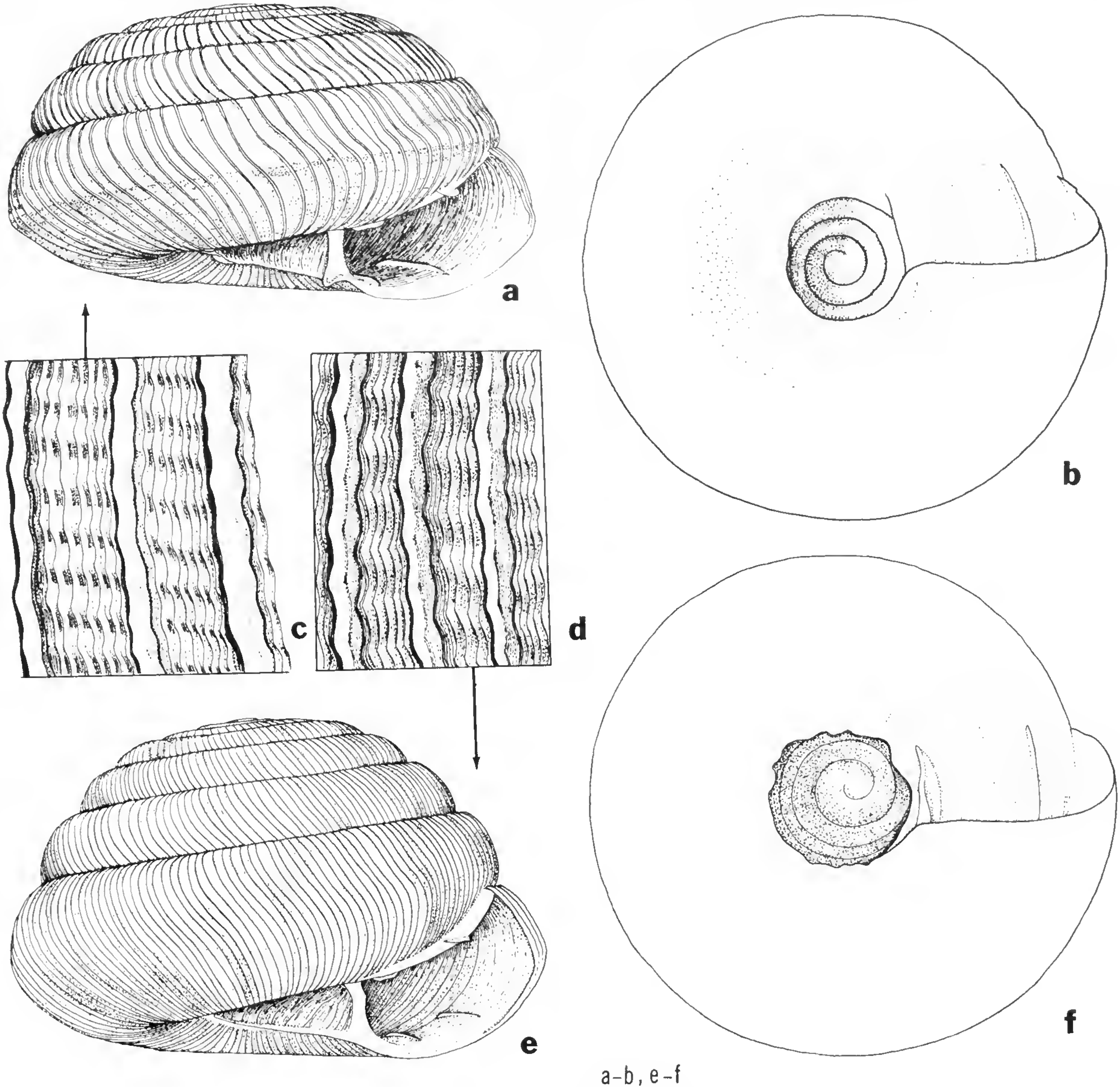

FIG. 174. **a-c**, *Libera bursatella bursatella* (Gould). Station 863, Mt. Aorai, 4,700-5,500 ft. elevation, Tahiti, Society Islands. Neotype of *Helix bursatella* Gould, 1846. BPBM 142059; **d-f**, *Libera bursatella orofenensis*, new subspecies. Station 946, Mt. Orofena, 5,500-5,700 ft. elevation, Tahiti, Society Islands. Paratype. BPBM 145587. Scale line equals 1 mm. Figures *c* and *d* have microsculpture omitted from major ribs and do not show microspiral ribbing. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

differences between populations in the two valleys. Unfortunately, Garrett did not name the valleys or indicate associated species. They were found "congregating in immense numbers on the underside of loose stones." (Garrett, 1884, p. 36). The large size of specimens from Garrett's collection (table CIII, BPBM 4881) probably reflects collection bias, Garrett having retained large specimens for his own collection.

Comments on the unusual form of umbilical closure are given below under *L. recedens*.

Libera recedens Garrett, 1884. Figures 170; 175 d-f.

Libera recedens Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 36, pl. 2, fig. 7 – one valley on west side of Moorea, Society Islands; Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), p. 42.

Helix (*Libera*) *recedens* (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 72, pl. 13, fig. 85.

Endodonta (*Libera*) *recedens* (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, pp. 23-24, pl. 9, fig. 34 (radula).

Diagnosis. – Shell of average size, diameter 5.36-6.67 mm. (mean 5.66 mm.), with 6⅝-7½ normally coiled whorls. Apex usually slightly

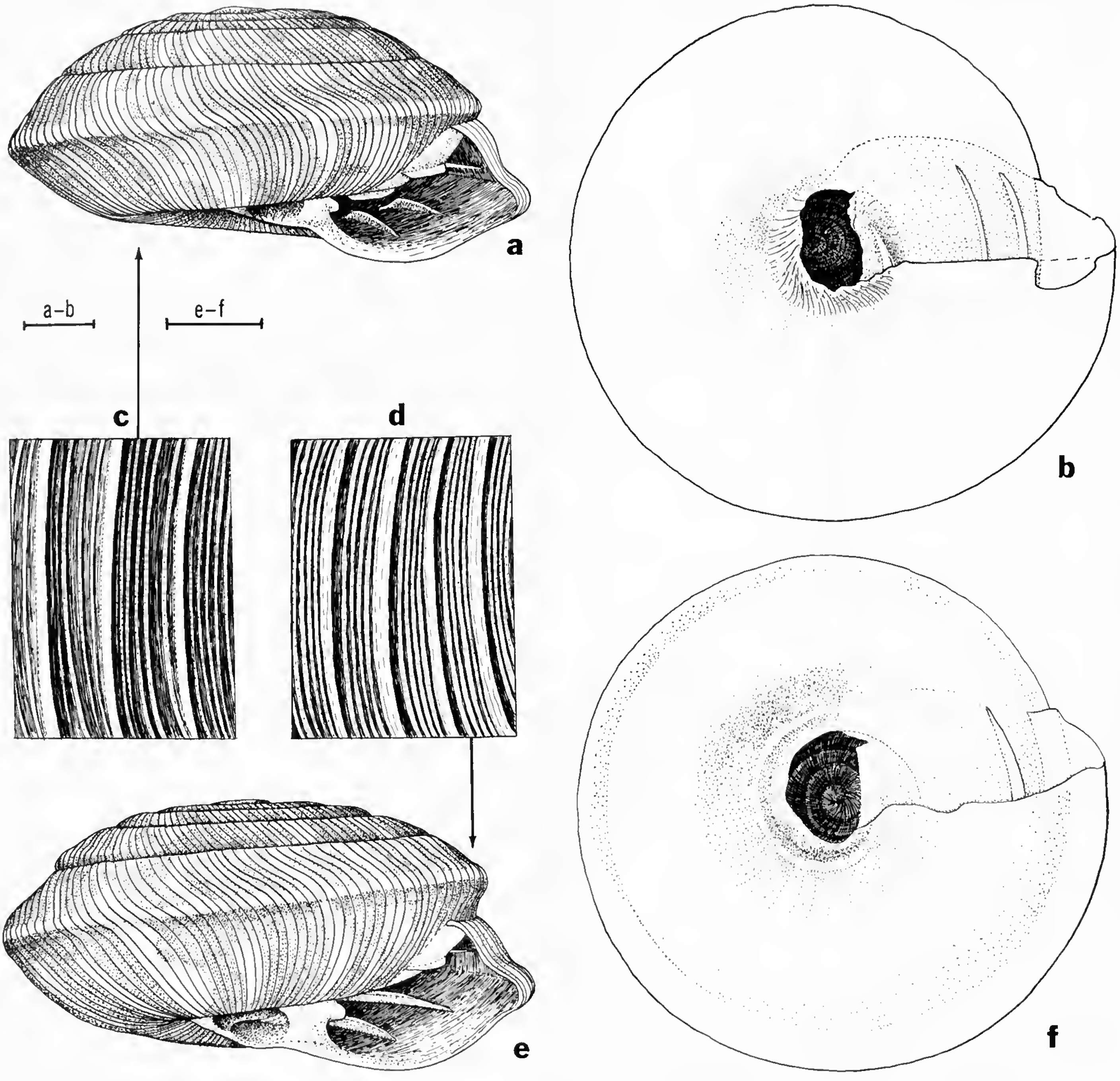

FIG. 175. **a-c**, *Libera gregaria* Garrett. Moorea, Society Islands. Paratype. BPBM 4881; **d-f**, *Libera recedens* Garrett. Moorea, Society Islands. Paratype. BPBM 2682. Scale lines equal 1 mm. Microsculpture on major ribs and microspirals omitted in *c* and *d*. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

elevated, lower whorls of spire descending progressively more rapidly, body whorl deflected drastically below periphery of penultimate whorl, H/D ratio 0.464-0.627 (mean 0.553). Umbilicus gradually narrowed at first by inward growth of baso-columellar margin, drastically narrowed on last whorl of growth by combination of parietal wall detachment and continued inward growth of baso-columellar margin, opening in adult very narrow and irregular so that measurements could not be made in a meaningful fashion. Postnuclear whorls with narrow, low, broadly V-shaped, protractively sinuated radial ribs, 152-198 (mean 178.2) on the body whorl, whose interstices are 3-5 times their width. Microsculpture a lattice of very fine radial riblets, five to eight between each pair of major ribs, crossed by distinctly finer and more crowded spiral riblets. A secondary sculpture of fine, rather widely and irregularly spaced spiral cords is visible on various portions of better preserved specimens. Sutures shallow, whorls flatly rounded down to prominent supraperipheral sulcus, periphery a broadly rounded and protruded keel, subperipheral sulcus stronger than supraperipheral, lower palatal and basal margins evenly and rather strongly rounded down to very prominent sulcus just before knife-edge baso-columellar margin. The extreme body whorl deflection and resultant parietal wall detachment has combined with the strong inward growth of the baso-columellar margin to produce a characteristic deep concavity on the columellar wall at the aperture which is not duplicated by other *Libera* (fig. 170). Aperture subquadrangular, more strongly rounded below than above, periphery markedly protruded, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper high and bladelike, slightly more elevated on posterior visible third, with very gradual anterior descension until just before termination; 2nd parietal about one-half length of upper parietal, recessed to midpoint of upper, equally high and expanded above posteriorly, with rather sharp descension, very rarely (2 of 95) with an anterior threadlike extension to point opposite end of upper parietal. Columellar wall distorted by pattern of growth, surmounted by a very broad and prominent, crescentic barrier that twists slightly upward from plane of coiling during its descent across middle of columellar callus. Palatal barriers 3, rarely with supraperipheral greatly reduced or absent, extending posteriorly about three-sixteenths of a whorl, deeply recessed within aperture: lower basal in position, high and slender, flattened above on posterior half with rather sharp anterior descension; 2nd midway between 1st palatal and periphery, slightly reduced in height, a little longer, with more gradual anterior descension; 3rd supraperipheral, located nearer periphery than parietal-palatal margin, greatly reduced in height, a ridgelike barrier with very gradual anterior descension, usually slightly shorter than 2nd palatal.

Adult specimens of *Libera recedens* can be separated from its close relatives, *L. gregaria,* by its smaller size, abrupt deflection of the body whorl below the periphery of the penultimate, absence of a threadlike anterior half to the 2nd parietal, and generally greater H/D ratio. Of the Tahitian species, only *L. bursatella* has similar appearing and spaced sculpture. It differs most obviously in its complete absence of a columellar barrier.

Description. — Shell of average size, with slightly more than 7⅛ normally coiled whorls. Apex and spire slightly elevated, weakly rounded above, last two-thirds of body whorl descending rapidly and strongly deflected below periphery, parietal wall partly detached, H/D ratio 0.494. Apical whorls 1½, sculpture mostly eroded. Postnuclear whorls with low, broadly rounded, protractively sinuated radial ribs, about 165 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by much finer and more crowded spiral riblets and a few irregularly spaced spiral cords that are most prominent on shell base. Sutures shallow, whorls flatly rounded above protruding periphery with prominent supraperipheral and subperipheral sulci. Color light yellow horn with narrow, crowded, zigzag, reddish flammulations. Umbilicus partially constricted by accelerating inward growth of baso-columellar margin over last whorl and a half, parietal wall detached and nearly closing umbilical opening. Aperture subcrescentic, with protruding periphery, inclined about 30° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper low and bladelike, becoming higher on posterior third; lower posteriorly equal in height but recessed to midpoint of upper, with sharper anterior descension. Columellar barrier high, broadly twisted up onto shell lobe, with gradual anterior descension. Palatal barriers 3, recessed, extending about three-sixteenths of a whorl: 2 lower subperipheral, thin, bladelike ridges with gradual anterior descension, flattened and expanded above on posterior two-thirds, with gradual anterior descension; upper a low, threadlike ridge situated one-third of way between periphery and upper palatal margin, shorter and more deeply recessed. Height of lectotype 2.94 mm., diameter 5.94 mm.

Lectotype. — Society Islands: west side of Moorea. Collected by Andrew Garrett. ANSP 47827.

Range. — Lower part of one valley on west side of Moorea, Society Islands (Garrett, 1884, p. 36).

Paratypes. — ANSP 290107, BPBM 2682.

Material. — Moorea (55 specimens, BPBM 2682, BPBM 167413, FMNH 46425, FMNH 156777, AMS, Edinburgh). Society Islands (5 specimens, ANSP 47827, ANSP 290107, FMNH 117054). No locality (1 specimen, Edinburgh).

Remarks. — The lectotype has the umbilical-parietal shield broken. It is almost certainly the specimen figured in Garrett (1884, pl. 2, fig. 7), and is more sharply angulated than most specimens.

L. recedens and *L. gregaria* are obviously closely related, differences in the body whorl deflection causing the size and shape changes (table C). Specific separation, rather than subspecific, is indicated because of the marked early whorl size difference (table CI) and lack of intermediate specimens. Rib counts of the two species are identical, 178.2 for *recedens* and 177.8 for *gregaria,* the significant difference in rib spacing, 9.57 in *recedens* and 8.16 in *gregaria,* being an artifact of reduced diameter in the former caused by greater whorl deflection.

Comparing mean dimensions of the two species (tables C, CI), *L. recedens* is 6.3 per cent smaller at three whorls; 8.4 per cent at four whorls; 12.1 per cent at five whorls; 15.8 per cent at adult size; but only 6.8 per cent less in adult height — reflecting the greater body whorl deflection. The increase of 9.9 per cent in mean H/D ratio for *L. recedens* is caused by the greater body whorl deflection and more than compensates for the slightly lower H/D ratio to be expected in a smaller shell.

Pilsbry (1893-1895, p. 23, pl. 9, fig. 34) illustrated eight radular teeth of *L. recedens* and reported a formula of 15-1-15. He did not differentiate between lateral and marginal teeth in the count, but did in his discussion. The figures show no differences from those of other *Libera* examined during this study that can not be interpreted as caused by differences in optical equipment.

Both *L. gregaria* and *L. recedens* have unusual umbilical closures that result in irregular narrowing of the openings, making meaningful measurements of the openings impossible. In both species the normal pattern of a slightly slanted columellar wall (fig. 184c, f) extending anteriorly of the lower palatal lip margin has been altered (fig. 175b, f). The columellar lip and a detached portion of the parietal wall are reflected inward almost perpendicular to the shell axis and progressively cover the umbilical opening (fig. 170) with a very thin plate. Many museum specimens have the plate partly broken, but whether this was an accident during years in the collections or resulted from the activities of emerging young is unknown. Specimens with intact closures, such FMNH 46359, have young retained inside the umbilicus. This altered form of umbilical closure, which occurs during the last whorl to whorl-and-a-quarter of growth, is an obvious adaptation to the low spire height in these two species. While other *Libera,* which have proportionately much higher spires, can take two whorls to gradually narrow the umbilicus and still preserve an adequate brood chamber, in *L. gregaria* and *L. recedens* the low spire results in a shallow chamber that would be very small if two whorls of narrowing were utilized. Hence the comparatively sudden and directly inward growth of the columellar wall and parietal callus maintains an adequate volume size to the brood chamber.

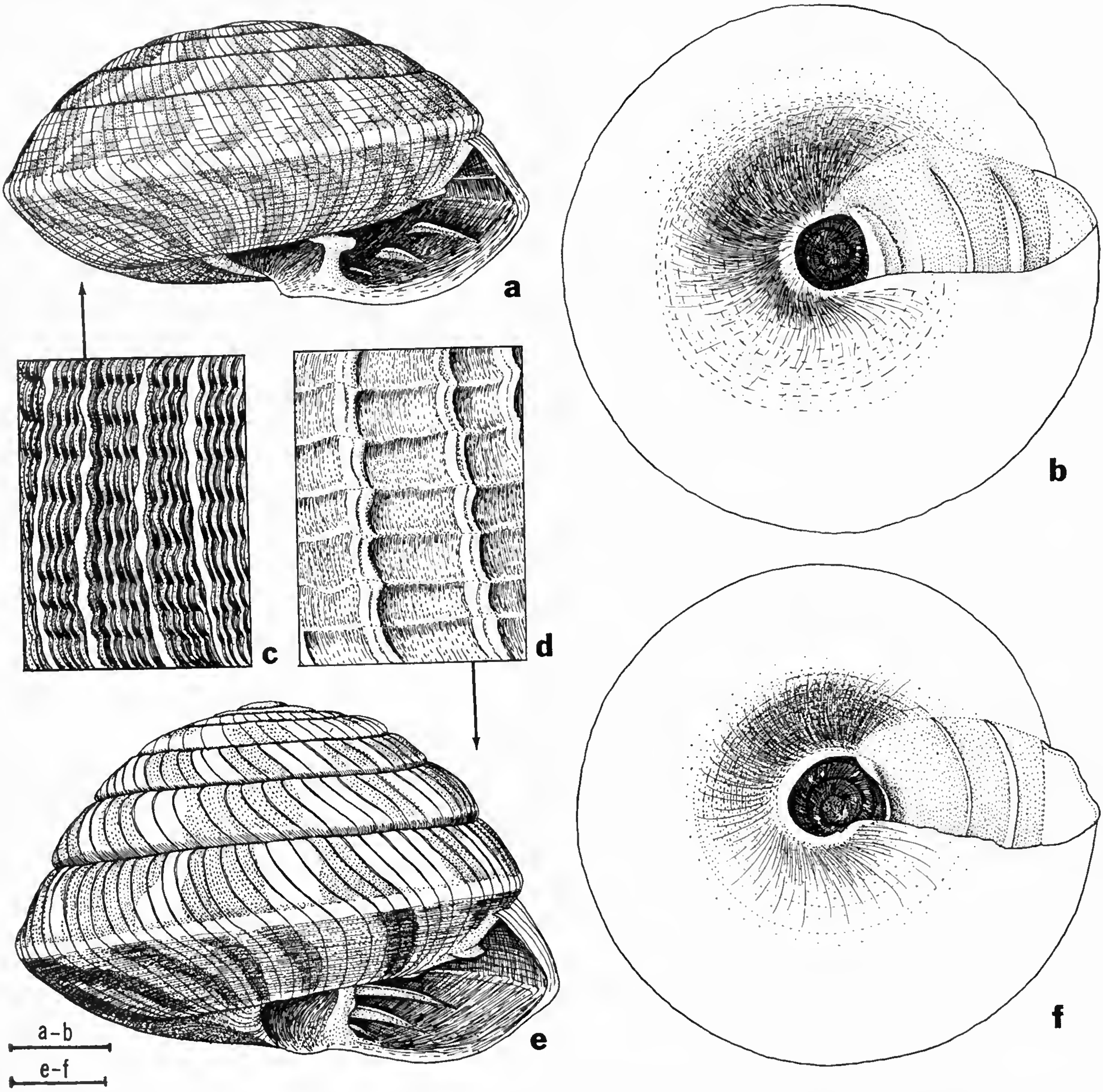

FIG. 176. *Libera dubiosa* Ancey: **a-c**, typical example. Moorea, Society Islands. BPBM 2235; **d-f**, gerontic individual. Moorea, Society Islands. BPBM 4916. Scale lines equal 1 mm. Microsculpture in *d* worn off, only major ribs and secondary spiral cording visible. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Libera dubiosa Ancey, 1889. Figure 176a-f.

Libera coarctata Garrett, 1884 (not Pfeiffer, 1850), Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), pp. 34-35, pl. 2, fig. 10 — valleys on north and east sides of Moorea, Society Islands.

Libera heynemanni var. *dubiosa* Ancey, 1889, Le Naturaliste, (2), **11**, (59), pp. 190-191 — locality unknown.

Diagnosis. — Shell slightly smaller then average, diameter 4.84-5.88 mm. (mean 5.35 mm.), with 6½-8 rather tightly coiled whorls. Apex and spire markedly elevated, rounded above, occasionally apex distinctly flattened, body whorl usually descending slightly below periphery of penultimate whorl, occasionally descending moderately, H/D ratio 0.525-0.697 (mean 0.587). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of baso-columellar margin over a little more than the last two whorls, resulting opening circular or subcircular, contained 3.85-7.00 times (mean 5.38) in the diameter. Postnuclear sculpture of low, narrow, somewhat crowded, protractively sinuated radial ribs, 111-138 (mean 125.2) on the body whorl, whose interstices are 3-6 times their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification. Secondary microsculpture of narrow, rather sharply defined and relatively widely spaced spiral cords, that become broader and much more crowded on shell base. Major radial sculpture usually reduced on shell base. Sutures shallow, whorls flatly rounded down to moderately protruded threadlike periphery, supraperipheral sulcus generally weak to absent, subperipheral sulcus relatively prominent, lower palatal wall strongly rounded down to basal margin which is flattened to distinct sulcus before baso-columellar margin. Aperture subovate, strongly flattened laterally above weakly protruded periphery, inclined about 30° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper parietal very high and slender on posterior third, gradually descending to anterior third which is a ridgelike lamellar blade; 2nd parietal with posterior portion equal in height to elevated posterior of upper parietal, descending to parietal wall at approximate midpoint of upper parietal, either with (33 per cent) or without (67 per cent) a threadlike anterior extension to point slightly in front of upper parietal termination. Columellar wall with prominent, high, broad, crescentic barrier that twists slightly upward from plane of coiling as it gradually descends across top of columellar callus. Palatal barriers 4, deeply recessed, extending posteriorly slightly more than one-eighth whorl: lower basal in position, flattened above on posterior third, with gradual anterior descension, often visible from apertural view only with difficulties; 2nd and 3rd slightly higher, longer, more flattened above, with progressively more gradual anterior descension, both subperipheral; 4th supraperipheral, located nearer periphery than parietal-palatal margin, greatly reduced in height, an elevated ridgelike barrier with very gradual anterior descension.

Both *Libera garrettiana* and *L. spuria* are closely related to *L. dubiosa*. *L. garrettiana*, from the northwest part of Tahiti, differs in its complete lack of major radial sculpture, smaller size, and lower whorl count. *L. spuria* is intermediate in sculpture, usually retaining major radial ribbing on the first three or four postnuclear whorls, but the major sculpture is absent from the lower spire and body whorl. The secondary spiral cording is very fine and crowded compared with *L. dubiosa*.

Types. — Ancey's material was not located. As in the case of *L. spuria*, I have chosen not to select a lectotype.

Range. — Valleys on north and west sides of Moorea, Society Islands (Garrett, 1884, p. 35).

Material. — Moorea (57 specimens, BPBM 2235, BPBM 4916, FMNH 156778, AMS, Zurich, RSM 1961.61.42). No locality (5 specimens, BPBM 8675, BPBM 10001, BPBM 170911, BPBM 170915, FMNH 46389).

Remarks. — Union of the shells that Garrett misidentified as "*coarctata*" with Ancey's *Libera dubiosa* from an unknown locality is based upon the distinctive sculpture, 4 palatal barriers and 5 mm. diameter mentioned by Ancey in his description. This combination of characters is found only in the material reported on by Garrett. It is not even partly duplicated by another species of *Libera*.

Normal specimens (fig. 176a-c) can readily be recognized as being closely related to *garrettiana*, but gerontic shells with reduced barriers and worn sculpture (fig. 176d-f) are more difficult to identify. Possibly *L. dubiosa* and *L. spuria* are only subspecifically separable, but the difference in whorl count and mean size is large enough that I am ranking them as species. Material from the various sources located (table CIII) probably all originated from Garrett. Except for the smaller size of the AMS set, there is no significant variation in size or shape.

The similarities of *L. dubiosa, L. spuria,* and *L. garrettiana* are obviously many, but their degree of relationship is uncertain. They show a progressive reduction in radial sculpture and intensification of spiral sculpture that is correlated with size reduction. The heavily sculptured *L. dubiosa* is much larger than those with reduced radial sculpture. Probably there is no direct phylogentic relationship between the three, but they were derived from a common stock. Certainly they retain the most generalized barrier structure in the genus.

Libera spuria Ancey, 1889. Figure 177a-b.

Libera heynemanni var. *Spuria* Ancey, 1889, Le Naturaliste, (2), **11**, (59), p. 190 — Tahiti.

Diagnosis. — Shell small, diameter 4.18-5.49 mm. (mean 4.83 mm.), with 5¾-6½ rather tightly coiled whorls. Apex and spire strongly elevated, usually rounded to slightly flattened above, body whorl normally not descending more rapidly, occasionally slightly deflected, H/D ratio 0.500-0.697 (mean 0.595). Umbilicus slightly narrowed secondarily to form a brood chamber by very gradual inward growth of baso-columellar margin, resulting opening normally circular, contained 4.00-7.80 times (mean 5.34) in the diameter. Postnuclear whorls with narrow, low, inconspicuous and relatively crowded radial ribs on upper spire that are absent from lower spire and body whorl. Microsculpture normally of very fine radial riblets, crossed by slightly finer and more crowded spiral riblets, with a secondary sculpture of low and quite crowded spiral cords that may, particularly on shell base, become more prominent than radial riblets. Sutures shallow, whorls flatly rounded down to weak or moderately prominent supraperipheral sulcus, periphery weakly protruded into a threadlike keel, normally without, sometimes with a subperipheral sulcus. Lower palatal wall evenly and more strongly rounded down to prominent sulcus and sharply protruded baso-columellar margin, columellar wall flattened internally. Aperture subquadrangular, more strongly rounded below than above slightly protruded periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper high and slender, weakly expanded above on posterior half, with gradual anterior descension; 2nd normally recessed to midpoint of 1st, equally high or slightly higher on posterior section, with rather sharp anterior descension, in juvenile and some adult individuals with a threadlike anterior extension to point opposite end of upper parietal. Columellar wall with single, high, crescentic, deeply recessed, slightly supramedial barrier, with gradual anterior descension almost to top of columellar callus, barely visible from normal apertural view. Palatal barriers variable in number, normally (87.1 per cent) 4, occasionally (9.7 per cent) with 1st absent, rarely (3.2 per cent) with both 1st and 4th absent, deeply recessed, extending posteriorly more than one-eighth whorl: lower normally basal in position, slightly to greatly reduced in height from 2nd and 3rd, sometimes absent, with rather gradual anterior descension; 2nd and 3rd subperipheral, quite high and prominent, weakly expanded and flattened above on posterior half, with progressively more gradual anterior descension, although descending more sharply than 1st; 4th, when present, a low and deeply recessed, threadlike to weakly lamellar supraperipheral trace.

Differences between *Libera spuria* and *L. garrettiana* are few, consisting primarily in *spuria* having major radial ribs present on the upper spire and generally rather indistinct secondary spiral cording. *L. garrettiana* has no trace of major radial ribbing on the shell and the secondary spiral cording normally is quite prominent. *L. dubiosa* from Moorea is slightly larger and has the major radial ribs extending on to

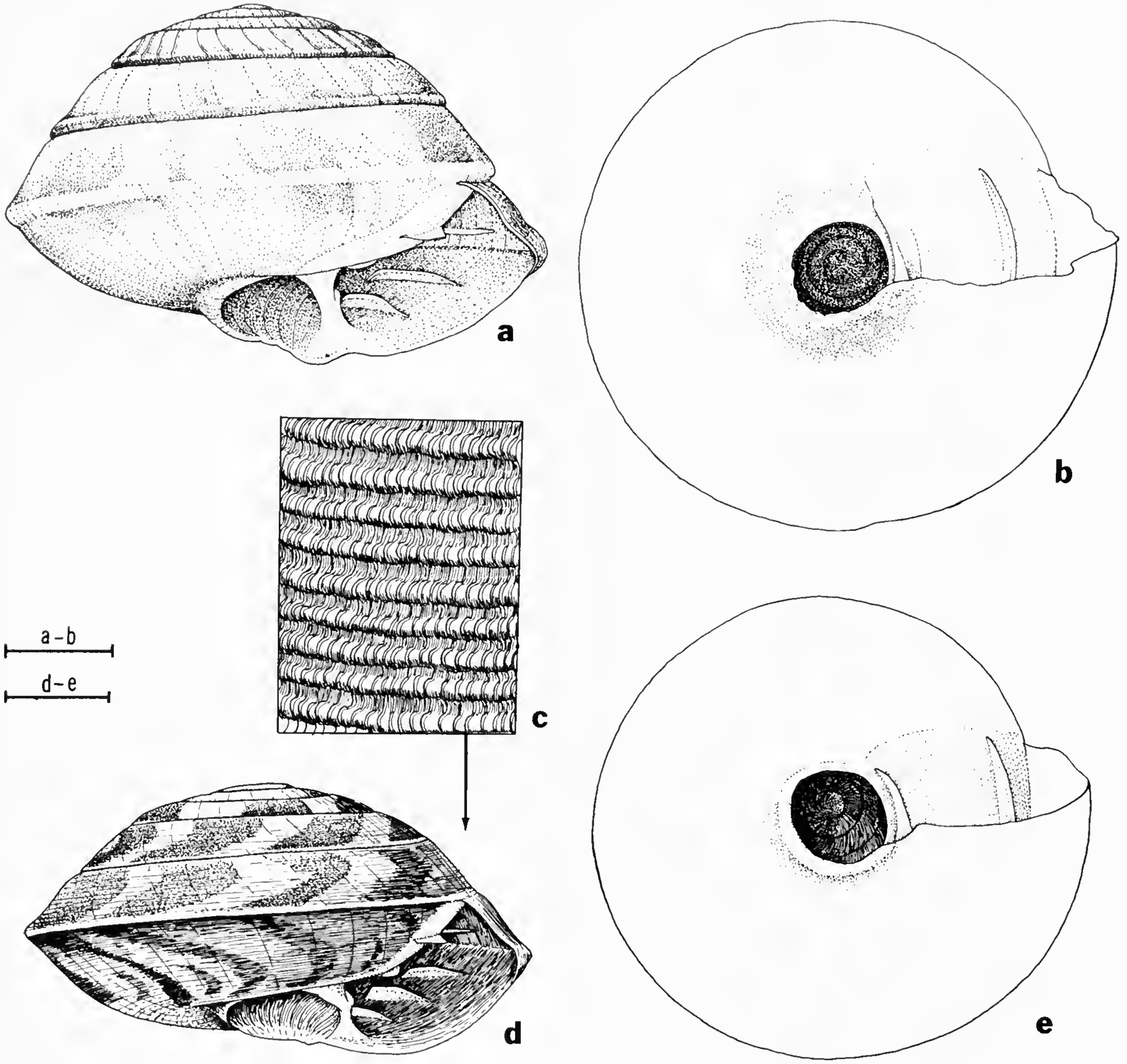

FIG. 177. **a-b**, *Libera spuria* Ancey. No locality. BPBM 9708; **c-e**, *Libera garrettiana*, new species. Tahiti, Society Islands. Holotype. BPBM 2234. Scale lines equal 1 mm. Microsculpture only suggested in c. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

both the lower spire and body whorl. The much larger *L. heynemanni* lacks all trace of major radial ribbing.

Types. — No material in the Bernice P. Bishop Museum, National Museum of Wales (Cardiff), and Institut Royal des Sciences Naturelles de Belgique (Brussels), the logical repositories for Ancey types, was labelled as this species. His types are so widely dispersed, however, that, in the absence of localized material, I have chosen not to select a neotype.

Range. — Probably Tahiti, but possibly Moorea, Society Islands.

Material. — Tahiti (30 specimens, FMNH 46417, FMNH 90622, FMNH 117051, Zurich, RSM). No locality (70 specimens, BPBM 9708, BPBM 189939, FMNH 7662, FMNH 73893, FMNH 156775, RSM 1961.61.44).

Remarks. — Ancey (*loc. cit.*) inferred that *Libera spuria* and *L. dubiosa* were from the same collection, but the latter is a Moorean species, while Ancey cited Tahiti as the habitat for *L. spuria*. Only new collections will settle the problem of locality. They are very similar in appearance, but the size and probable locality difference combined to suggest specific separation.

None of the Bishop Museum material had exact locality and apparently this was not a species collected

TABLE CIII. - LOCAL VARIATION IN SOCIETY ISLAND LIBERA

	Number of specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
recedens						
BPBM 2682, BPBM 167413	10	3.07±0.063 (2.61-3.27)	5.55±0.030 (5.42-5.69)	0.553±0.0123 (0.476-0.602)	7+ (6 5/8-7 1/4)	
ANSP 47827, ANSP 290107	4	3.02±0.062 (2.94-3.20)	5.62±0.125 (5.42-5.95)	0.539±0.0210 (0.494-0.590)	7 1/8 (7-7 1/4)	
RSM 1961.61.48	33	3.14±0.036 (2.81±3.59)	5.65±0.056 (5.10-6.73)	0.557±0.0057 (0.500-0.627)	7+ (6 1/8-7 1/2)	
gregaria						
RSM 1961.61.56	46	3.30±0.042 (2.75-3.99)	6.67±0.032 (6.27-7.12)	0.494±0.0052 (0.437-0.577)	7 1/8- (6 5/8-7 3/4)	
BPBM 4881	5	3.58±0.073 (3.46-3.86)	7.01±0.104 (6.73-7.25)	0.512±0.0121 (0.482-0.546)	7 3/8- (7 1/8-7 1/2)	
BPBM 167412	13	3.43±0.058 (3.14-3.73)	6.79±0.055 (6.41-7.06)	0.505±0.0067 (0.466-0.540)	7 1/4 (6 3/4-7 1/2)	
retunsa						
BPBM 2233, BPBM 167410, BPBM 170906, BPBM 170913	9	2.84±0.071 (2.48-3.14)	4.35±0.077 (3.92-4.64)	0.654±0.0190 (0.567-0.758)	6 3/8+ (6-7)	4.17±0.203 (3.38-5.00)
streptaxon						
Paris A	5	3.32±0.114 (2.88-3.46)	6.24±0.129 (5.95-6.67)	0.554±0.0103 (0.520-0.582)	8- (7 3/4-8)	7.13±0.264 (6.54-8.06)
Paris B	6	3.28±0.070 (3.07-3.53)	6.20±0.064 (5.95-6.41)	0.529±0.0118 (0.500-0.575)	7 3/4- (7 1/2-8)	6.44±0.249 (5.53-7.38)
heynemanni						
BPBM 170907-8	6	3.44±0.142 (2.94-3.86)	6.30±0.238 (5.23-6.67)	0.547±0.0094 (0.522-0.578)	6 3/4- (6 1/4-7)	4.64±0.261 (4.00-5.72)
incognata						
BPBM 167407, BPBM 175610	3	4.66±0.434 (3.92-5.42)	7.04±0.087 (6.86-7.12)	0.661±0.0548 (0.571-0.761)	8 1/8+ (7 5/8-8 7/8)	5.99±1.057 (3.89-7.27)
BPBM 43.4.5.187-8	5	5.05±0.086 (4.71-5.16)	7.48±0.076 (7.32-7.71)	0.675±0.0130 (0.631-0.705)	8+ (7 1/2-8 1/2)	5.55±0.483 (3.80-6.58)
dubiosa						
BPBM 2235	4	3.09±0.129 (2.88-3.46)	5.25±0.056 (5.10-5.36)	0.589±0.0245 (0.561-0.662)	7 1/8+ (7-7 5/8)	No Measurement
BPBM 4916	6	3.15±0.171 (2.75-3.79)	5.39±0.075 (5.23-5.62)	0.583±0.0245 (0.525-0.682)	7 1/8- (6 5/8-7 7/8)	No Measurement
AMS (subadult)	5	2.70±0.045 (2.58-2.81)	5.00±0.072 (4.87-5.23)	0.538±0.0067 (0.525-0.563)	6 3/4 (6 1/2-7)	4.48±0.313 (3.85-5.65)
Zurich	15	3.21±0.070 (2.78-3.74)	5.45±0.040 (5.10-5.70)	0.588±0.0096 (0.540-0.657)	7 1/4- (7-7 1/2)	5.68±0.225 (4.58-7.00)
RSM 1961.61.42	14	3.41±0.045 (3.20-3.66)	5.59±0.048 (5.36-5.88)	0.611±0.0075 (0.570-0.655)	7 1/4+ (6 7/8-7 5/8)	5.79±0.176 (4.55-7.00)
spuria						
BPBM 9708, BPBM 189939	7	2.68±0.092 (2.22-2.94)	4.56±0.092 (4.18-4.84)	0.590±0.0230 (0.500-0.672)	6 1/8 (5 3/4-6 3/8)	4.94±0.329 (4.00-6.09)
Zurich	6	2.77±0.062 (2.48-2.91)	4.64±0.063 (4.54-4.93)	0.597±0.0114 (0.547-0.627)	6 1/4 (6-6 1/2)	5.72±0.147 (5.27-6.20)
RSM 1961.61.44	60	2.92±0.035 (2.42-3.46)	4.89±0.031 (4.44-5.49)	0.596±0.0056 (0.513-0.697)	6 5/8+ (6 1/8-7 1/2)	5.35±0.107 (4.00-7.80)
garrettiana						
BPBM 2234	7	2.82±0.066 (2.55-3.07)	5.04±0.084 (4.71-5.29)	0.559±0.0087 (0.534-0.603)	6 5/8- (6 3/8-7)	5.27±0.147 (4.71-5.79)
AMS C50, AMS C28644	7	2.66±0.087 (2.35-2.91)	4.79±0.065 (4.57-5.07)	0.555±0.0140 (0.503-0.607)	6 3/8 (6-6 3/4)	4.75±0.246 (3.81-5.68)

by Garrett. Thus the small size of the BPBM sets (table CIII) indicates nothing of significance except trading bias by collectors. The origin of the large set from the Fulton collection (RSM 1961.61.44) could not be established.

Libera garrettiana, new species. Figure 177c-e.

Libera heynemanni Garrett, 1884 (not Pfeiffer, 1862), Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 35, pl. 2, fig. 9 – several valleys on northwest part of Tahiti, Society Islands.

Helix (*Libera*) *heynemanni* Tryon, 1887 (not Pfeiffer, 1862), Man. Conchol., (2), **3**, pl. 13, fig. 82. Copied from Garrett (1884, pl. 2, fig. 9).

Diagnosis. – Shell small, diameter 4.51-5.29 mm. (mean 4.85 mm.), with 5⅝-7 normally coiled whorls. Apex and spire rather strongly elevated, distinctly rounded above, last whorl only rarely descending more rapidly, H/D ratio 0.503-0.607 (mean 0.559). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of baso-columellar margin over last two whorls, resulting opening circular, contained 3.81-5.57 times (mean 4.91) in the diameter. Postnuclear whorls without major radial ribbing, having a velvety appearance under low (20×) magnification. Microsculpture consisting of very fine and crowded radial riblets with much finer and extremely crowded spiral riblets that are visible only under 96× magnification, normally with a secondary sculpture of rather prominent spiral cords that are exaggerated in Figure 177c. Sutures reduced to an impressed line, whorls flat or very gently rounded down to shallow supraperipheral sulcus, periphery right or acutely angled, very weakly protruded, lower palatal and basal margins gently and evenly rounded down to prominent sulcus before knife-edge sharp baso-columellar margin, walls of columella flat internally. Aperture subquadrangular, slightly more strongly rounded below than above weakly protruded periphery, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper high and bladelike, expanded and distinctly elevated on posterior three-eighths, with very gradual anterior descension; 2nd recessed to point slightly in front of midpoint of upper parietal, equally elevated and expanded above posteriorly, with rather sharp anterior descension. Columellar wall with high, prominent, broadly rounded crescentic barrier, with gradual anterior descension almost to top of columellar callus, deeply recessed within aperture. Palatal barriers normally 4, rarely (4.6 per cent) with upper absent, deeply recessed, extending posteriorly slightly less than one-eighth whorl: lower basal in position, much lower than 2nd and 3rd, flattened above on posterior third, with gradual anterior descension; 2nd and 3rd elevated and bladelike, flattened above on posterior half to five-eighths, weakly expanded above, with progressively more gradual anterior descension, deeply recessed within aperture; 4th supraperipheral, greatly reduced in height, a threadlike to low, ridgelike lamellar trace, with very gradual anterior descension.

Libera garrettiana is distinguished by its complete absence of major radial ribbing and the general predominance of secondary spiral cording. *L. spuria* is extremely similar, but generally is slightly more elevated and has major radial ribbing retained on the upper spire. In general, specimens of *L. spuria* have the whorls more strongly rounded and there is a greater tendency toward size reduction and loss of the 1st palatal. The other species without major radial sculpture, *L. heynemanni,* differs in its much larger size (mean diameter 6.52 mm.) and the apparent total absence of any sculpture.

Description. – Shell of average size, with 6⅛ relatively loosely coiled whorls. Apex and spire markedly elevated, rounded above, last whorl not descending more rapidly, H/D ratio 0.538. Sutures very shallow, whorls of apex and spire flattened above. Body whorl with slightly protruding, acutely angulated keel, lower palatal wall more strongly rounded. Embryonic whorls 1⅝, sculpture of extremely fine radial ribs, whose interstices are about 1½ times their width, with very fine crowded spirals. Post apical whorls with radial sculpture of exceedingly fine, closely spaced radial riblets, crossing much larger and more prominent rounded spiral cords (fig. 177c). Color light yellow horn, with prominent, reddish flammulations that become zigzagged below periphery. Umbilicus constricted by expansion of last two whorls and sharp inward protrusion of basal lip. Opening nearly circular, contained 4.87 times in the diameter. Aperture subquadrangular with rounded basal margin, inclined about 25° from shell axis. Parietal wall with 2 barriers that extend posteriorly more than one-quarter whorl: upper high and lamellate for entire length, slightly expanded and minutely serrated above; lower deeply recessed, extending about one-eighth whorl, equal in height to upper. Columellar barrier a high, broadly rounded ridge, moderately deeply recessed within aperture, descending gradually to top of columellar callus. Columellar margin of lip extending sharply anteriorly. Palatal barriers 4, deeply recessed: lower 3 high and bladelike, extending about one-eighth whorl with gradual anterior descension, lowest one smaller than upper 2; upper palatal a low, thin supraperipheral lamellar ridge. Height of holotype 2.74 mm., diameter 5.10 mm.

Holotype. – Society Islands: northwest part of Tahiti, Society Islands. Collected by Andrew Garrett. BPBM 2234.

Range. – Valleys on northwest part of Tahiti, Society Islands (Garrett, 1884, p. 35).

Paratypes. – Same as list of material.

Material. – Tahiti (62 specimens, BPBM 2234, BPBM 87514, BPBM 170905, FMNH 156774, Zurich, AMS C50, AMS C28644, RSM 1961.61.43). No locality (51 specimens, BPBM 9709, BPBM 8603, BPBM 170904, BPBM 170909-10, BPBM 170912, BPBM 170914).

Remarks. – Garrett's confusion of this species with *L. heynemanni* is readily understandable, particularly in view of the poor descriptions and illustrations available to Garrett. The original measurements of *heynemanni* cite a diameter of 5½ mm., which is above the maximum recorded size for this species and within the range of what I am calling *heynemanni.* That species has no secondary spiral cording and normally lacks the 4th palatal.

Probably the true size of *L. garrettiana* is between that cited for the BPBM 2234 examples (biased to large size) and those in the AMS (biased for small size) (table CIII). Unfortunately, no exact locality is known for this species.

Great pleasure is taken in naming this species after Andrew Garrett, pioneer collector and student of Pacific land mollusks.

Libera umbilicata, new species. Figure 178a-c.

Diagnosis. – Shell smallest in genus, diameter 3.66-3.79 mm. (mean 3.71 mm.), with 6½-7½ normally coiled whorls. Apex and spire strongly and almost evenly elevated, slightly rounded above, whorls of lower spire descending progressively more rapidly, body whorl at most only slightly deflected below periphery, H/D ratio 0.625-0.736 (mean 0.673). Umbilicus slightly narrowed to form brood chamber by very gradual inward growth of baso-columellar margin, remaining widely open, circular in outline, contained 2.94-3.41 times (mean 3.16) in the diameter. Postnuclear sculpture of prominent, very

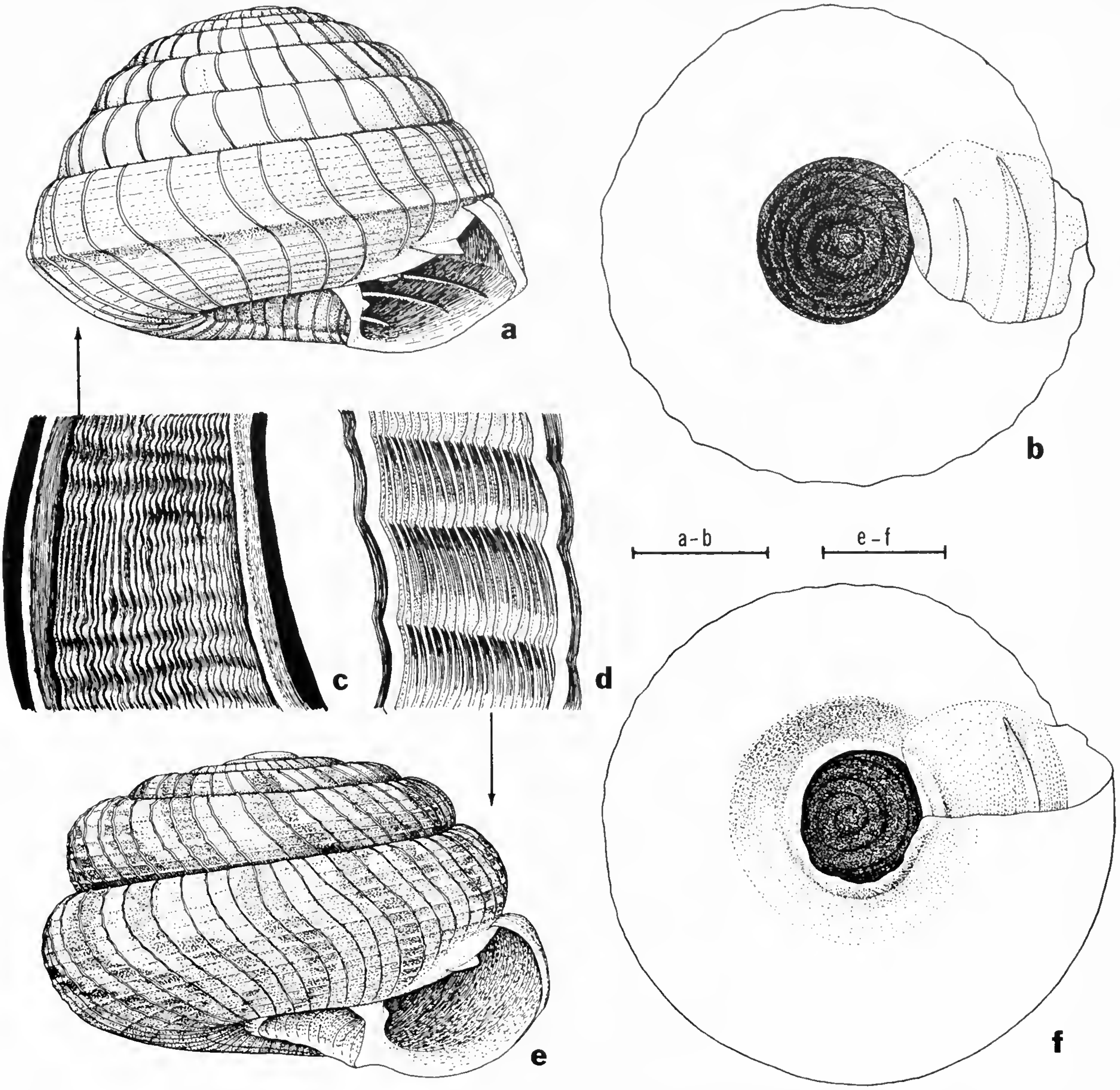

FIG. 178. **a-c,** *Libera umbilicata,* new species. Station 949, Mt. Orofena, 4,500 ft. elevation, Tahiti, Society Islands. Holotype. BPBM 145820; **d-f,** *Libera retunsa* (Pease). Tahiti, Society Islands. Lectotype. BPBM 170913. Scale lines equal 1 mm. Microspiral sculpture not shown in *c* and *d*, all microsculpture omitted from major ribs. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

broadly V-shaped, widely spaced, strongly protractively sinuated radial ribs, 26-32 (mean 29.3) on the body whorl, whose interstices are 7-10 times their width. Microsculpture a lattice of very fine radial riblets, approximately 30 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Lower spire and base of shell with indistinct, broadly rounded, irregularly spaced secondary spiral cords. Sutures shallow, whorls rather flatly rounded down to weak supraperipheral sulcus, periphery a weak threadlike keel with distinct subperipheral sulcus present, lower palatal and basal margin gently and almost evenly rounded down to approximately right-angled baso-columellar margin, with columellar wall flattened. Aperture subquadrangular, more strongly rounded above than below the threadlike keeled periphery, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision: upper high and slender, weakly expanded above on posterior visible half with very gradual anterior descension; 2nd parietal equally high and expanded above on visible posterior half, descending rather rapidly to anterior third which is much lower, but gradually and more evenly descending than upper parietal to point behind or in front of upper's termination. Columellar wall with a large, crescentic, quite broad, deeply recessed barrier, reaching to top of thin columellar callus. Palatal barriers 3, moderately deeply recessed, all subperipheral in position: lower very near baso-columellar margin, much less elevated than parietal, flattened above, with relatively sharp anterior descension; 2nd and 3rd progressively reduced in height, more elongated, and with much more gradual anterior descension.

Libera umbilicata is characterized by its extremely small size, very widely spaced radial ribs, threadlike keel, relatively wide umbilicus, and the extremely long parietal barriers. The most similar species, *L. retunsa*, differs in its total lack of palatal barriers, absence of a keel, much stronger secondary spiral sculpture, and possession of 43-54 major radial ribs on the last whorl. All other *Libera* with reduced major radial sculpture are at least 1 mm. larger in mean adult size.

Description. – Shell very small, with 7½ rather tightly coiled whorls. Apex and spire strongly elevated, slightly rounded above, last whorl not descending more rapidly. H/D ratio 0.736. Apical whorls 1½, sculpture completely eroded, visible in umbilicus as traces of major radials with one to two microriblets between. Postnuclear whorls with very widely spaced, broadly V-shaped, protractively sinuated radial ribs, 30 on the body whorl, whose interstices are 6-9 times their width. Microsculpture of exceedingly fine radial riblets, about 30 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets, with vague secondary spiral cording visible on body whorl above periphery and base of shell (fig. 178c). Ground color light yellow horn, with extremely broad, reddish flammulations that almost coalesce above periphery, become zigzagged and fade out on shell base. Umbilicus broadly U-shaped, only slightly secondarily narrowed to form brood chamber by inward growth of baso-columellar margin, opening circular, contained 3.35 times in the diameter. Aperture subquadrangular, more strongly rounded above than below threadlike peripheral keel, inclined about 30° from shell axis. Parietal barriers 2, extending posteriorly beyond line of vision, upper very high and thin, posterior visible half slightly elevated and more expanded, with very gradual anterior descension; 2nd parietal equally high on visible posterior half, rather abruptly descending to a raised threadlike anterior third that terminates slightly behind end of upper parietal. Columellar wall with a weak callus, surmounted by a very broad, high and crescentic barrier that reaches barely to top of columellar callus. Palatal barriers 3, subperipheral, moderately deeply recessed, extending posteriorly almost three-sixteenths of a whorl; lower very near baso-columellar margin, slightly higher, shorter and with more abrupt anterior descension than 2nd and 3rd, which are progressively longer, lower and with more gradual anterior descension. Height of holotype 1.75 mm., diameter 3.73 mm.

Holotype. – Society Islands: Tahiti, Station 949, east side, south ridge of Mt. Orofena at 4,500 ft. elevation. Collected by Harold St. John on September 20, 1934. BPBM 145820.

Range. – Mt. Orofena at 4,500 ft. elevation, Tahiti, Society Islands.

Paratypes. – Same as list of material.

Material. – Tahiti: east side, south ridge of Mt. Orofena (Station 949), at 4,500 ft. elevation (4 specimens, BPBM 145820).

Remarks. – The only species of similar size, *Libera retunsa*, also has widely spaced radial ribs, but differs in the sharp descension of the body whorl, rounded periphery, loss of apertural barriers, and the much greater development of spiral cording (fig. 178d-e). In retaining a columellar barrier and 3rd palatal, *L. umbilicata* is rather generalized, but the very widely spaced sculpture, stronger keel and very high spire are specialized conditions. Possibly the specimens were slightly subadult and the umbilicus could become narrower, but I suspect that only slightly greater inward growth would be probable. The relatively high whorl count (7-) suggests adult size and all specimens showed at least a slight area of adult growth.

Libera retunsa (Pease, 1864). Figure 178d-f.

Helix retunsa Pease, 1864, Proc. Zool. Soc. London, **1864**, p. 670 – no locality; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 220; Pfeiffer, 1876, *op. cit.*, **7**, p. 256.

Ptys retunsa (Pease), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 475 – Tahiti, Society Islands.

Libera retunsa (Pease), Garrett, 1884, Jour. Acad. Nat. Sci., Philadelphia, **9**, (1), p. 35, pl. 2, fig. 8 – south side of Tahiti, Society Islands; Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), p. 41.

Helix (Libera) retunsa (Pease), Tryon, 1887, Man. Conchol., (2), **3**, p. 71, pl. 13, fig. 81.

Endodonta (Libera) retunsa (Pease), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 24.

Diagnosis. – Shell very small, diameter 3.86-4.64 mm. (mean 4.30 mm.), with 5¾-7 normally coiled whorls. Apex and early spire slightly and evenly elevated, lower whorls descending much more rapidly, body whorl deflected significantly below level of penultimate whorl periphery. H/D ratio 0.567-0.758 (mean 0.644). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of baso-columellar margin on last two whorls, opening roughly ovate, slight indication of parietal callus detachment, opening contained 3.28-5.00 times (mean 4.08) in the diameter. Postnuclear sculpture of low, narrow, widely spaced, strongly protractively sinuated radial ribs, 43-55 (mean 51.2) on the body whorl, whose interstices are 4-7 times their width. Microsculpture of prominent radial riblets, five to ten between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are barely visible under 96× magnification, with a secondary sculpture of relatively narrow, quite prominent, widely spaced spiral cords that are present over most of shell surface. Sutures impressed, whorls strongly rounded down to very obtusely rounded or weakly angulated periphery, lower palatal margin more strongly and evenly rounded than in most *Libera*, baso-columellar margin protruded, columellar wall flattened. Aperture ovate, strongly rounded above and slightly less strongly rounded below obtusely rounded periphery, inclined about 30° from shell axis. Parietal wall with a single low blade, extending posteriorly slightly more than one-quarter whorl, normally a little supramedial in position, occasionally (1 of 11) with a short and deeply recessed lower 2nd parietal. Columellar wall with or without a single very deeply recessed, broadly rounded, submedial lamellar swelling, visible only by extreme tilting of aperture when present. Palatal wall normally without barriers, often (2 of 11) with two very short and low, deeply recessed, threadlike, subperipheral traces present.

The two species of similar size, *Libera umbilicata* and *L. micrasoma*, both have two very large parietals of equal length, prominent palatal barriers, and differ considerably in sculpture character. *L. micrasoma* has normal endodontid ribbing with more than one hundred rather closely spaced ribs on the body whorl. *L. umbilicata* has even more widely spaced major radial ribbing, but differs in its greatly reduced secondary spiral cording and in having about 30 very fine microradials between each pair of major ribs. *L. streptaxon* has very similar sculpture, but is immediately separable by its much larger size, more depressed shape, and presence of 2 prominent parietals and 3 palatal barriers.

Description. – Shell small, with 5¾ relatively tightly coiled whorls. Apex and early spire somewhat flattened, later whorls descending quite rapidly, body whorl strongly deflected. H/D ratio 0.652. Embryonic whorls 1½, sculpture of equally spaced radial riblets, overshadowing smaller, much more closely spaced spiral cords. Remaining whorls with low, protractively sinuated lamellar radial ribs with hairlike periostracal projections, widely spaced, whose interstices are 6-9 times their width. Almost equally prominent is a sculpture of widely spaced spiral cords, particularly prominent on shell base. Microsculpture (fig. 178d) of low, crowded lamellar radial riblets, five to ten between each pair of major ribs, plus very fine and crowded spiral riblets. Sutures relatively deep, whorls strongly rounded above and down to faint trace of peripheral angulation, evenly rounded down to sulcus before baso-columellar margin. Umbilicus narrowed to form a brood chamber by inward growth of parietal-palatal margin, slight detachment of parietal callus, ovate, contained 4.78 times in the diameter. Color light horn, with broad, widely spaced, reddish flammulations becoming sinuated below periphery. Aperture ovate, flattened columellar margin, inclined about 30° from shell axis. Parietal wall with 1 moderately low barrier, extending slightly more than three-sixteenths of a whorl. Columellar wall with thin callus and moderately prominent, broadly rounded, deeply recessed barrier. Palatal wall without barriers. Height of lectotype 2.94 mm., diameter 4.38 mm.

Lectotype. – Society Islands: Tahiti. Collected by Andrew Garrett. BPBM 170913.

Range. – South side of Tahiti, Society Islands (Garrett, 1884, p. 35).

Paratypes. – BPBM 2233, BPBM 170913.

Material. – Tahiti (10 specimens, BPBM 2233, BPBM 167410, BPBM 170913, FMNH 46266). No locality (1 specimen, BPBM 170906).

Remarks. – Two of the 11 specimens retained very small and deeply recessed palatal barriers. The remaining nine examples had no palatals. Although reported as common on the south side of Tahiti (Garrett, 1884, p. 35), no material has been collected in this century and very few specimens were located in museums. The complete absence of any peripheral angulation or keeling, extreme deflection of the body whorl and general absence of palatal barriers effectively separate this species from the other *Libera*. While the effect of the sculpture in *L. retunsa* is the same as in *L. streptaxon*, the components are quite different. Only the Cook Island *L. tumuloides* goes further in reduction of apertural barriers.

Libera streptaxon (Reeve, 1852). Figure 179a-c.

Helix bursatella Gould, 1846, Proc. Boston Soc. Nat. Hist., **2**, p. 175 – Tahiti and Moorea (part); Gould, 1852, U. S. Explor. Exped., Wilkes, **12**, pp. 51-53 (part); Gould, 1860, Atlas of Shells, U. S. Explor. Exped., Wilkes, pl. 4, figs. 52b, c, d, e.

Helix coarctata Pfeiffer, 1850 (Jan-June) (not Montagu, 1803, or Deshayes, 1840), Proc. Zool. Soc. London, **1849**, pp. 128-129 – Tahiti, Society Islands; Pfeiffer, 1850 (April), Zeits. Malak., **6**, p. 74.

Helix streptaxon Reeve, 1852, Conchol. Icon., **Helix**, pl. 112, fig. 641 – Tahiti, Society Islands.

Helix turriculo Hombron and Jacquinot, 1852 (not Lowe, 1833), Voy. Pol. Sud, Astrolabe et Zélée, pl. 6, figs. 21-24 – Tahiti, Society Islands; Rousseau, 1854, *loc. cit.*, **5**, pp. 19-20.

Helix cavernula Pfeiffer, 1853 (not Hombron and Jacquinot, 1852 or Lowe, 1833), Syst. Conchyl. Cab., 1, **12**, (3), pp. 297-298, pl. 125 (issued in 1852), figs. 29-31.

Helix (*Libera*) *coarctata* Pfeiffer (not Montagu or Deshayes), Tryon, 1887, Man. Conchol., (2), **3**, p. 71, pl. 13, figs. 78-80.

Libera streptaxon (Reeve), Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), pp. 41-42.

Diagnosis. – Shell larger than average, diameter 5.23-6.67 mm. (mean 6.06 mm.), with 6⅝-8 very tightly coiled whorls. Apex at most barely protruding, upper spire flat, last two whorls descending rapidly, body whorl drastically deflected beneath periphery of penultimate whorl, H/D ratio 0.434-0.616 (mean 0.542). Umbilicus secondarily narrowed to form brood chamber by drastic inward growth of baso-columellar margin, opening very narrow and irregular, closure involving partial detachment of parietal wall, umbilical opening contained 3.75-8.06 times (mean 6.45) in the diameter. Postnuclear sculpture of prominent, broadly V-shaped, widely spaced, protractively sinuated radial ribs, 36-55 (mean 46.4) on the body whorl, whose interstices are 4-6 times their width, and which become greatly reduced on shell base. Microsculpture of fine radial riblets, twelve to twenty between each pair of major ribs, with exceedingly fine and crowded spiral riblets, visible only under 96× magnification. Secondary sculpture of prominent, relatively crowded spiral cords over entire shell surface. Sutures shallow, whorls evenly rounded down to shallow supraperipheral sulcus, periphery protruded into a broad threadlike keel that is acutely angled in juvenile specimens, becoming right-angled with adulthood. Lower palatal margin flatly rounded after subperipheral sulcus, basal margin gently and evenly rounded down to distinct sulcus before protruded baso-columellar margin. Aperture subquadrangular, more strongly rounded below than above protruded periphery, inclined about 35° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper high and thin, markedly elevated and weakly expanded above on posterior visible quarter, descending quickly to anterior visible two-thirds that descends very gradually; 2nd parietal deeply recessed, slightly shorter and higher than upper posteriorly, with rather abrupt anterior descension to a short threadlike portion that terminates about one-third to one-half length of upper parietal within aperture in adults, extending to or beyond end of upper parietal in juveniles. Columellar wall with broadly rounded, relatively prominent, deeply recessed barrier reaching just to top of columellar callus, rarely (4 per cent) absent. Palatal barriers 3, moderately to deeply recessed, extending posteriorly about three-sixteenths of a whorl: lower basal in position, elevated and bladelike, flattened above on posterior third, with gradual anterior descension; 2nd palatal distinctly more elevated, flattened above on posterior five-eighths, with more abrupt anterior descension, longer than 1st, situated midway between 1st palatal and periphery; 3rd palatal supraperipheral, deeply recessed, reduced in height, short, crescentic, bladelike with very gradual anterior descension.

Libera recedens is the only other species having the same abrupt body whorl descension. It differs from *L. streptaxon* in its very numerous radial ribs (mean 178), distinctly more elevated spire and less prominent peripheral sulci. *Libera retunsa* is much smaller, lacks the lower parietal and usually all palatal barriers, although it is very similar in sculpture.

Description. – Shell slightly larger than average, with 7 tightly coiled whorls. Apex and early spire slightly depressed, main part of spire flat, later whorls descending much more rapidly, body whorl strongly deflected below periphery of penultimate, H/D ratio 0.434. Embryonic whorls 1¼, sculpture of narrow and rounded radial riblets, approximately equally spaced, crossed by very low and crowded spiral riblets. Some ribs on the embryonic whorls appear slightly larger than others, but there is no regular sequence. Remaining whorls with very widely spaced, V-shaped, sinuately protractive radial ribs, 46 on the body whorl, becoming reduced on shell base, crossing rounded, equally spaced spiral cords that are most strongly developed on shell base. Microsculpture of fine radial riblets, 10-20 between each pair of major ribs and barely visible, extremely crowded spiral riblets. Sutures moderately shallow, whorls strongly rounded on upper spire, somewhat protruded, acute keel, evenly rounded below. Umbilicus with irregularly ovate opening, constricted by inward growth of body whorl baso-columellar margin, contained 3.75 times in the diameter. Part of closure effected by detachment of lower parietal wall. Color yellowish-white with many

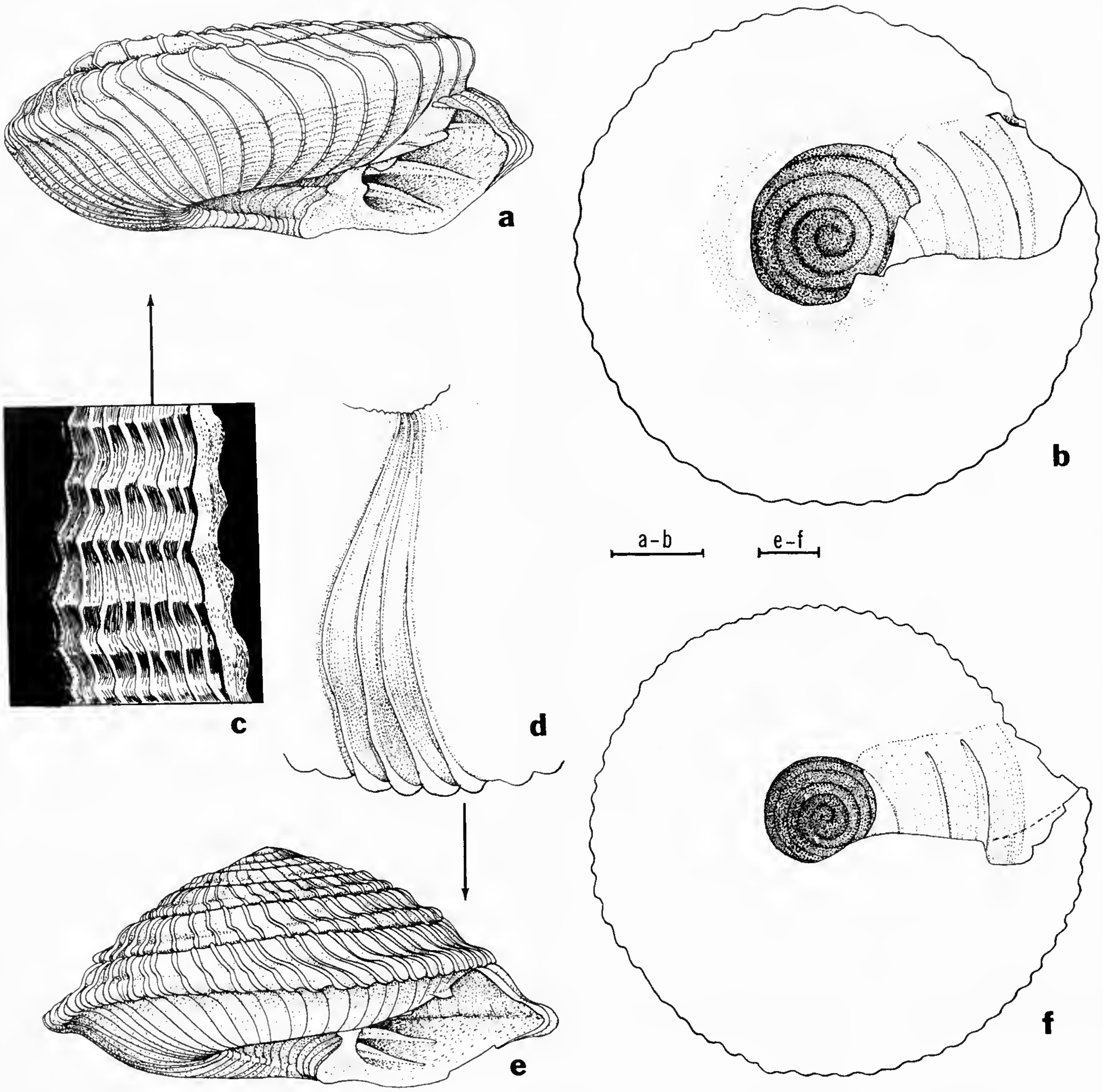

FIG. 179. **a-c,** *Libera streptaxon* (Reeve). Tahiti, Society Islands. Neotype of *Helix streptaxon* (Reeve, 1852). BPBM 167411; **d-f,** *Libera jacquinoti* (Pfeiffer). Tahiti (?), Society Islands. BPBM 167409. Scale lines equal 1 mm. Microsculpture in *c* and *d* with spirals omitted. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

reddish tessellations. Aperture subquadrangular, inclined about 25° from shell axis. Parietal wall with 2 barriers, extending posteriorly to line of vision: upper lamellate for entire length, distinctly higher on posterior quarter; lower with anterior half low and threadlike, terminating opposite end of upper parietal. Columellar barrier high, V-shaped, with gradual descension to top of columellar callus. Palatal wall with 3 barriers, moderately recessed, extending posteriorly three-sixteenths of a whorl: lower 2 high and bladelike, with gradual anterior descension, subperipheral; upper much lower, supraperipheral, with more gradual anterior descension. Height of neotype 2.55 mm., diameter 5.88 mm.

Neotype. — Society Islands: Tahiti. BPBM 167411.

Range. — Probably Tahiti, Society Islands.

Material. — Tahiti (22 specimens, BPBM 167411, FMNH 117009, SMF 165418, Paris); Moorea (1 specimen, BMNH 1908.7.2.41). "Marquesas" (1 specimen, FMNH 155933). No locality (2 specimens, BMNH).

Remarks. — Since no type material could be located in the British Museum (Natural History), I have selected the illustrated specimen as neotype. The general appearance is sufficiently similar to that of *L. retunsa* that type selection seems required. Although the neotype is not fully adult, its sculpture is well preserved and shows clear differences from possibly related species.

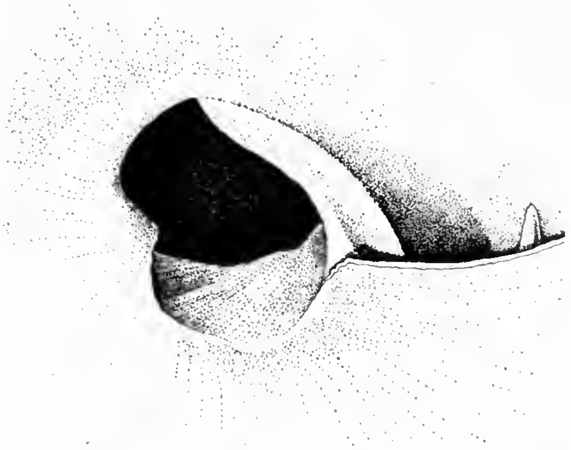

FIG. 180. Umbilicus of *Libera streptaxon* showing exit hole from brood chamber. FMNH 117009. (SH).

Umbilical closure is a modification of the pattern seen in *L. gregaria* and *L. recedens*. It undoubtedly is related to the depressed spire of *L. streptaxon*. For the first whorl of closure, detachment of the parietal wall is primarily responsible, but for the last whorl (or fraction thereof) there is the normal slight intrusion of the baso-columellar margin. In several specimens there was clear evidence of the juvenile having eaten its way out of the umbilical opening, leaving a distinct "notch" in the columellar wall (fig. 180).

At first glance, the sculpture seems to be very similar to that found in *L. retunsa,* but they are quite different. In *L. streptaxon* there are 12 to 20 microradials (fig. 179c) between each pair of major ribs and the very prominent secondary spiral cording extends over the entire surface; in *L. retunsa* there are only 5 to 10 (fig. 178d) much more widely spaced microradials between each pair of major ribs and the secondary spiral cording is much finer in character. The effect is the same, but it has been arrived at independently.

Apparently, *L. streptaxon* was not uncommon at the time of its original description, but only scattered specimens could be located at this time. None were accompanied by exact locality data and the citations of "Tahiti" and "Moorea" in early references provide no data of significance. Garrett (1884, p. 34) had not seen this shell and placed the references as synonyms of what I call *Libera dubiosa*. These species are quite different in appearance, although the original figures could be misinterpreted. The habitat and exact relationships of *L. streptaxon* are unknown.

Libera heynemanni (Pfeiffer, 1862). Figure 181 c-f.

Helix heynemanni Pfeiffer, 1862, Malak. Blätt., **9**, pp. 151-152 – Tahiti, Society Islands; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 219; Pfeiffer, 1876, *op. cit.*, **7**, p. 255.

Pitys heynemanni (Pfeiffer), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 475.

Patula heinemanni (sic) (Pfeiffer), Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 93.

Libera heynemanni (Pfeiffer), Ancey, 1889, Le Naturaliste, (2), **11**, (59), pp. 190-191 (partly); Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), pp. 42-43.

Helix (Libera) heynemanni Pfeiffer, Tryon, 1887, Man. Conchol., (2), **3**, p. 72 – description only, figure of *garrettiana*.

Endodonta (Libera) heynemanni (Pfeiffer), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 24.

Diagnosis. – Shell large, diameter 5.23-8.43 mm. (mean 6.52 mm.), with 6¼-8⅜ normally coiled whorls. Apex and spire markedly elevated, slightly to strongly rounded above, last whorl not to strongly deflected beneath periphery of body whorl. H/D ratio 0.484-0.578 (mean 0.538). Umbilicus narrowed to form brood chamber by gradual inward growth of baso-columellar margin for last two whorls, opening subcircular, contained 4.00-6.78 times (mean 5.05) in the diameter. Postnuclear whorls macroscopically smooth, under moderate to high magnification only low and very irregular growth wrinkles visible. Sutures shallow, whorls flatly rounded down to weak supraperipheral sulcus, periphery a very slightly protruded threadlike keel, right-angled, lower palatal margin much more strongly rounded than upper palatal down to sulcus before baso-columellar margin. Walls of columella flat. Aperture subovate, flattened laterally above protruded periphery, inclined about 30° from shell axis. Parietal barriers 2, occasionally (1 of 15) with a 3rd, extending posteriorly to line of vision: upper high and bladelike, expanded and more highly elevated on posterior third, with gradual anterior descension; 2nd deeply recessed, equal in height or slightly higher than posterior portion of upper, with rather sharp anterior descension to parietal wall at approximately midpoint of upper parietal, with or without a threadlike anterior extension to point near termination of upper parietal; 3rd, when present, a lower version of 2nd parietal. Columellar wall with a medial, very deeply recessed, broadly rounded crescentic barrier that is not visible from direct front view of aperture. Palatal barriers normally 3, occasionally (2 of 15) a 4th one present, moderately recessed, extending posteriorly about three-sixteenths of a whorl: lower two basal in position, high and slender, flattened above on posterior half, with progressively more gradual anterior descension, subperipheral; 3rd supraperipheral, greatly reduced in height, short, deeply recessed, elevated, and ridgelike; 4th, when present, subperipheral, with relative positions of 1st and 2nd palatals shifted.

The complete absence of major radial sculpture and secondary spiral cording combine with the very large size to immediately identify this species. *L. incognata* is similar in size and barriers, but has very strong and prominent major radial ribbing above the periphery. *L. garrettiana*, the only other species that lacks major radial ribbing, has quite fine but prominent secondary spiral cording and is much smaller in size.

Type. – No potential type material was located.

Range. – Unknown, probably Tahiti, Society Islands.

Material. – Tahiti (15 specimens, BPBM 170907-8, Paris, Zurich, Brussels, Edinburgh).

Remarks. – None of the limited material seen could be traced back to a possible association with Pfeiffer. What I am interpreting as this species is a comparatively large shell without any prominent sculpture, and retaining well-developed apertural barriers. Garrett (1884, p. 35) identified a much smaller species which has prominent spiral cording and 4 palatals (see above as *L. garrettiana*) as *heynemanni*, but the original description comes much closer to the shells listed above. Since no localized or syntypic material is known, I prefer not to select a type specimen at this time.

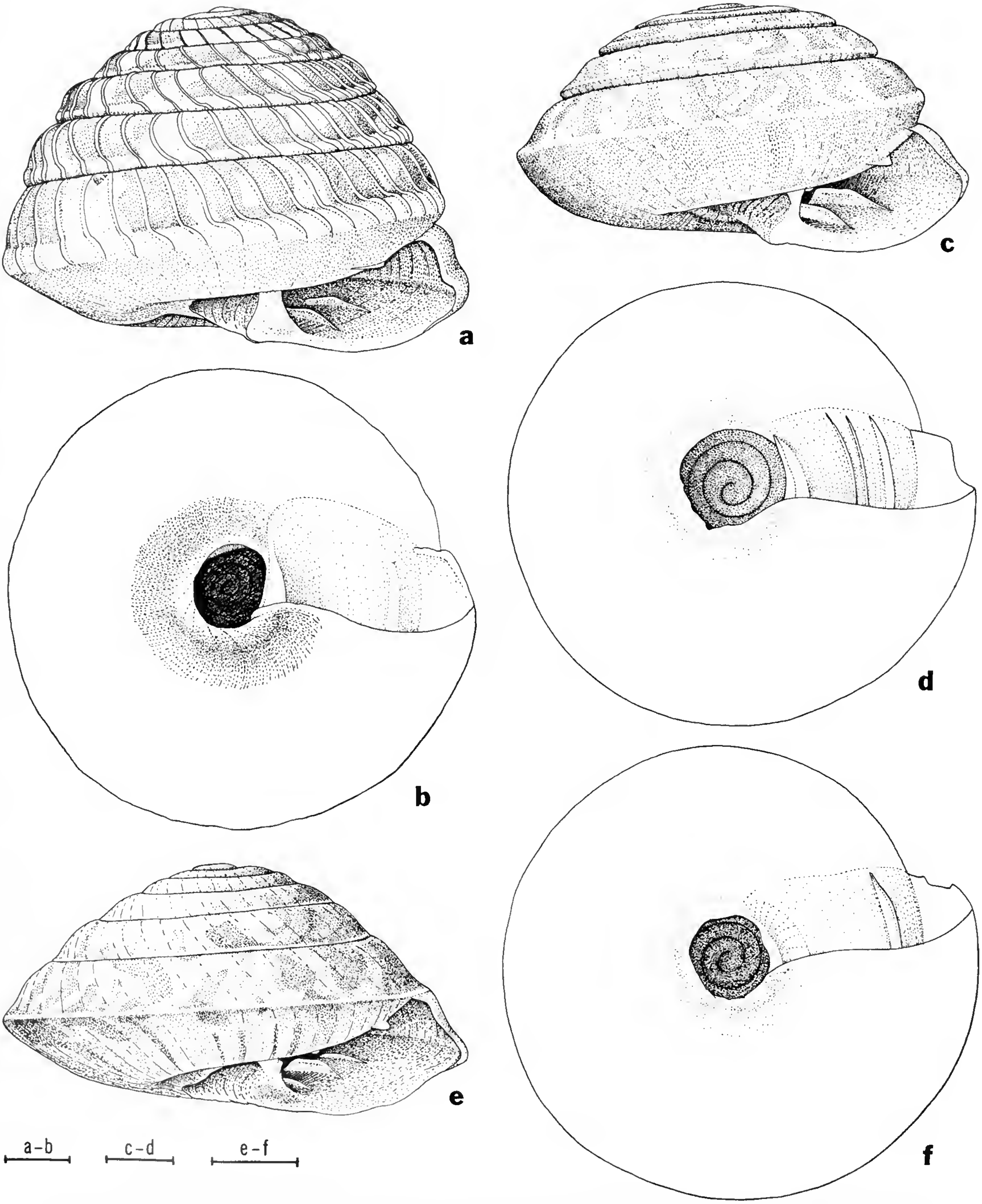

FIG. 181. **a-b**, *Libera incognata*, new species. Tahiti (?), Society Islands. Holotype. BPBM 167407; **c-f**, *Libera heynemanni* (Pfeiffer). *c-d*, gerontic shell. Society Islands. BPBM 170907; *e-f*, younger specimen. Tahiti, Society Islands. BPBM 170908. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Libera incognata, new species. Figure 181a-b.

Helix bursatella Gould, 1846, Proc. Boston Soc. Nat. Hist., **2**, p. 175 – partly; Gould, 1852, U. S. Explor. Exped. Wilkes, **12**, pp. 51-53 – partly; Gould, 1860, Atlas of Shells, U. S. Explor. Exped. Wilkes, pl. 4, figs. 52, a; ?Pfeiffer, 1853, Syst. Conchyl. Cab., **I**, **12**, (3), p. 296, pl. 125, figs. 23-25 – probably (plate issued in 1852).

Helix bursatella Reeve, 1852 (not Gould, 1846), Conchol. Icon., *Helix*, pl. 111, fig. 635 – Tahiti, Society Islands.

Helix (*Libera*) *bursatella* Tryon, 1887 (not Gould, 1846), Man. Conchol., (2), **3**, p. 71, pl. 13, fig. 86 (copy of Conchol. Icon., pl. 111, fig. 635).

Diagnosis. – Shell very large, diameter 6.80-7.97 mm. (mean 7.30 mm.), with 7½-8⅞ rather tightly coiled whorls. Apex and spire markedly elevated, distinctly flattened and rounded above, last part of body whorl descending slightly more rapidly in gerontic individuals, H/D ratio 0.571-0.761 (mean 0.650). Umbilicus secondarily narrowed to form brood chamber by inward growth of very sharply edged baso-columellar margin, remaining opening subcircular, contained 3.80-7.27 times (mean 5.62) in the diameter. Postnuclear whorls with prominent, broadly rounded, strongly protractive, rather closely spaced radial ribs, 43-55 (mean 49.8) on the body whorl, that become greatly reduced and irregular during gerontic growth and are absent from base of shell. Microsculpture reduced to very fine radial riblets, often interrupted by growth wrinkles and irregularities on major ribs, surface of all material too worn for detection of microspiral sculpture. No indication of secondary spiral cording. Sutures shallow, whorls flatly rounded down to weak supraperipheral sulcus, periphery broadly threadlike, very weakly protruded, approximately right angled, lower palatal wall flatly rounded down to weak sulcus before the extremely sharp edged baso-columellar margin. Walls of columella flat and internally with very thick callus. Aperture subquadrangular, more strongly rounded below than above periphery, inclined about 25° from shell axis. Parietal barriers 2, extending posteriorly to line of vision, rarely with a weak accessory trace: upper parietal high and bladelike, slightly higher and weakly expanded above on posterior third, with rather sharp anterior descension just before termination; 2nd parietal equally high and elevated on posterior third, descending moderately to raised threadlike anterior half that may terminate in back of, at, or beyond end of upper parietal. Columellar wall without (76.5 per cent) or with (23.5 per cent) a low, broadly rounded and deeply recessed lamellar ridge. Palatal wall normally (64.7 per cent) with two deeply recessed, short, subperipheral barriers that extend about one-eighth whorl posteriorly, frequently (23.5 per cent) with two additional barriers, one sub- and the other supraperipheral, and often (11.8 per cent) with only the additional supraperipheral: all palatals slender and elevated, flattened above posteriorly, with relatively gradual anterior descension.

Libera incognata is characterized by its domed shape, very heavy radial sculpture above the periphery, absence of major sculpture below the periphery, absence of secondary spiral cording, and extremely large size. *Libera subcavernula* from Rarotonga is superficially similar, but has the sculpture greatly reduced on the lower spire and, in specimens of similar size, average 1½ whorls less.

Description. – Shell very large, with 8⅞ tightly coiled whorls. Apex and spire strongly elevated, rounded above, last one-eighth of body whorl descending slightly, H/D ratio 0.761. Whorls somewhat flattened laterally with only marginally indented sutures. Embryonic whorls and early spire with sculpture eroded except for faint traces of larger and smaller radial ribbing in the sutures. Postnuclear whorls with low, broadly rounded, protractively sinuated radial ribs that become greatly reduced on last part of body whorl. On upper whorls ribs spaced 3-6 times their width. Microsculpture generally eroded with only traces of exceedingly fine radial riblets remaining. Base of shell with only irregular growth wrinkles. Body whorl bluntly keeled, supra- and subperipheral sulci weak, flattened above, rounded below. Color yellow-white, with numerous, broad, wine-red flammulations. Umbilicus contracted to form brood chamber by broad expansion of entire last whorl, baso-columellar margin sharp-edged, opening ovate, contained 7.27 times in the diameter. Aperture subquadrangular, flattened laterally, sinuately rounded below, inclined about 40° from shell axis. Parietal wall with 2 moderately high barriers, extending posteriorly to line of vision: upper broken posteriorly, worn anteriorly; lower deeply recessed within the aperture, half length of upper, moderately elevated. Columellar wall with high white callus, no trace of a barrier. Palatal wall with 2 deeply recessed and moderately elevated, bladelike barriers, each about one-eighth whorl in length. Height of holotype 5.43 mm., diameter 7.13 mm.

Holotype. – Society Islands: Tahiti. BPBM 167407 ex Fulton collection.

Range. – Unknown, but probably Tahiti, Society Islands.

Paratypes. – Same as list of material.

Material. – Tahiti (9 specimens, BPBM 167407, FMNH 117003, FMNH 156773, Zurich, Brussels). No locality (8 specimens, BPBM 175610, SMF 165411, BMNH 43.4.5.187-8).

Remarks. – Although apparently well known in collections formed prior to 1860, this species does not seem to have been collected by Garrett and has not been taken subsequently. Presumably it lived on either Tahiti or Moorea, but no data are available concerning its habitat. No credence can be placed on the "Tahiti" label in old collections, since this probably was copied from the early references.

The apertural barriers, except for the columellar, are like those of *L. bursatella*, and the sculpture of *L. incognata* can be derived rather easily from that of *L. bursatella*. I suspect that the former was (or is) a Tahitian species. Possibly the variation in palatal barriers is caused by age, since the larger individuals had only 2 and the smaller, younger shells had 3 or 4 palatals. The very broad and irregular radial ribs are quite different in appearance from those of *L. jacquinoti* or the Cook Islands species, although the rib spacing is very similar to the former.

Libera jacquinoti (Pfeiffer, 1850). Figure 179d-f.

Helix jacquinoti Pfeiffer, 1850 (Jan.-June), Proc. Zool. Soc. London, **1849**, p. 128 – Tahiti and Marquesas; Pfeiffer, 1850 (Apr.), Zeits. Malak., **6**, pp. 73-74; Reeve, 1852, Conchol. Icon., *Helix*, pl. 111, fig. 631; Pfeiffer, 1853, Syst. Conchyl. Cab., I, **12**, (3), pp. 296-297, pl. 125, figs. 26-28 (a different shell from the type, plate issued in 1852).

Helix cavernula Hombron & Jacquinot, 1852, Voy. Pol. Sud, Astrolabe et Zéleé, Atlas, pl. 6 figs. 33-36 – Tahiti, Society Islands; Rousseau, 1854, *loc. cit.*, **5**, pp. 17-18.

Helix (Libera) cavernula Hombron & Jacquinot, Tryon, 1887, Man. Conchol., (2), **7**, pp. 69-70, pl. 13, figs. 75-77 (copied from Hombron & Jacquinot, *loc. cit.*).

Helix (*Libera*) *jacquinoti* Pfeiffer, Tryon, 1887, *loc. cit.*, p. 71 – description only, figures are of *excavata*.

Libera jacquinoti (Pfeiffer), Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), p. 39.

Diagnosis. – Shell extremely large, diameter 7.45-9.28 mm. (mean 8.46 mm.), with 6⅞-9 normally coiled whorls. Apex and spire strongly and almost evenly elevated, at most very slightly rounded above, body whorl sometimes deflected slightly beneath periphery of penultimate whorl, H/D ratio 0.446-0.617 (mean 0.539). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of last whorl and one-quarter, resulting opening subcircular, variable in size, contained 3.78-8.93 times (mean 6.49) in the diameter. Postnuclear whorls with prominent, broad but sharply defined, strongly protractively sinuated radial ribs that generally become moderately to greatly reduced on body whorl, an estimated 47-67 (mean 55.0) on adult specimens, whose interstices are 2-3 times their width. Microsculpture of very fine radial riblets, more than 10 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures very shallow, whorls flatly rounded down to broad and shallow supraperipheral sulcus, periphery quite strongly protruded into a sharp threadlike keel, generally with an even shallower subperipheral sulcus, lower palatal and basal margins gently and evenly rounded down to weak sulcus just before very sharp edged baso-columellar margin. Aperture subovate, more strongly rounded below than above markedly protruded periphery, inclined about 40° from shell axis. Parietal barriers 2, extending posteriorly to or slightly beyond line of vision: upper very high and slender, slightly more elevated above on posterior visible third, with very gradual anterior descension until just before termination; 2nd parietal equally high on posterior third, with rather sharp anterior descension to point opposite midpoint of upper parietal, with or without a threadlike anterior extension reaching slightly beyond termination of upper parietal. Columellar wall with a broadly rounded, relatively low, very deeply recessed crescentic barrier, with very gradual anterior descension and slightly slanting upwards across top of columellar callus. Palatal barriers normally 4, rarely (3.8 per cent) with upper absent, deeply recessed, extending posteriorly about three-sixteenths of a whorl: lower basal in position, generally slightly reduced in height, with relatively sharp anterior descension; 2nd and 3rd subperipheral, slightly to moderately higher than 1st, flattened above on posterior half, with progressively more gradual anterior descension; 4th supraperipheral, situated midway between periphery and parietal-palatal margin, low and threadlike to moderately elevated, bladelike, with very gradual anterior descension.

The extremely large size, prominent radial ribbing above the periphery, retention of 4 palatal barriers, and relatively straight-sided spire combine to separate *Libera jacquinoti* from all other known species. *L. incognata* appears at first glance to have similar sculpture, but is a much more elevated and smaller shell with the ribbing much coarser and the individual ribs more broadly rounded. *L. fratercula* is at once separated in having the radial ribbing retain its prominence below the body whorl periphery.

Description. — Shell very large, with 8 moderately tightly coiled whorls. Apex and spire strongly and almost evenly elevated, sides only slightly convex, H/D ratio 0.545. Apical whorls 1⅜, sculpture mostly eroded with traces of broadly rounded, low radial ribs visible in the suture. Postnuclear whorls with moderately widely spaced, broad, slightly protractively sinuated radial ribs, 62 on the body whorl, whose interstices are 1½-3 times their width, and which are slightly to moderately expanded on crossing periphery. Microsculpture of extremely fine and crowded radial riblets crossed by barely visible spiral riblets. Major ribs finely denticulate periphery, moderately to strongly reduced in prominence on base of shell. Sutures very shallow, whorls flatly rounded above with prominent supraperipheral sulcus. Periphery protruded into acutely angulated keel with only slightly less prominent subperipheral sulcus and flatly rounded basal margin. Color faint yellowish-white, with irregular, zigzag, reddish flammulations above, absent from base of shell. Umbilicus small, strongly constricted by diagonal inward growth of last whorls, opening nearly circular, contained 6.70 times in the diameter. Aperture subquadrangular with peripheral keel and flatly rounded basal margin, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly about one-quarter whorl: upper a narrow lamellate ridge gradually becoming quite high posteriorly, with very slow descension over anterior two-thirds, moderately rapid descension at anterior edge; 2nd parietal less than two-thirds length of upper, deeply recessed, equally high and narrow posteriorly, with sharp anterior descension. Columellar wall with heavy white opaque callus and prominent, ridgelike, deeply recessed columellar barrier visible only at an extreme angle. Palatal barriers 4, extending slightly more than one-eighth whorl: lower palatal a small, lamellate ridge near basal margin; 2nd much higher, bladelike posteriorly, with very gradual anterior descension; 3rd intermediate in length, between 1st and 2nd; 4th a narrow, V-shaped, supraperipheral ridge situated just above supraperipheral sulcus. All palatals moderately to deeply recessed within aperture. Height of lectotype 4.78 mm., diameter 8.76 mm.

Lectotype. — "Society Islands." BMNH 1962707/1 ex Hugh Cuming.

Range. — Unknown, but most probably Tahiti or Moorea, Society Islands.

Paratypes. — BMNH 1965707/2-3.

Material. — "Society Islands" (3 specimens, BMNH 1965707/1-3). "Tahiti" (17 specimens, BPBM 167409, FMNH 46349, Paris, AMS). "Tubuai" (3 specimens, FMNH 156769, AMS C28645). "Marquesas" (1 specimen, BPBM 189941). Unknown (5 specimens, FMNH 117316, AMS).

Remarks. — None of the specimens were accompanied by meaningful locality data and the range of *Libera jacquinoti* remains unknown. Its superficial appearance is very much like the Cook Islands *L. fratercula* and *L. subcavernula,* but the great reduction in ribbing below the body whorl periphery, narrower and more sharply defined radial ribs, and great size (tables C, CVI) are more similar to the Society Islands species. This is by far the largest species of *Libera*. Eventual discovery that it is from a locality other than the Cook or Society Islands would not surprise me.

Gambiodonta grandis from Mangareva is similar in general appearance, but the totally different form of umbilical closure and greatly increased number of apertural barriers found in the latter immediately differentiate the two species. *G. grandis* also is much larger at the same whorl count.

Libera fratercula (Pease, 1867)

More material was available for this species than for any other endodontid studied. Besides the 2,899 individuals cited below, 865 vaguely localized shells in older collections were quickly inspected for peculiarities, but not assigned to subspecific units or measured. Additional thousands of specimens are present in the mixed Pease material at the Museum of Comparative Zoology.

A detailed discussion of population size and structure in the Rarotonga shells is presented elsewhere (Solem, 1969a), together with a fuller analysis of variational trends.

Although Garrett (1881, p. 392) reported this species from Aitutaki, I saw no material from that island. Material from Mauke, Atiu, Mangaia, and the satellite islands of Rarotonga agreed rather closely in respect to size, shape, and sculpture (tables CIV, CV). Those from Rarotonga are significantly larger (table CIV), generally have fewer palatal barriers, and often a prominent columellar. With some hesitation, this difference is recognized as subspecific, the Rarotonga populations being described as a new subspecies, *Libera fratercula rarotongensis.*

Apparently, *Libera fratercula* is unique within the family as to its habitat. It lives at low elevations very near the shore and persists under obviously disturbed ecological conditions. It has been collected a few feet above the tide mark among coral boulders. In this habitat on Rarotonga it reaches a mean population density of 39.87 ± 3.49/ft.^{2}, with an estimated total population in one colony of 43,000,000 ± 3,770,000. In this relatively exposed habitat, it is subject to fluctuating moisture conditions and shows considerable local variation (Solem, 1969a). There are no inland records for *L. fratercula.* Accidental transport by waves during severe storms may account for its wide distribution in the Cook Islands.

Probably because of its habitat among coral boulders, with an essentially unlimited supply of calcium, *L. fratercula* has adopted its peculiar mode of releasing young from the brood pouch. Full details are given in Solem (1969a), but here it can be summarized briefly. During narrowing of the brood chamber, the animal gradually vacates the upper spire whorls, filling in behind itself with calcium. The upper spire becomes solid calcium while the eggs are in the brood chamber. After the young hatch, they chew their way into the sides of the umbilicus and eventually create an apical or subapical hole through which they exit. What percentage of the adults die before this process is completed remains unknown. Of the semi-quantitative samples (Stations R-1 through R-10) taken on Rarotonga, 44.5 per cent of live collected adults had hatched young in their brood chambers. An additional 27 specimens (4.3 per cent of 623 adults), which were collected alive, had the apex missing and the brood chamber considerably "chewed." It is possible that some of the damage occurred in the preservative or during handling, but most of the specimens represented post-reproductive material that had survived exiting of the young.

Both of the inland Rarotonga species, *Libera subcavernula* and *L. tumuloides,* are obvious derivatives of *L. fratercula.* Distinguishing features are mentioned under the diagnoses of these species. Of the other *Libera,* only *L. jacquinoti* and *L. incognata* might be confused. The former is much larger, has more widely spaced ribbing which is greatly reduced below the body whorl periphery and has 3 or 4 palatals. *L. incognata* agrees more closely in barriers, but has fewer and broader major ribs (mean 49.8) and is larger in size.

Libera fratercula fratercula (Pease, 1867). Figure 182e-f.

Helix sculptilis Pease, 1864 (not Bland, 1858), Proc. Zool. Soc. London, **1864**, pp. 669-670 — Mangier (error for Mangaia, Cook Islands); Pfeiffer, 1868, Monog. helic. viv., **5**, p. 217.

Helix fratercula Pease, 1867, Amer. Jour. Conchol., **3**, (1), p. 104 — new name for *sculptilis* Pease, 1864, not Bland, 1858; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 253 — Gambier Islands (error, possibly based on a *Gambiodonta*).

Libera fratercula (Pease), Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, **8**, (4), p. 392 — Aitutaki and Atiu, Cook Islands; Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), pp. 38-39.

Diagnosis. — Shell of average size, diameter 4.84-6.54 mm. (mean 5.60 mm.), with 5½-7¾ rather tightly coiled whorls. Apex and spire strongly elevated, normally rounded or slightly flattened above, last whorl rarely descending more rapidly, H/D ratio 0.475-0.696 (mean 0.570). Umbilicus strongly narrowed to form brood chamber by gradual inward growth of baso-columellar margin over last two whorls, opening circular or irregularly subcircular, contained 5.20-13.0 times (mean 7.40) in the diameter. Postnuclear whorls with very large, broadly rounded, strongly protractively sinuated radial ribs, 65-112 (mean 81.5) on the body whorl, whose interstices are about equal to their width. Microsculpture of extremely fine radial riblets, five to eight between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets, both generally worn off peripheral portion of major ribs. Sutures shallow, whorls strongly rounded down to very deep supraperipheral sulcus, periphery a markedly protruded threadlike keel with a deep subperipheral sulcus, lower palatal and basal margins rather strongly and evenly rounded down to baso-columellar margin which is marked by only a weak sulcus. Aperture subovate, strongly rounded above and below markedly protruded periphery, inclined about 35° from shell axis. Parietal barriers 2, extending posteriorly to line of vision; upper slightly more elevated and weakly expanded above on posterior third, with very slight anterior descension until just before termination, when barrier descends abruptly; 2nd parietal normally recessed two-thirds to one-half the length of upper, equally high and expanded on posterior elevated part with rather abrupt descension to point just behind or in front of midpoint of upper parietal, sometimes with a weak anterior threadlike extension that rarely reaches end of upper parietal. Columellar wall slightly convex inside aperture, with a heavy callus, but no noticeable columellar barrier from apertural view, occasionally a vague central elevation visible by extreme tilting of aperture. Palatal barriers normally 4, rarely (5 per cent) with supraperipheral trace absent, deeply recessed, extending posteriorly more than one-eighth whorl: lower basal in position, ridgelike, partly to completely hidden in apertural view by strong columellar callus, with very gradual anterior descension to point just behind top of baso-columellar callus margin; 2nd moderately elevated, weakly expanded above on posterior third, with very gradual anterior descension, much higher than 1st; 3rd midway in height between 1st and 2nd, subperipheral, with even more gradual anterior descension; 4th, when present, supraperipheral, a low to moderately elevated and deeply recessed threadlike trace.

Libera fratercula fratercula differs on the average in size and spire elevation from *L. fratercula rarotongensis,* but is systematically differentiated by retaining 3 subperipheral palatal barriers, and in having no conspicuous columellar barrier. The other Cook Islands species differ in their reduced major radial ribbing and less pronounced peripheral protrusion, while the very large *L. jacquinoti* also differs in its greatly reduced radial ribbing.

TABLE CIV. - ISLAND VARIATION IN LIBERA FRATERCULA

Island	Ribs[1]	Ribs/mm.[1]	Height[2]	Diameter[2]	H/D Ratio[2]	Whorls[2]
Atiu	80.0±1.81 (66-93)	5.01±0.100 (4.23-5.77)	2.91(2.55-3.33)	5.26(5.03-5.56)	0.553(0.494-0.653)	6 1/8+(5 1/2-6 1/2)
Mauke	78.9±2.18 (66-93)	4.53±0.158 (3.65-5.60)	3.10(2.81-3.99)	5.57(5.16-6.27)	0.556(0.517-0.640)	6 1/4+(6-7)
Mangaia	83.5±1.22 (72-104)	4.86±0.068 (3.81-6.13)	3.27(2.48-4.44)	5.67(4.77-6.54)	0.574(0.475-0.680)	6 1/2+(5 1/2-7 3/4)
Rarotonga	83.0±2.84 (66-105)	4.22±0.135 (3.31-5.44)	4.32(3.13-6.18)	6.59(5.43-8.15)	0.656(0.519-0.844)	7 3/8+(6-8 3/4)

1. N = 20 for Atiu; 18 for Mauke; 39 for Mangaia; 17 for Rarotonga.
2. Based on all measured adults, not cited "n" for ribs and ribs/mm.

TABLE CV. - LOCAL VARIATION IN LIBERA FRATERCULA

Name	Number of Specimens Examined	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
fratercula fratercula						
Atiu						
BPBM 94950	15	2.86±0.053 (2.55-3.20)	5.21±0.037 (4.90-5.42)	0.549±0.0088 (0.494-0.620)	6 1/8- (5 1/2-6 1/2)	7.15±0.245 (5.71-8.77)
Mauke						
BPBM 95162	20	3.00±0.032 (2.81-3.20)	5.49±0.037 (5.16-5.75)	0.547±0.0036 (0.524-0.578)	6 1/8+ (6-6 1/2)	
Mangaia						
BPBM 97492-3	15	2.92±0.068 (2.55-3.40)	5.36±0.076 (4.84-5.88)	0.544±0.0067 (0.512-0.598)	6 1/8+ (5 7/8-6 1/2)	
BPBM 97477	23	3.27±0.056 (2.81-3.66)	5.62±0.043 (5.23-5.95)	0.580±0.0069 (0.529-0.647)	6 5/8+ (6 1/4-7)	7.36±0.159 (6.14-9.45)
BPBM 97436-7	16	3.57±0.097 (3.07-4.44)	5.99±0.060 (5.56-6.54)	0.594±0.0115 (0.527-0.680)	7 1/2- (6 1/4-7 3/4)	7.83±0.255 (6.07-9.78)
BPBM 97556	17	3.58±0.052 (3.07-3.99)	5.93±0.055 (5.62-6.34)	0.604±0.0068 (0.534-0.651)	7- (6 1/2-7 1/8)	
"Mangier"						
BMNH 1965705/1-5	5	2.85±0.161 (2.48-3.20)	5.49±0.239 (4.77-6.08)	0.518±0.0112 (0.475-0.539)	6+ (5 1/2-6 1/2)	6.93±0.452 (6.08-8.28)
Satellite islands of Raratonga						
FMNH 152745 Sta. R-18	90	3.50±0.034 (2.91-4.46)	5.71±0.034 (5.05-6.47)	0.607±0.0076 (0.541-0.674)	6 5/8+ (4 3/8-7 1/4)	
FMNH 153784 Sta. R-19	19	3.60±0.067 (2.91-4.08)	5.74±0.097 (4.79-6.53)	0.614±0.0089 (0.514-0.687)	6 3/4- (5 1/2-7 1/4)	
FMNH 152742 Sta. R-17	106	3.80±0.022 (3.36-4.53)	6.17±0.021 (5.69-6.99)	0.617±0.0025 (0.559-0.690)	7- (6 1/2-7 5/8)	
fratercula rarotongensis						
BPBM 167428 (pre-1890)	14	4.08±0.102 (3.66-4.97)	6.41±0.109 (6.08-7.65)	0.635±0.0091 (0.582-0.683)	7- (6 1/2-7 1/2)	7.04±0.291 (4.26-9.36)
BPBM 95356-7 (1929)	21	3.96±0.064 (3.53-4.64)	6.34±0.038 (6.01-6.60)	0.623±0.0090 (0.571-0.725)	7- (6 3/8-7 1/2)	7.44±0.300 (6.12-8.91)
BPBM 95363, -5, -8 (1929)	14	4.20±0.096 (3.59-4.77)	6.49±0.097 (6.01-7.19)	0.647±0.0104 (0.573-0.717)	7 1/4- (6 5/8-7 3/4)	7.51±0.222 (6.12-9.00)
FMNH 144514 -5 Sta. 1, 1964)	40	3.89±0.063 (3.13-5.00)	5.54±0.038 (5.07-6.05)	0.702±0.0093 (0.583-0.844)	6 7/8- (6-7 3/8)	6.93±0.231 (5.09-13.38)
FMNH 144556, -8 Sta. 6, 1964	35	4.72±0.077 (3.88-5.39)	6.92±0.055 (6.25-7.57)	0.682±0.0088 (0.593-0.788)	7 3/4- (6 7/8-8 3/8)	7.97±0.148 (6.67-10.40)
FMNH 144557 Sta. 6, 1964	170	4.58±0.037 (3.49-5.72)	6.75±0.023 (5.92-7.50)	0.678±0.0041 (0.540-0.821)	7 5/8+ (6 1/2-8 1/2)	7.69±0.071 (5.11-9.82)
FMNH Sta. R-1 - R-10	367	4.24±0.017 (3.23-6.18)	6.62±0.001 (5.43-8.15)	0.641±0.0025 (0.519-0.813)	7 1/2- (6-8 3/4)	

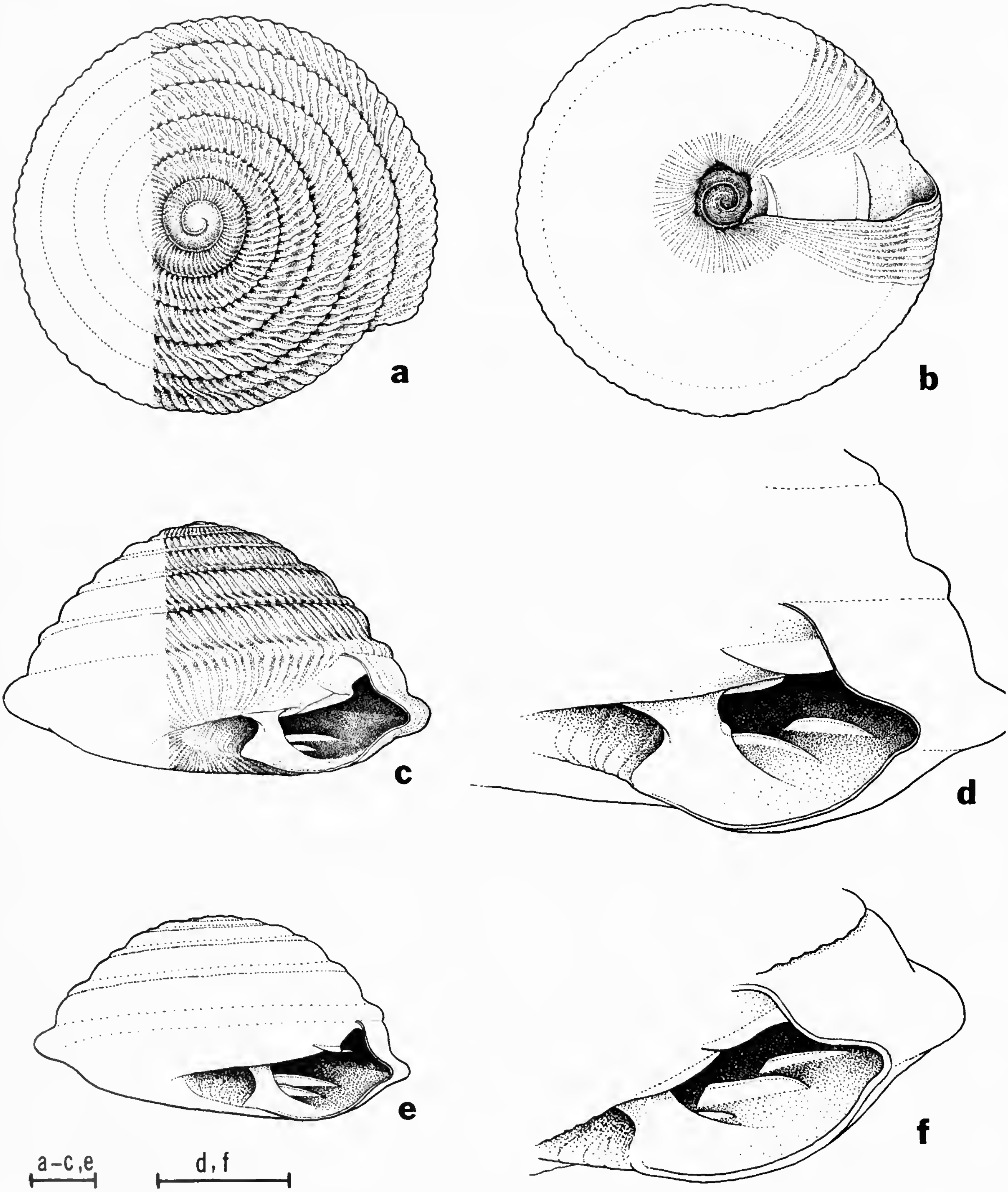

FIG. 182. **a-d**, *Libera fratercula rarotongensis*, new subspecies. Tupapa, Rarotonga, Cook Islands. Holotype. BPBM 95386; **e-f**, *Libera fratercula fratercula* (Pease). South of Oneroa, Mangaia, Cook Islands. BPBM 97503. Scale lines equal 1 mm. (SH).

Description. – Shell of average size, with 6½ moderately tightly coiled whorls. Apex and spire strongly elevated, rounded above, last whorl not descending more rapidly, H/D ratio 0.539. Embryonic whorls 1½, sculpture of moderately prominent, rounded radial ribs, eroded on upper portion. Postnuclear whorls with prominent, broadly rounded, protractively sinuated radial ribs, about 84 on the body whorl, whose interstices are almost the same as their width, and which become more broadly rounded on crossing periphery. Microsculpture occasionally visible as very fine radial riblets crossed by much finer and more crowded spiral riblets. Major ribs denticulate periphery of body whorl upon crossing, becoming slightly narrower and less prominent on shell base. Sutures shallow, whorls flatly rounded above with deep supraperipheral sulcus. Periphery a protruded, acutely rounded keel with slight subperipheral sulcus, base of shell flatly rounded. Umbilicus minute, strongly constricted by inward growth of last whorl, contained 8.28 times in the diameter. Color light yellowish-white, with faint, irregular, reddish maculations on upper spire. Aperture subquadrangular with beaklike carina and gently rounded basal margin. Parietal barriers 2, extending posteriorly one-quarter whorl: upper narrow, bladelike, sharply descending anteriorly, weakly expanded and with very fine serrations on posterior half; lower parietal less than two-thirds length of upper, deeply recessed within aperture, higher posteriorly with much more gradual anterior descension. Columellar wall with heavy opaque white callus extending slightly onto basal margin. Palatal barriers 4, deeply recessed, extending about one-eighth whorl: lower basal in position, partially hidden by anterior extension of callus, a very low lamellar ridge; 2nd high, bladelike, flattened above posteriorly, with gradual anterior descension; 3rd of same length and appearance as 2nd, but slightly lower in height; upper a low, rounded, V-shaped ridge, situated just above supraperipheral sulcus. Height of lectotype 3.21 mm., diameter 5.95 mm.

Lectotype. – Cook Islands: Mangier (= Mangaia). BMNH 1962705/1 ex Hugh Cuming, W. H. Pease.

Range. – Mauke, Aitutaki, Atiu, Mangaia and satellite islets of Rarotonga, Cook Islands.

Paratypes. – BMNH 1962705/2-5, BPBM 1399.

Material. – Mangaia (8 specimens, BPBM 97600, BPBM 97560, FMNH 117047): south of Oneroa, 200 yd. inland at 50 ft. elevation (162 specimens, BPBM 97477-83, collected December 22, 1929 by P. H. Buck); south of Oneroa, 200 yd. inland at 50 ft. elevation (213 specimens, BPBM 97490-8, BPBM 97503-4 collected December 16, 1929 by P. H. Buck); north of Oneroa, 200 yd. inland at 50 ft. elevation (115 specimens, BPBM 97435-40 collected December 16, 1929 by P. H. Buck); northwest coast, 200-850 yd. inland at 50-150 ft. elevation (2 specimens, BPBM 97430 collected by P. H. Buck on December 14, 1929); north of Orongo, 200 yd. inland at 20 ft. elevation (77 specimens, BPBM 96555-8 collected February 3, 1930 by Peter H. and Margaret Buck); Orongo, 150 yd. inland at 50 ft. elevation (153 specimens, BPBM 97618-23 collected February 10, 1930 by P. H. Buck); Orongo, 400 yd. inland at 50 ft. elevation (22 specimens, BPBM 97625-6).

Mauke (7 specimens, BPBM 95272, AMS C18487): Taunganui, 300-600 yd. inland at 50-70 ft. elevation (163 specimens, BPBM 95162-3, BPBM 95211-3, BPBM 95285, BPBM 95596 collected September 9 to November 25, 1929); Utu, 100 yd. inland at 50 ft. elevation (58 specimens, BPBM 95229-31 collected September 15, 1929 by P. H. Buck).

Atiu (3 specimens, BPBM 87406): Taunganui track, one-half mile inland at 30-70 ft. elevation (197 specimens, BPBM 94950-4, BPBM 94958-9 collected August 15, 1929 by P. H. Buck); Torapaka, one-quarter to one-half mile inland at 30-70 ft. elevation (43 specimens, BPBM 94973-4, BPBM 94979, BPBM 94995-7, BPBM 95016-7 collected August 23, 1929 by P. H. Buck); Matai track, one-quarter mile inland at 30 ft. elevation (2 specimens, BPBM 95116 collected September 1, 1929 by P. H. Buck); Mokoero, one-half mile inland at 30 ft. elevation (134 specimens, BPBM 95123, BPBM 95135-40).

Satellite islands of Rarotonga: Oneroa, Station R-19 (29 specimens, FMNH 153784); Motutapu, Stations R-17 – R-18 (307 specimens, FMNH 152742-5).

Inadequate data or "Mangier" (50 specimens, BMNH 1962705/1-5, DMW 8840, FMNH 46616, FMNH 73868, FMNH 90614, FMNH 90631, FMNH 91760).

Remarks. – The remnant of the type set preserved in the British Museum (BMNH 1965705/1-5) contains slightly subadult examples. These were obtained by Pease from a Dr. Dean (Garrett, 1881, p. 392). Although Garrett collected many specimens from Atiu, Aitutaki, Mauke, and Mangaia, no museum material from this period retained sufficient geographical data to warrant restudy. Garrett (*loc. cit.*) stated that the Rarotonga examples (here described as *L. f. rarotongensis*) were larger and with a more elevated spire; the Mangaia specimens a "uniform luteous horn color"; and the Atiu examples smaller, darker and frequently variegated with reddish brown. Partial analysis of the material collected by the Bucks on Atiu, Mangaia, and Mauke in 1929-1930 showed mean size differences between the islands (table CIV) and moderate to considerable variation between populations (table CV). The Atiu populations are smaller, but there is no significant difference between the Mauke and Mangaia populations. In general, the reported color differences were confirmed, but no statistical analysis of color variation was attempted.

Specimens from the low coral islets of Motutapu and Oneroa off the coast of Rarotonga (Stations R-17, R-18, R-19) had the barrier number (4 palatals) and were closer to the size range (table CIV) of the nominate race. They are classified with this subspecies, rather than with the Rarotongan race.

A scatter diagram of ribs and ribs/mm. (fig. 183) shows the essential similarity of the various populations, with only a slight offset distinguishing the smaller Atiu and larger Rarotonga shells.

Specimens from both Mauke (BPBM 95162) and Mangaia (BPBM 7492) were dissected and found to agree with the structures of *L. f. rarotongensis* in everything except penial length. The penes were 2.5-2.8 mm. long in the Mauke and Mangaia examples, compared with 3.3-3.5 mm., in the Rarotonga shells.

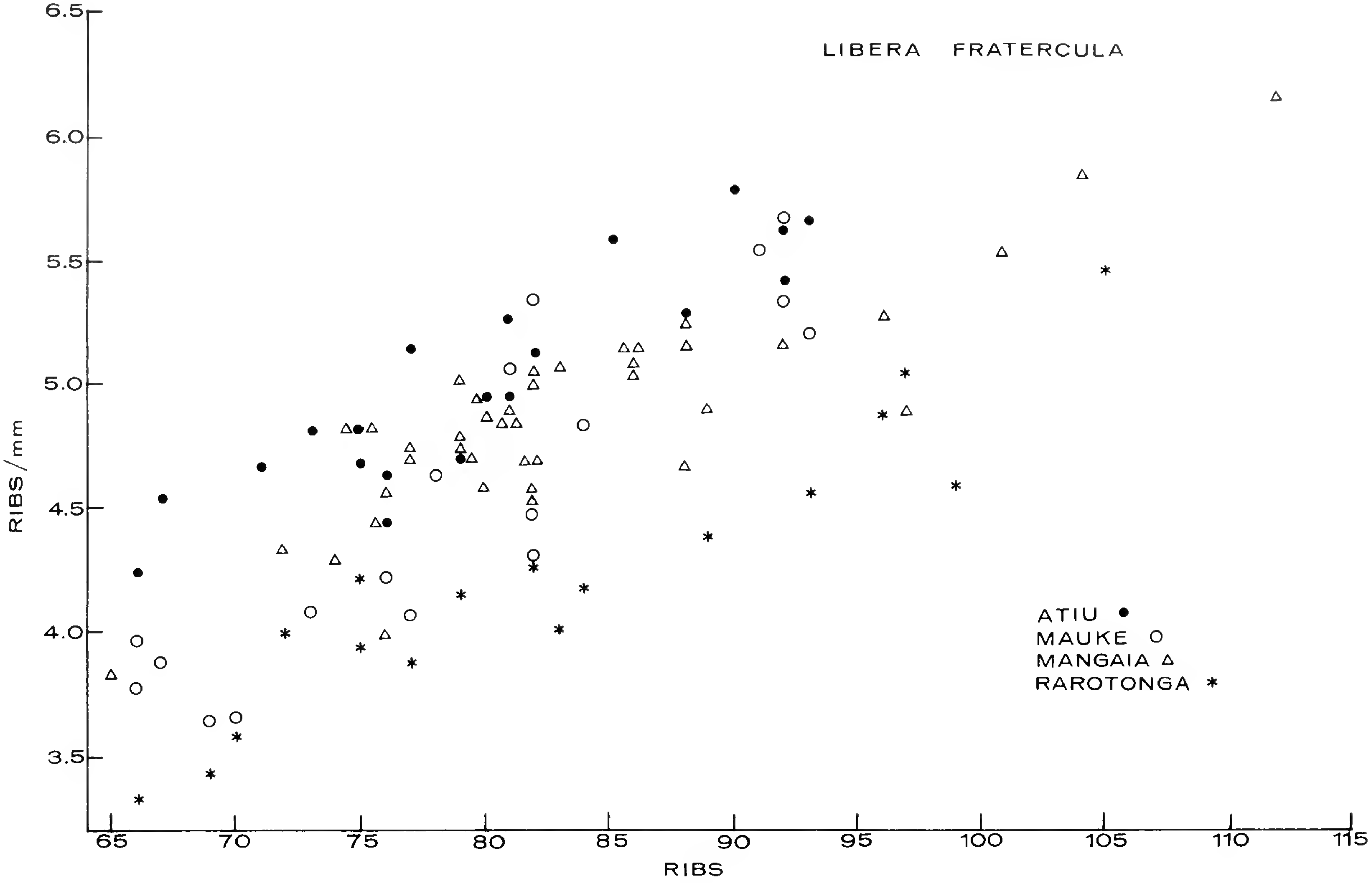

FIG. 183. Scatter diagram relating ribs and ribs/mm. in populations of *Libera fratercula* from Rarotonga, Mauke, Mangaia and Atiu.

The internal pilaster structure was identical in the several populations.

Libera fratercula rarotongensis, new subspecies. Figures 172c-g; 182a-d.

Pitys fratercula Pease, 1871, Proc. Zool. Soc. London, 1871, p. 475 – Rarotonga, Cook Islands.

Helix (*Libera*) *fratercula* (Pease), Tryon, 1887, Man. Conchol., (2), 3, p. 70, pl. 13, figs. 64-66.

Endodonta (*Libera*) *sculptilis* Pease (not Bland), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 24 – corrected on p. 339 (1895) to *fratercula*.

Diagnosis. – Shell large, diameter 5.43-8.15 mm. (mean 6.59 mm.), with 6-8¾ rather tightly coiled whorls. Apex and spire strongly elevated, slightly rounded above, last whorl rarely descending more rapidly, H/D ratio 0.519-0.844 (mean 0.656). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of last two whorls, resulting opening usually quite narrow, circular or subcircular in outline, contained 4.26-13.4 times (mean 7.55) in the diameter. Postnuclear whorls with prominent, broadly rounded, strongly protractively sinuated radial ribs, 66-105 (mean 83.0) on the body whorl, whose interstices are about equal to their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets. Sutures shallow, whorls strongly rounded down to deep and narrow supraperipheral sulcus, periphery strongly protruded into a threadlike keel with shallower subperipheral sulcus, lower palatal wall strongly rounded down to flattened basal margin with very weak sulcus just before knife-edge baso-columellar margin, columellar wall inside umbilicus flattened. Aperture subovate, strongly rounded above and below markedly protruded periphery, inclined about 35° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper moderately elevated, slightly higher above on posterior third with very gradual anterior descension until just before termination; 2nd parietal recessed two-thirds to three-quarters length of upper, markedly reduced in height, very weakly expanded above posteriorly, with rather sharp anterior descension, occasionally in juveniles with a threadlike anterior trace reaching almost to end of upper parietal. Columellar wall slightly convex inside aperture, heavily callused, either with or without a low to moderately prominent, very deeply recessed barrier that is barely visible by extreme tilting of aperture. Palatal barriers 2, very deeply recessed, extending posteriorly about one-eighth whorl, subperipheral; lower occupying position of 2nd palatal in nominate subspecies, a raised ridgelike barrier with very gradual anterior descension; 2nd occupying position of 3rd palatal in nominate subspecies, equal to, slightly larger than, or slightly smaller than 1st palatal, usually with more gradual anterior descension.

Libera fratercula rarotongensis is immediately separable from the nominate race in lacking the 1st and 4th palatals. Usually it has a columellar barrier. Size differences are considerable, although overlap exists. *Libera subcavernula* has the sculpture greatly reduced on the spire and absent on the lower whorls, while the periphery is much less strongly protruded. *Libera tumuloides* differs in having no major radial sculpture and retaining only 1 parietal and 1 palatal barrier in adult specimens.

Description. – Shell relatively large, with 7⅛ moderately tightly coiled whorls. Apex and spire strongly elevated, slightly rounded above, last whorl not descending more rapidly, H/D ratio 0.626. Embryonic whorls 1½, sculpture partially eroded with remnants of fine radial ribs persisting near suture. Postnuclear whorls with broadly rounded, prominent, protractively sinuated radial ribs, about 90 on the body whorl, whose interstices are equal to or slightly narrower than their width. Microsculpture of fine radial riblets crossed by exceedingly fine and crowded spiral riblets continuing onto and on top of the major radial ribs. Major ribs finely denticulating peripheral keel on crossing, somewhat reduced in prominence on shell base. Sutures shallow, with denticulated edge, whorls strongly rounded above with deep, concave sulcus above periphery, weaker sulcus below. Body whorl with protruded denticulated carina. Umbilicus strongly constricted by expansion of last whorl-and-one-half, opening narrow, somewhat irregular in shape, contained 8.25 times in the diameter. Color a light yellow-white, with a few brownish tessellations on the upper spire, fading out after 5th whorl. Aperture subquadrangular with protruded beaklike carina, with evenly rounded basal margin, inclined about 35° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper moderate in size, becoming slightly higher on posterior half; lower deeply recessed, becoming lamellate posteriorly, about half length of upper. Columellar wall with heavy thick white callus, a deeply recessed, low columellar barrier barely visible within aperture, gradually descending behind columellar callus. Palatal barriers 2, extending slightly less than one-eighth whorl, moderately elevated with gradual anterior descension, both subperipheral in position and very deeply recessed. Height of holotype 4.05 mm., diameter 6.47 mm.

Holotype. – Cook Islands: Rarotonga, 200 yd. inland from Tupapa at 10 ft. elevation. Collected by Margaret Buck on October 4, 1929. BPBM 95368.

Range. – Rarotonga, Cook Islands, but not the small satellite islands of Oneroa and Motutapu.

Paratypes. – Same as list of material.

Material. – Rarotonga (46 specimens, BPBM 167428, FMNH 90630): 200 yd. inland at 10 ft. elevation, Tupapa (178 specimens, BPBM 95356-68 collected by Margaret Buck on October 4, 1929); 1.6-2.8 miles east (Stations R-1 through R-10, R-14, R-15) of Avarua (930 specimens, FMNH 152743-4, FMNH 153372-4, FMNH 153376-9, FMNH 153393, FMNH 153418, FMNH 153421 collected by Laurie Price in November 1965); Avarua (Stations 1, 6) and Avatiu Harbour area (247 specimens, FMNH 144514-5, FMNH 144556-8 collected by Laurie Price in October to November, 1964). Cook Islands (13 specimens, FMNH 91073, FMNH 91842).

Remarks. – A particularly large colony of *Libera fratercula rarotongensis* is found 1.6-2.8 miles east of Avarua on both sides of the main road. Except for scattered houses, where the coral boulders and part of the undergrowth have been cleared away, the colony is continuous. It starts just inside the vegetation above the storm high-tide mark and continues through the coral boulder zone, fading out about 150 yd. inland, congruent with the end of the boulders. The vegetation consists of typical lowland scrub, coconut palms, and a few large trees. Samples of all living individuals within a 15-in.-square quadrat were taken at 200 yd. intervals. The mean density of living individuals was 39.87 ± 3.49 per sq. ft. The total population of the colony, just between the main road and the high tide mark, is estimated at about 43,000,000 living snails. Full discussion of variation in this colony is given in Solem (1969a). Summary measurements are given in Table CV. The 1964 locality, Station 6, is from part of this same colony.

For comparison, data on material from pre-1890 collecting (BPBM 167428) and two segregates from the 1929 collecting (BPBM 95356-7 and BPBM 95363, -5, -8) are presented in Table CV. It is obvious that there are no significant differences between the populations from different time intervals. There is, however, a significant difference between material from the 1964 collection at Station 1 (FMNH 144514-5) and the remaining samples discussed above. The Avatiu Harbour examples are much smaller and slightly higher, reaching the diameter and whorl count, but not the height or H/D ratio, range of the nominate subspecies. This area is much less heavily vegetated, and hence drier, than the other major sampling area. The dwarfing of these specimens is not exceptional under the drier conditions.

That there is a genetic base to the differences between the nominate race and *rarotongensis* is suggested by the barrier counts in juveniles, where young *rarotongensis* have only 2 palatals and young *fratercula fratercula* have 3 palatals below the periphery. Whether the larger size of the *rarotongensis* shells merely represents more favorable moisture and nutrient conditions on Rarotonga compared with the offshore atolls and other Cook Islands, or is the result of more complex factors is unknown.

There were no unusual anatomical features in the material dissected.

Description of soft parts. — Foot and tail slender, length about equal to shell diameter, tapering slightly then rounded posteriorly, truncated anteriorly with head projecting slightly in front of foot. Pedal grooves relatively low on sides of foot, suprapedal slightly weaker than pedal, both uniting across tail. No caudal horn, caudal foss or middorsal groove. Slime network weakly rectangular, rather inconspicuous.

Body color in preservative light yellow-white, eyespot small and black, rest of ommatophore with dense black speckles.

Mantle collar (MC) of average width, thin, with slight protrusion of mantle glands onto roof. Pneumostome masked by thickened edges of mantle collar but without distinct lobes. Anus and pneumostome sharing common opening, relative positions as in *Endodonta fricki.*

Pallial cavity (fig. 172e) extending apically for about three-quarters whorl. Lung roof clear, without any white or black specklings. Kidney (K) narrow, less than one-third length of pallial cavity, abutting on loop of intestine, a significant portion reaching hindgut. Ureter (KD) short and conspicuous, following curve of kidney and reflexing to anterior edge of rectal kidney arm, then opening directly onto pallial cavity. No secondary ureter present. Hindgut (HG) paralleling parietal-palatal angle to anus, not enlarged. Heart (H) rather large, slightly less than half length of kidney. Principal pulmonary vein (HV) conspicuous, running along periphery of shell from anterior end of kidney, reaching the very slight protrusion of mantle gland onto lung roof, no conspicuous secondary venation.

Ovotestis (G) imbedded in digestive gland just above stomach-intestine reflexion, consisting of numerous clumps of palmately clavate alveoli, slightly iridescent basally, strung along single collecting tubule. Ovotestis stopping well short of digestive gland apex (fig. 172f). Hermaphroditic duct (GD) a slim, opaque, slightly iridescent tube running along basal margin of whorl past base of stomach, narrowing abruptly at base of albumen gland (GG), then running into latter to join buried stalk of talon (GT). Albumen gland white, of loose, fine-textured acinar tissue, squeezed between loops of intestine with head of spermatheca (S) lying on outer surface. Talon a blind duct with expanded head tapering to a slender tube, expanded to form carrefour just before union with hermaphroditic duct. Prostate (DG) composed of three rows of large acini opening into a slender tube partly obscured by uterine tube. Uterus (UT) a very thin-walled circular tube above, past midpoint of prostate uterus broadening into a large chamber (fig. 172f), tapering to start of free oviduct (UV). Vas deferens (VD) a continuation of tube from prostate, passing down to penioviducal angle where it then passes up alongside penis, but not bound to it, before entering just below apical insertion of penial retractor (PR). Latter very long and rather thick, arising from diaphragm at level of spermathecal head and inserting on head of penis (P). Latter a thin-walled muscular tube extending about 3.5 mm. long, moderately swollen medially, tapering gradually to both ends, internally (fig. 172d) with two longitudinal, high, glandular pilasters, one with a secondary broad extension medially. Pilasters uniting in atrium (Y), which is quite short.

Free oviduct (UV) about one-and-one-half times as long as prostate-uterus, slightly swollen apically, tapering to a slender tube scarcely wider than duct of spermatheca. Spermatheca (S) with very slender duct lightly bound to free oviduct and margin of prostate-uterus to midpoint of latter, then passing up surface of prostate and starting to expand just before base of albumen gland. Head of spermatheca pressed against albumen gland surface, bulbously expanded, shaft inserting directly onto penioviducal angle, being tightly bound to free oviduct for last 2 mm.

Gross appearance of digestive system differing from *Endodonta* only in having the esophagus larger in diameter (probably an artifact in preservation), and less striking constrictions at the stomach-intestine junction. Digestive gland extending to apex of soft parts, occupying full whorl and a half above apex of ovotestis, but stopping several whorls short of apex in gerontic individuals (see p. 95).

Free muscle system simple. Right ommatophoral retractor passing through penioviducal angle, uniting with right rhinophoral retractor two-thirds of way to tentacular union with tail fan. Columellar muscle broad and elongated, extending up to midlevel of stomach. Buccal retractor not split, joining columellar retractor at its tip.

Penis enervated from right cerebral ganglion. Main nerve to base of penis, with second largest branch to vas deferens in penioviducal angle, secondary branches to free oviduct and atrium.

Jaw of narrow plates, about four times as long as wide, with slight trace of medial fusing.

Radula with central about 13μ long, 8μ wide, laterals 6 to 7, endocone becoming prominent at point of transition where ectocone starts splitting. By outer of 10 to 13 marginals, endocone and mesocone subequal, ectocone split into three or four smaller cusps, basal plates broadly rectangular.

(Based on BPBM 95356 and FMNH 114556, 10 adult specimens.)

Libera subcavernula (Tryon, 1887). Figure 184 a-c.

Pitys cavernula Garrett, 1872 (not *Helix cavernula* Hombron & Jacquinot, 1852, which is a synonym of *Libera jacquinoti* Pfeiffer), Amer. Jour. Conchol., 7, (4), pp. 226-227, pl. 19, fig. 16 — in mountain ravines of Rarotonga, Cook Islands; Pfeiffer, 1876, Monog. helic. viv., 7, p. 568.

Libera cavernula (Garrett), Garrett, 1881 (not Hombron and Jacquinot, 1852) Jour. Acad. Nat. Sci., Philadelphia, 8, (4), p. 392.

Helix (Libera) subcavernula Tryon, 1887, Man. Conchol., (2), **3**, p. 70, pl. 13, figs. 67-69 — new name for *cavernula* Garrett, 1872, not Hombron and Jacquinot, 1852.

Endodonta (Libera) subcavernula (Tryon), Pilsbry, 1893, *op. cit.*, (2), **9**, pp. 23, 24, pl. 5, figs. 45-48.

Libera subcavernula (Tryon), Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), p. 38.

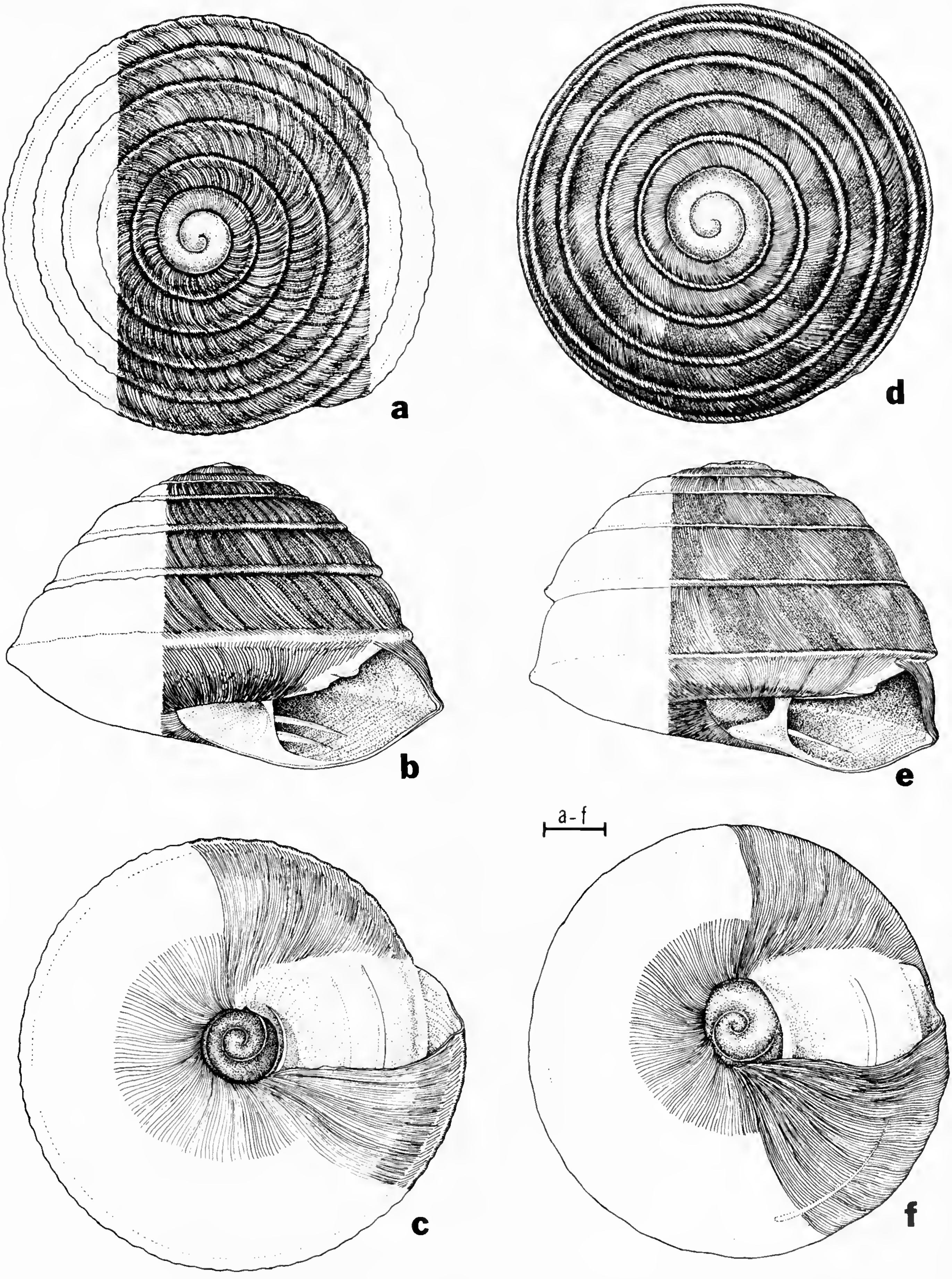

FIG. 184. **a-c**, *Libera subcavernula* (Tryon). Rarotonga, Cook Islands. BPBM 2240; **d-f**, *Libera tumuloides* (Garrett). Rarotonga, Cook Islands. BPBM 2239. Scale lines equal 1 mm. (MM).

Diagnosis. — Shell large, diameter 5.29-7.63 mm. (mean 6.29 mm.), with 5½-7¼+ normally coiled whorls. Apex and spire strongly elevated, rounded above, last whorl not descending more rapidly, H/D ratio 0.548-0.711 (mean 0.618). Umbilicus secondarily narrowed to form brood chamber by gradual inward protrusion of basocolumellar margin for last two whorls, resulting opening circular or subcircular, contained 3.58-8.09 times (mean 5.68) in the diameter. Postnuclear sculpture of relatively low, rounded, protractively sinuated radial ribs, whose interstices are about twice their width, and which become reduced to irregularity on body whorl and are absent from base of shell in adults. Microsculpture of fine, rather widely spaced radial riblets, three to five between each pair of major ribs, crossed by exceedingly fine and crowded spiral riblets that are visible only under 96× magnification. Sutures shallow, whorls evenly rounded down to relatively shallow supraperipheral sulcus, periphery a moderately protruded threadlike keel with weak supraperipheral sulcus, lower palatal and basal margins rather strongly and evenly rounded down to very slight sulcus before sharply angled basocolumellar margin. Aperture subquadrangular, more strongly rounded above than below protruded periphery, inclined about 25° from shell axis. Parietal barriers 2, rarely (2.3 per cent) with lower absent, extending posteriorly to line of vision: upper high and bladelike, distinctly more elevated and expanded above on posterior third, with very gradual descension until just before anterior termination; 2nd recessed to about midpoint of upper, lower but more broadly expanded above posteriorly with rather sharp anterior descension to normal termination, often with a weak, threadlike anterior extension to point opposite end of upper parietal. Columellar wall with a low to moderately elevated, broadly rounded, very deeply recessed barrier that merges into top of columellar callus. Palatal barriers 2, rarely (4.7 per cent) with a 3rd present, moderately deeply recessed, extending posteriorly about three-sixteenths of a whorl: lower at lower palatal-basal margin, flattened and weakly expanded above on posterior third, with gradual anterior descension; 2nd slightly less elevated, flattened above on posterior half, with slightly sharper anterior descension; 3rd, when present, a low lamellar blade, very short, situated between columellar and 1st palatal.

Libera subcavernula differs from *Libera fratercula rarotongensis* primarily in degree rather than in kind. The latter has the regular sculpture much stronger and more regularly spaced, the peripheral keel is much more strongly protruded, the sulci are deeper, and apparently is restricted to lowland habitats near the ocean. *L. subcavernula* was an inland species with much less prominent radial ribbing and smaller peripheral keel. *L. tumuloides* has lost the radial ribbing, generally has only a single palatal barrier and always has only a single parietal.

Description. — Shell large, with slightly less than 6½ normally coiled whorls. Apex and spire strongly elevated, form dome shaped, last whorl not deflected, H/D ratio 0.607. Apical whorls 1⅜, sculpture of fine, moderately widely spaced radial riblets, whose interstices are 3-5 times their width, with a microreticulated sculpture of radial and spiral riblets. Postnuclear whorls with low, rounded, rather widely spaced radial ribs, whose interstices are 2-3 times their width, and which denticulate the sutures, becoming obsolete on last half of body whorl. Microsculpture of fine radial riblets crossed by much finer and more crowded spiral riblets. Sutures margined by a protruding threadlike keel, denticulated by radial ribs on early whorls. Whorls flatly rounded above threadlike keel, with a distinct supraperipheral groove, evenly rounded on elongated basal margin. Color yellowish-horn with numerous, somewhat irregular, reddish flammulations that fade out near umbilicus. Umbilical region strongly constricted by growth of last whorl-and-one-half, opening almost circular, contained 4.86 times in the diameter. Aperture subcrescentic with protruding peripheral keel and evenly rounded margins, inclined about 20° from shell axis. Parietal barriers 2, extending more than one-quarter whorl: upper parietal with anterior half a low, raised lamellar ridge becoming high and bladelike on posterior half; lower parietal similar posteriorly but with anterior half low and threadlike. Columellar wall with a heavy callus, surmounted by a deeply recessed, broad, lamellar barrier. Palatal wall with two subperipheral barriers, deeply recessed, extending three-sixteenths of a whorl: lower palatal high and bladelike, with gradual anterior descension; upper palatal lower with more gradual anterior descension and slightly more deeply recessed. Height of lectotype 4.05 mm., diameter 6.67 mm.

Lectotype. — Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47813.

Range. — Mountain ravines of Rarotonga, Cook Islands (Garrett, 1881, p. 392).

Paratypes. — BPBM 2240, ANSP 290112.

Material. — Cook Islands (21 specimens, BPBM 189937, FMNH 90609, FMNH 91884, FMNH 99849): Rarotonga (52 specimens, BPBM 2240, BPBM 167429, FMNH 73892, ANSP 47813-4, AMS, AMS C18488, ANSP 290112, USNM 77110, USNM 98745, USNM 203454).

Remarks. — Although Garrett (1881, p. 392) implied that this species was widely dispersed and "Found plentifully in the mountain ravines," no specimens were collected in 1964 and 1965. Apparently it was an inland replacement of *Libera fratercula rarotongensis. L. subcavernula* almost certainly was derived by reduction of the keel and ribbing. No intermediate examples were seen. The lectotype is a rather flat and heavily sculptured specimen, but is the best preserved example in the type set.

Many small samples in older museum collections (table CVI) were seen. Variation was only in size, reflecting retention of large specimens by Garrett (BPBM 2240) and the presence of small individuals in the Hedley (AMS) and Fulton (RSM) collections. There is no indication of variation between populations as in *Thaumatodon multilamellata.*

Libera tumuloides (Garrett, 1872). Figure 184d-f.

Pitys tumuloides Garrett, 1872, Amer. Jour. Conchol., **7**, (4), pp. 225-226, pl. 19, fig. 15 — high up in a mountain ravine on Rarotonga, Cook Islands.

Endodonta tumuloides (Garrett), Binney, 1875, Proc. Acad. Nat. Sci., Philadelphia, **1875**, p. 248, pl. 21, fig. 6 (radula).

Helix tumuloides (Garrett), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 567.

Libera tumuloides (Garrett), Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, **8**, (4), p. 393; Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), pp. 40-41.

Helix (Libera) tumuloides (Garrett), Tryon, 1887, Man. Conchol., (2), **3**, p. 70, pl. 13, figs. 70-71.

Endodonta (Libera) tumuloides (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, pp. 23-24, pl. 9, fig. 26 (radula).

Diagnosis. — Shell large, diameter 6.18-7.17 mm. (mean 6.51 mm.), with 6⅛-7½ normally coiled whorls. Apex and spire rather strongly elevated, broadly rounded above, last whorl normally slightly to moderately deflected below periphery of penultimate whorl, H/D ratio 0.553-0.812 (mean 0.671). Umbilicus secondarily narrowed to form brood chamber by gradual inward growth of basocolumellar margin over last two whorls, inward growth accelerating in later stages, resulting opening somewhat irregular, contained 3.62-

TABLE CVI. - LOCAL VARIATION IN LIBERA SUBCAVERNULA, L. TUMULOIDES AND L. JACQUINOTI

	Number of Specimens	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
subcavernula							
AMS C.18488	5		3.70±0.064 (3.53-3.92)	5.93±0.126 (5.62-6.27)	0.624±0.0076 (0.607-0.651)	6 1/4- (6-6 1/2)	5.55±0.353 (4.77-6.69)
RSM 1961.61.51	11		3.70±0.123 (3.07-4.25)	6.05±0.129 (5.29-6.80)	0.610±0.0124 (0.548-0.677)	6 1/8+ (5 3/4-6 3/4)	5.64±0.365 (3.58-8.09)
ANSP 47812	7		3.81±0.114 (3.46-4.31)	6.16±0.130 (5.75-6.80)	0.619±0.0166 (0.549-0.688)	6 1/4 (5 7/8-6 5/8)	5.95±0.454 (4.52-7.84)
ANSP 47814	10		3.99±0.149 (3.33-4.97)	6.42±0.216 (5.56-7.58)	0.622±0.0120 (0.560-0.668)	6 1/2 (6-7 1/4)	5.89±0.253 (5.00-7.31)
ANSP 47813, ANSP 290112	6		3.92±0.139 (3.59-4.51)	6.44±0.113 (6.01-6.80)	0.609±0.0208 (0.576-0.711)	6 1/2- (6-7)	5.47±0.347 (4.84-6.93)
BPBM 2240	5		4.35±0.196 (3.66-4.84)	6.93±0.068 (6.67-7.06)	0.628±0.0246 (0.549-0.698)	7- (6 1/4-7 1/8)	5.64±0.295 (4.91-6.70)
tumuloides							
Zurich	8		4.25±0.177 (3.53-5.10)	6.34±0.083 (6.14-6.86)	0.670±0.0270 (0.574-0.812)	6 3/4- (6 1/8-7 1/2)	4.88±0.308 (3.62-6.00)
Zurich	6		4.52±0.078 (4.25-4.71)	6.44±0.050 (6.21-6.54)	0.702±0.0102 (0.670-0.735)	6 3/4+ (6 1/2-7 1/8)	4.93±0.216 (4.16-5.55)
ANSP 47815, ANSP 290098	10		4.43±0.068 (4.25-4.90)	6.46±0.049 (6.21-6.73)	0.686±0.0117 (0.640-0.773)	7 (6 5/8-7 1/4)	5.09±0.161 (4.23-6.18)
BPBM 2239, BPBM 167427	9		4.45±0.124 (4.05-4.97)	6.67±0.081 (6.34-7.12)	0.667±0.0163 (0.603-0.732)	7- (6 1/2-7 1/4)	5.42±0.350 (3.74-6.93)
jacquinoti							
BPBM 167409, BPBM 189941	3	60.0±5.72 (53-67)	4.34±0.367 (3.79-5.03)	8.13±0.602 (6.93-8.82)	0.534±0.0254 (0.485-0.570)	7 3/8 (7-7 7/8)	5.20±0.987 (3.78-7.10)
AMS	5	54.0±2.45 (47-60)	4.47±0.183 (3.86-4.84)	8.35±0.270 (7.45-9.02)	0.535±0.0140 (0.500-0.580)	7 1/2 (7-7 7/8)	6.39±0.622 (4.75-7.82)
Paris	5	53.0±2.90 (47-62)	5.05±0.162 (4.58-5.49)	8.93±0.105 (8.69-9.28)	0.565±0.0152 (0.522-0.617)	8+ (7 5/8-9)	8.35±0.215 (7.82-8.93)

6.93 times (mean 5.08) in the diameter. Early postnuclear whorls with narrow, strongly protractive major radial ribs, that are absent from last few whorls and very reduced and irregular on early spire. Microsculpture of fine radial riblets, broader and more widely spaced below than on upper spire, crossed by extremely fine and crowded spiral riblets that are barely visible under 96× magnification. Sutures very shallow, whorls flatly rounded down to prominent supraperipheral sulcus, periphery a narrow, rather sharply protruded threadlike keel with weaker subperipheral sulcus, lower palatal and basal margin evenly and rather broadly rounded down to distinct sulcus before protruded baso-columellar margin. Aperture subquadrangular, rounded above and below strongly protruded periphery, inclined about 30° from shell axis. Parietal wall with single barrier, extending posteriorly to or beyond line of vision, high and slightly more expanded above on visible posterior quarter, with gradual anterior descension to midpoint, anterior half a raised threadlike ridge. Columellar wall normally (71.8 per cent) without, often (28.2 per cent) with a low and broadly rounded, very deeply recessed barrier, visible only by extreme tilting of aperture. Palatal wall normally with a single subperipheral, medially located, moderately deeply recessed barrier, extending posteriorly three-sixteenths of a whorl, occasionally (5.2 per cent) with a second, slightly lower, barrier: major barrier high and slender, flattened above on posterior half, with gradual anterior descension; 2nd, when present, located nearer columellar margin, slightly reduced in height.

The complete loss of major radial ribbing on the lower spire and body whorl combine with presence of only 1 parietal and 1 palatal to immediately separate *Libera tumuloides* from the other Rarotongan species. Society Islands species with reduced radial sculpture, such as *L. heynemanni* and *L. garrettiana,* differ immediately in the greater number of apertural barriers.

Description. — Shell relatively large, with slightly less than 7¼ tightly coiled whorls. Apex strongly elevated, whorls descending rapidly, form dome shaped, body whorl slightly deflected, H/D ratio 0.686. Apical whorls 1½, sculpture eroded except for traces of radial ribbing in the sutures. Postnuclear whorls with low, rounded, rather widely spaced radial ribs that weakly denticulate the suture on the upper whorls, becoming obsolete on the lower spire and body whorl. Microsculpture of very fine radial riblets, crossed by much finer and more crowded spiral riblets. Sutures shallow, margined by protruded threadlike keel. Whorls flatly rounded above periphery and partly flattened on basal margins. Color light yellow horn, with broad, irregular, light- to dark-toned, reddish flammulations. Umbilicus strongly constricted to form brood chamber by last whorl-and-a-half, opening subcircular, contained 5.10 times in the diameter. Aperture subquadrangular with flattened upper palatal margin and elongated, gently rounded basal margin, inclined about 25° from shell axis. Parietal wall with single long barrier, low and threadlike anteriorly, becoming high and bladelike posteriorly, running beyond line of vision. Columella with a heavy, white callus on which a broad, deeply recessed radial swelling occurs. Lower palatal lip with a single, medial, deeply recessed, bladelike barrier, extending slightly more than one-eighth whorl, recessed almost one-eighth whorl within aperture. Height of lectotype 4.57 mm., diameter 6.67 mm.

Lectotype. — Cook Islands: Rarotonga, high up in a mountain ravine. Collected by Andrew Garrett. ANSP 47815.

Range. — A small area of about one-half acre located nearly 2 miles inland, Rarotonga, Cook Islands (Garrett, 1881, p. 393).

Paratypes. — BPBM 2239, ANSP 290098.

Material. — Cook Islands (11 specimens, USNM 77940, USNM 98742, FMNH 91146, FMNH 91841): Rarotonga (61 specimens, BPBM 2239, BPBM 167427, FMNH 73891, FMNH 117279, ANSP 47815, ANSP 290098, AMS, Zurich, USNM 77037, USNM 203452).

Remarks. — Of an original "over 300 specimens," only 72 were located in museum collections. There was little variation in size and shape (table CVI). The highly restricted range of "one-half an acre" would be difficult to find even if a valley name had been furnished. Probably at least 3,400 acres of Rarotonga would lie "nearly two miles inland" by foot (or more). Providing the species is not extinct, much more thorough collecting will be required than was possible in 1964 and 1965 to locate the colony. Since no material of *L. subcavernula* was found, I suspect both may be extinct.

L. tumuloides has lost the major radial ribbing and retains only 1 parietal and 1 palatal barrier. It shows intensification of the trends seen in *L. subcavernula* when compared with *L. fratercula*, and probably was directly derived from this stock.

I could not locate the radular material figured by Binney (1875) and Pilsbry (1893-1895). Their drawings show no peculiarities that would separate them from species studied during preparation of this report.

Libera sp.

Helix excavata Hombron & Jacquinot, 1841 (not Bean, 1830), Ann. Sci. Nat., Zool., (2), **16**, p. 64 — Tahiti; Hombron and Jacquinot, 1852, Voy. Pol. Sud, Astrolabe et Zélée, Atlas, pl. 6, figs. 9-12 — Tahiti, Society Islands; Rousseau, 1854, *op. cit.*, **5**, pp. 17-18; Ponsonby, 1910, Proc. Malacol. Soc. London, **9**, (1), p. 43.

Helix (*Libera*) *jacquinoti* Tryon, 1887 (not Pfeiffer, 1850), Man. Conchol., (2), **3**, pl. 13, figs. 72-74.

Range. — Unknown.

Material. — "Tahiti" (3 specimens, BPBM 167408, ex Fulton). No locality (10 specimens, BPBM 8599, BPBM 8690 ex Garrett, FMNH 117007).

Remarks. — Ponsonby (*loc. cit.*) and Cooke (manuscript notes) considered that *Helix excavata* of Hombron and Jacquinot was a variety of *Libera heynemanni.* I disagree, since the type figures clearly show radial ribbing on the upper shell surface (but absent below periphery) while *heynemanni* lacks all ribbing. The figures show a very tiny umbilicus and 2 strong parietal barriers, the lower deeply recessed, but no palatals. Lack of the latter in the illustration has no significance, since they are absent in the other *Libera* on the same plate. Rousseau's (*loc. cit.*) description was based only on the figures and is worthless in determining its identity. The specimens cited above, ranging from 5.30 - 6.15 mm. in diameter, agree fairly well with the figures, although slightly smaller than the 7 mm. size cited by Rousseau. They are slightly larger and higher than most *L. dubiosa*, but may be only extreme variants of that species.

Until localized material agreeing with the type figures is rediscovered, there is no reason to rename the pre-occupied *Helix excavata* Hombron & Jacquinot. I prefer to leave it as a dubious species. Ponsonby (1910, p. 43) indicated that the type specimens are not in the Paris Museum and I could not locate any specimens during my visits to that institution.

Libera sp.

Helix bursatella var. *alpha*, Gould, 1846, Proc. Boston Soc. Nat. Hist., **2**, p. 175 – Tahiti and Eimeo (Moorea), Society Islands; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 185; Gould, 1852, U. S. Explor. Exped., Wilkes, **12**, p. 52.

Material. — Location unknown (2 specimens, BPBM 189935).

Remarks. — The large, nearly smooth shell closely matches Gould's description of variety *alpha*. It appears to be a large form or close relative of *heynemanni*, but without new material from a precise locality, no nomenclatural recognition is warranted. The largest shell is 8.17 mm. in diameter with 8½ whorls, H/D ratio 0.640.

Libera sp.

Libera n. sp., Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, 8, (4), p. 393 – lowland forest at Aitutaki, Cook Islands.

Remarks. — Garrett (*loc. cit.*) reported that five shells of this, "the smallest species in the genus," were deposited in the Museum Godeffroy, Hamburg. These collections were destroyed during World War II. No collecting has been done on Aitutaki since Garrett's time.

Genus **Gambiodonta,** new genus

Extremely large Endodontidae in which the umbilicus is modified to form a brood chamber by inward growth of the last whorl. Apical sculpture consisting of very broad and rounded major ribs interspersed with finer riblets. Postnuclear sculpture of narrow to broadly rounded, strongly protractive radial ribs that denticulate the slight to very strong peripheral keel and may be reduced or absent on base of shell. Strong secondary spiral cording usually present. Whorl count generally more than 6 (except in *G. mirabilis*), spire strongly elevated, dome shaped above. Parietal barriers extending more than one-quarter whorl, 2-5 major barriers (usually 4-5) and five to eight accessory traces (except in *G. grandis*). One columellar barrier usually with a single accessory trace. Major palatal barriers 4, lower almost reduced to size of accessory traces (not differentiated in *G. mirabilis* and *G. grandis*), with three to twelve accessory traces. Anatomy unknown.

Type species. — *Gambiodonta pilsbryi pilsbryi*, new species.

Both *Libera* and *Pseudolibera*, the other two Polynesian genera with an umbilical brood chamber, have a greatly reduced number of apertural barriers, different apical sculpture (fig. 22a-c), and quite different postnuclear sculpture. Formation of an umbilical brood chamber has produced many similarities in form and general appearance, but the patterns of sculpture, apertural barriers and rate of umbilical closure are completely different in *Libera*, *Pseudolibera*, and *Gambiodonta*.

The apertural barriers in *Gambiodonta* are essentially identical to those of *Anceyodonta*, differing only in minor details such as having the lower palatal much more reduced in size (accentuating a trend present in many *Anceyodonta*) and an increased number of accessory traces (probably reflecting the greater area of the parietal and palatal walls, hence more room for accessory traces). The reduction of elevated parietals to 2 or 3 (*G. mirabilis* and *G. agakauitaiana*) reflects secondary shell modifications and small size, respectively, while the development of 5 relatively low parietals in *G. pilsbryi* correlates with depressed shape and strongly protruded keel of that species. Placement of the accessory traces, with two or three above the upper palatal and parietal barriers, with one or two between each pair of major barriers, follows the exact pattern seen in those *Anceyodonta* with accessory traces present.

Sculptural similarities of *Anceyodonta* and *Gambiodonta* are marked. The secondary spiral cording present in many *Anceyodonta* is very strongly developed in most *Gambiodonta*, being absent only in the highly modified *G. mirabilis* and *G. grandis*. Three *Gambiodonta*, *G. mirabilis*, *G. mangarevana*, and *G. agakauitaiana*, have the same narrow ribbing found in *Anceyodonta*; the other three species, *G. pilsbryi*, *G. tumida*, and *G. grandis*, have developed quite broadly rounded ribs. Most species have a basically identical color pattern, except for *G. mirabilis*. It is noteworthy that the larger species have modified ribbing, the smaller typical endodontid ribs. *Gambiodonta* differs most obviously in sculpture by its very large major apical ribs (fig. 22a-c).

Comparisons of form are negated by the vastly different umbilical structures. In *Anceyodonta* the umbilicus generally is minute or constricted internally with the last whorl decoiling to form a wider opening (*A. labiosa*, *A. subconica*, *A. soror*, and *A. difficilis*) and only in *A. andersoni* and *A. alternata* (fig. 82c, f) is the umbilicus broadly open internally. In *Gambiodonta* the juvenile umbilicus is very broadly open (fig. 189d) with a sharp marginal angulation developed after about 3½-5½ whorls. In *G. pilsbryi aukenensis*, for example, within slightly more than one-half whorl after this, the angulation has become a weak keel. Very suddenly, an extremely sharp inward projection of this keel starts from the baso-columellar margin (fig. 185). The inward growth continues for about one-quarter to one-third whorl, and at the end, the columellar wall has been grossly elongated, slanted downward and inward, obscuring approximately one-third of the umbilical width. Inward growth stabilizes at this point, with the subsequent half whorl of umbilical margin growth irregularly maintaining the same distance from the columellar margin of the preceeding whorl. This is particularly obvious in Figures 186b; 187b, e; and 188b. When this inward growth of the baso-columellar margin stabilizes, the basal wall remains roughly parallel to the plane of coiling, while the inner columellar wall slants diagonally toward the shell axis (from top to bottom). The

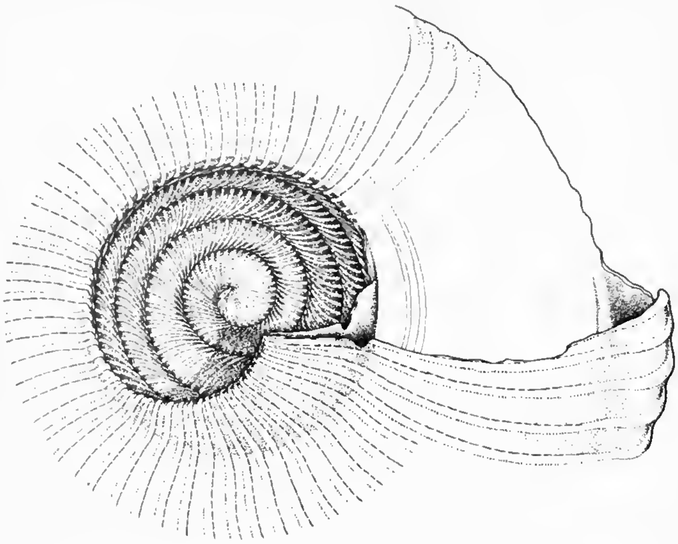

FIG. 185. Form of umbilical closure in *Gambiodonta pilsbryi aukenensis*. Aukena, Mangareva, Gambier Islands. BPBM 138711. (MM).

inclination of the aperture is such that a distinct "leading edge" of columellar wall growth is visible in each bottom view. In all intact adult specimens examined, this "leading edge" stops either at or just short of the point at which the sudden inward projection of the baso-columellar margin started. Hence closure of the umbilical brood chamber in *Gambiodonta* is completed within one whorl of growth. Effective narrowing of the umbilicus takes less than one-third whorl, and, with only very minor deviations, growth ceases one whorl after umbilical closure begins. The same pattern is repeated in the other species of *Gambiodonta*, the starting point of inward whorl growth varying from the 4th to 7th whorl, depending on the whorl count of the individual adult shell.

All *Gambiodonta* collected by the Mangarevan Expedition were taken from cave deposits, washed loose from road-cut and open-ground deposits, or taken from semi-consolidated sand deposits. As a result, the umbilici and apertures of all specimens were tightly clogged with dirt and/or small pebbles. Time did not permit more than a partial sampling of specimens for cleaning, since removal of sufficient apertural debris to establish the number of elevated parietals and cleaning enough of the umbilicus to check for apical encroachment by the embryos took up to 20 min. per specimen. Where material permitted, at least five specimens of each form (in addition to those previously cleaned by the Bishop Museum staff) were cleaned sufficiently to check parietal elevation and establish palatal trace counts. Since only a small percentage of the available material was checked for the trace counts, these figures in Table CVII cannot be considered statistical, but only reflect the observed range of variation. More specimens were checked for parietal elevation than trace counts, and no variation in number was observed.

Specimens which had the umbilicus completely cleaned showed no indication of apical encroachment and embryos were found only in two specimens of *Gambiodonta tumida*.

Variational trends within the genus are comparatively simple. As mentioned above, three species – *G. grandis, G. mirabilis,* and *G. tumida* – have the radial ribs greatly widened, rounded, and markedly reduced or absent on the shell base, while the other three retain the typical ribbing seen in *Anceyodonta*. The characteristic secondary spiral cording is very well developed in all species but *G. mirabilis* and *G. grandis.* Peripheral keel protrusion is weakest in *G. mangarevana,* only slightly more strongly developed in *G. tumida,* very strongly developed in *G. pilsbryi aukenensis* and *G. grandis,* with *G. mirabilis* having two additional keels developed. There is thus no correlation between changes in ribbing, secondary sculpture, and the development of the peripheral keel. The size range (table CVII) is strongly skewed by the presence of *G. grandis.* From the smallest, *G. agakauitaiana,* to the second largest, *G. tumida,* there is a percentage size increase of 8.5-20.9 per cent from species to species and a total increase in mean diameter of only 65.7 per cent from the smallest to largest. The difference in mean diameter between *G. tumida* and *G. grandis* is 98.4 per cent. The gigantic size of *G. grandis* is only partly accounted for by an increase in whorl count (from a mean of 6⅜+ to 7⅜), with the rest of the difference resulting from whorl enlargement. First whorl diameter is 0.64-0.69 mm. in *G. pilsbryi* and *G. agakauitaiana*; 0.76-0.82 in *G. mirabilis* and *G. tumida*; and 1.05-1.15 mm. in *G. grandis.*

Distribution patterns are relatively simple. Mangareva Islet has four species – *G. mangarevana, G. pilsbryi pilsbryi, G. tumida,* and *G. mirabilis;* Aukena Islet has three species – *G. pilsbryi aukenensis, G. grandis,* and *G. mirabilis*; and Agakauitai has two species – *G. agakauitaiana* and *G. grandis.* Two species, *G. grandis* and *G. mirabilis,* were collected on two islets without subspecific differentiation, while *G. pilsbryi* is represented by different subspecies on two islets. No *Gambiodonta* were collected on Akamaru or any of the smaller islets. Indeed, all known material of the genus was collected by the B. P. Bishop Museum Mangarevan Expedition between May 23 and June 11, 1934 except for a single shell (BMNH 1886.6.9.919) without exact locality data received by the British Museum (Natural History) from J. L. Lambert. The lip is badly broken and the shell is 4.78 mm. in diameter, H/D ratio 0.836, with 7⅛ whorls. The sculpture is very much like that of *G. pilsbryi,* but the shell is much more elevated than any other *Gambiodonta* examined. It very probably represents an unnamed species, but is not described since it is without adequate locality data.

The derivation of *Gambiodonta* from the same stock that produced *Anceyodonta* would be logical,

TABLE CVII. - RANGE OF VARIATION IN GAMBIODONTA

Name	Number of Specimens Examined	Ribs	Height	Diameter	H/D Ratio	Whorls	Pr	C	P
agakauitaiana	17	52.0(45-57)	2.69(2.50-2.83)	3.73(3.91-4.05)	0.675(0.633-0.716)	6 1/8+(6-6 3/8)	3+5-8	1	4+5-6
pilsbryi pilsbryi	88	89.6(74-99)	2.85(2.35-3.14)	4.89(4.58-5.29)	0.582(0.514-0.652)	6 3/4-(6 1/8-7 1/8)	5+7-8	1+1-2	4+6-8
pilsbryi aukenensis	79	77.5(69-85)	2.83(2.61-3.01)	5.07(4.64-5.36)	0.559(0.519-0.605)	6 3/8-(6-6 5/8)	5+5-8	1+0-1	4+6-8
mangarevana	6	70.7(67-77)	3.07(2.88-3.27)	4.51(4.38-4.58)	0.686(0.657-0.715)	6 5/8	4+6-8	1+1	4+5-7
mirabilis	41	45.5(38-56)	3.39(3.07-3.86)	5.54(5.03-5.75)	0.612(0.552-0.694)	5 3/8-(5-5 7/8)	2+5-8	1+1	3[1]+7-12
tumida	33	60.6(53-66)	4.34(3.60-4.71)	6.18(5.88-6.41)	0.702(0.604-0.758)	6 3/8+(6-6 3/4)	4+6-8	1+1	4+4-6
grandis	259	56.7(46-65)	7.26(5.60-8.70)	12.26(10.9-13.4)	0.591(0.509-0.721)	7 3/8-(6 1/4-8)	4+0-1	1+1	3[1]+3-6

[1] Lower palatal of other species so reduced that it is not separable from accessory traces.

except for the vast difference in umbilical contour between the *Minidonta simulata* group and the juvenile *Gambiodonta*. I think it more probable that *Gambiodonta* diverged after the *Anceyodonta* evolutionary level had been obtained. A series of mutations from such a start as could be represented by the *A. andersoni* and *A. alternata* pair (fig. 82c-f) provides a clear indication of how the transition could have occurred. While the smallest *Gambiodonta*, *G. agakauitaiana*, barely falls within the size range of *Anceyodonta*, its strongly developed peripheral keel, secondarily reduced number of elevated parietals, and quite high spire suggest that this is a comparatively specialized species, rather than being near a generalized ancestral state. Although the type of *G. mangarevana* presents the most generalized appearance found in known *Gambiodonta*, even this species seems too far removed from the pattern of *Anceyodonta* to be considered a linking or intermediate form. The gap between *Anceyodonta* and *Gambiodonta* is fully equivalent to the gap seen between *Mautodontha* and *Libera*.

No phylogenetic ordering of species within *Gambiodonta* seems possible, except to note that *G. mirabilis* and *G. grandis* are highly specialized, while the others show combinations of generalized and specialized features. More information could be expected after stratigraphically oriented collections have been made on the Mangareva islets. On Mangareva Islet, for example, material from Stations 142 and 277, which are within a few hundred feet of each other at most, differ markedly in species abundance:

Species	Station	
	142	277
G. mirabilis	7	28
G. p. pilsbryi	26	62
G. tumida	23	1

The collections were made at different times and by different people – Station 142 on June 3, 1934, by C. M. Cooke and Yoshio Kondo; Station 277 on June 26, 1934, by Donald Anderson – so that the possibility of personal bias in collection must be considered. Since similar discordant numbers were found in *Anceyodonta*, where the small size range would negate any sampling bias under field conditions, I have no doubt that the differences between thanatocoenoeses are real. The Mangarevan Expedition collectors were primarily interested in live material, and sampling of the fossil deposits was not done with any idea of studying time distribution of the material. While Cooke (1935, p. 42) concluded that "These fossil beds are not of any considerable age but represent lowland fauna that probably existed after the arrival of the Polynesians," the different species content between stations and obviously great difference in preservation seen among available material, combine to suggest that quantitative stratigraphic sampling of the Aukena, Mangareva, and Akamaru beds might provide sequential data. Obviously, fossils are present in sufficient quantity to allow use of radiometric dating methods, so that possible changes in species abundance and, potentially, information concerning their time of appearance might be gained. Unfortunately, the extent and depth of these beds are unknown, so that preliminary exploration would be required before the advisability of intensive study could be determined. These are the only known major Polynesian deposits of endodontid shells. In view of the great amount of minor evolution that took place on Mangareva, further study of these is greatly needed.

Key to the Genus *Gambiodonta*

1. Body whorl with periphery keeled or protruded, but no other keels present 2
Body whorl with three prominent keels (fig. 188c).
Gambiodonta mirabilis, new species
2. Diameter at 6 whorls less than 7.00 mm.; many parietal traces.
3
Diameter at 6 whorls more than 9.50 mm.; few parietal traces.
Gambiodonta grandis, new species
3. Major radial ribbing prominent on base of shell 4
Major radial ribbing absent from base of shell (fig. 188a).
Gambiodonta tumida, new species
4. More than 60 ribs on body whorl; adult diameter more than 4.25 mm 5
Less than 60 ribs on body whorl; adult diameter less than 4.15 mm .... *Gambiodonta agakauitaiana*, new species
5. Major parietal barriers 5, weakly elevated posteriorly; spire relatively low, mean H/D ratio less than 0.600 6
Major parietal barriers 4, strongly elevated posteriorly; spire strongly elevated, mean H/D ratio more than 0.650.
Gambiodonta mangarevana, new species
6. Periphery strongly protruded (fig. 187a); mean ribs on body whorl about 90; Mangareva Islet.
Gambiodonta pilsbryi pilsbryi, new species
Periphery less strongly protruded (fig. 187d); mean ribs on body whorl about 78; Aukena Islet.
Gambiodonta pilsbryi aukenensis, new subspecies

Gambiodonta agakauitaiana, new species (Solem & Cooke). Figures 22c-e; 186a-b.

Diagnosis. – Shell very small, diameter 3.91-4.05 mm. (mean 3.73 mm.), with 6-6⅜ tightly coiled whorls. Apex and spire markedly elevated, slightly rounded above, last whorl only slightly deflected below periphery, H/D ratio 0.633-0.716 (mean 0.675). Umbilical opening irregularly ovate, modified internally to form brood chamber. Postnuclear sculpture of high, broad, sharply delineated, strongly protractively sinuated radial ribs, 45-57 (mean 52.0) on the body whorl, whose interstices are less than twice their width. Microsculpture typical, five to eight microradials between each pair of major ribs, spiral cording most strongly developed on base of shell. Sutures shallow, whorls sloping directly to edge of deeply and sharply outlined supraperipheral sulcus, periphery sharply and narrowly protruded into a threadlike keel. Aperture compressedly ovate, strongly marked internally both by protrusion of peripheral keel and upper edge of supraperipheral sulcus, inclined about 30° from shell axis. Major parietal barriers 3, extending well beyond line of vision, with five to eight accessory traces: in undamaged specimen, major parietals threadlike to beyond line of vision, when apertural edge is broken, 3rd parietal can be seen to elevate one-quarter whorl behind aperture; upper 2 becoming weakly elevated somewhat posterior of this point. Accessory traces in normal position. Columellar barrier a high lamellar blade, parallel to plane of coiling, reaching almost to lip edge, with gradual anterior descension. Major palatal barriers 4, extending nearly one-quarter whorl, with five or six accessory traces: lower palatal very greatly reduced in height, barely larger than neighboring accessory trace; 2nd and 3rd palatals high, bladelike, deeply recessed, with very gradual anterior descension; 4th palatal supraperipheral in position, reduced in height, a V-shaped ridge. Palatal traces in normal position.

The very small size, deep supraperipheral sulcus, strong but narrow peripheral keel, and presence of only 3 major parietal barriers that are very deeply recessed within the aperture combine to separate *Gambiodonta agakauitaiana* from other species of the genus. The only species that approaches this in size, *Gambiodonta mangarevana*, has only a faint indication of a supraperipheral sulcus, much finer and more crowded ribbing, and only faint indication of a protruded peripheral keel.

Description. — Shell very small, with 6 tightly coiled whorls. Spire dome shaped, rounded above, last whorl slightly deflected, H/D ratio 0.706. Embryonic whorls 1¾, with very heavy protractive radial ribs. Postnuclear whorls with high, wide, protractively sinuated radial ribs, 54 on the body whorl, whose interstices are less than twice their width. Microsculpture of exceedingly fine radial riblets, much finer and more crowded spiral riblets, and a secondary sculpture of close-set spiral cords. Spiral ribbing strongest on base but also prominent in supraperipheral sulcus, weaker above. Sutures shallow, whorls strongly rounded above deep, prominent supraperipheral sulcus. Radial ribbing weaker in sulcus, becoming more prominent in crossing the somewhat protruded threadlike carination, but little reduced on base of shell. Umbilicus ovately open, constricted below, enlarged interiorly to form brood chamber. Aperture roughly ovate with sinuate upper margin, somewhat flattened below, inclined about 30° from shell axis. Parietal wall with 12 barriers, the next to lowest becoming high and lamellate posteriorly, others threadlike to past the line of vision. Columellar barrier a high lamellate ridge, lying parallel to plane of coiling. Major palatal barriers 4, with numerous accessory traces: 1st palatal reduced in size, a short threadlike ridge; other 3 long, relatively low, the upper located just above periphery of body whorl. Height of holotype 2.76 mm., diameter 3.92 mm.

Holotype. — Gambier Islands: Mangareva, Station 195, Agakauitai Islet, northwest side. Collected on sandy soil by Donald Anderson on June 8, 1934. BPBM 138903.

Range. — Agakauitai Islet, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Agakauitai (Station 195) on northwest side (17 specimens, BPBM 138903).

Remarks. — The six adult specimens showed comparatively little variation in size, shape or apertural barriers. *Gambiodonta agakauitaiana* is remarkable for the reduced size of the palatal barriers and the very deep recession of the lamellate parietals. The reduction to 3 parietals probably is correlated with the very small size.

All specimens were taken at the single station, where *G. grandis* was twice as numerous.

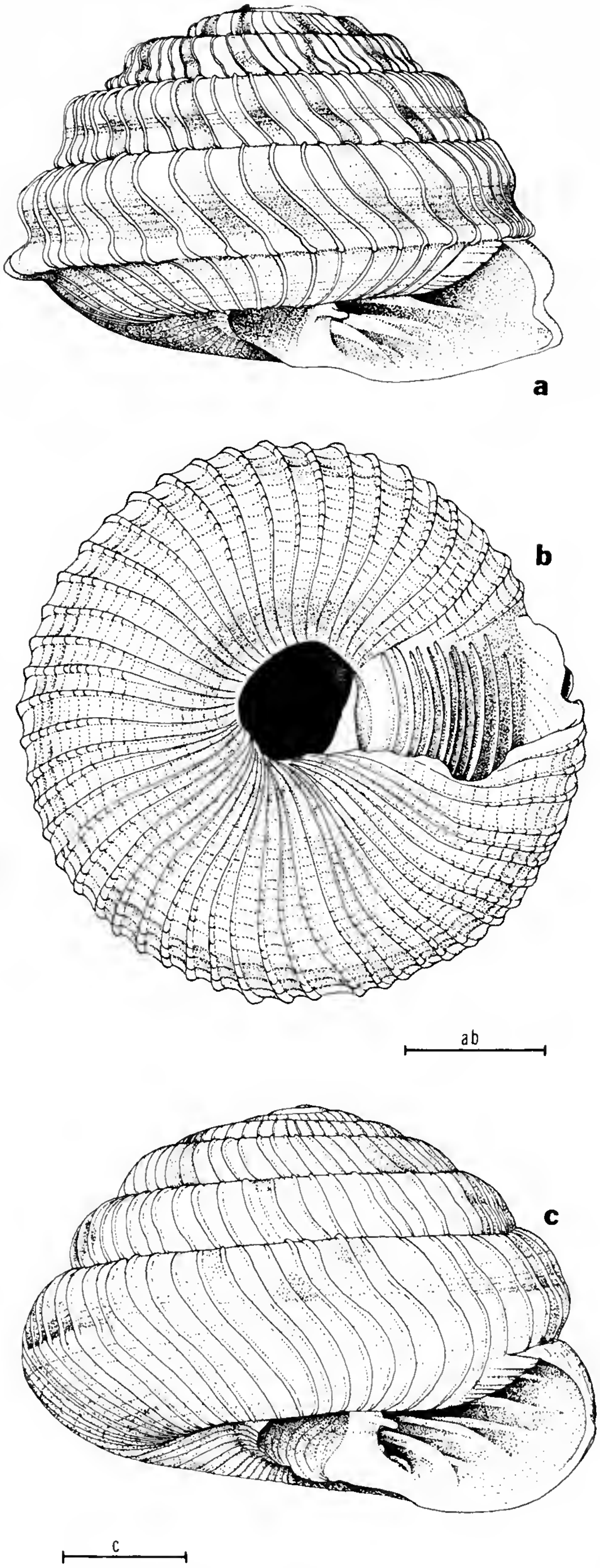

FIG. 186. **a-b**, *Gambiodonta agakauitaiana*, new species. Station 195, Agakauitai Islet, Mangareva, Gambier Islands. Holotype. BPBM 138903; c, *Gambiodonta mangarevana*, new species. Station 189, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 141695. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Gambiodonta pilsbryi pilsbryi, new species and subspecies (Cooke & Solem). Figure 187a-c.

Diagnosis. – Shell of average size, diameter 4.58-5.29 mm. (mean 4.89 mm.), with 6⅛-7⅛ normally coiled whorls. Apex and spire moderately elevated, weakly flattened above, last whorl slightly deflected below periphery, H/D ratio 0.514-0.652 (mean 0.582). Umbilical opening irregularly oval, internally modified to form brood chamber. Postnuclear sculpture of narrow, prominent, strongly protractively sinuated, rather crowded radial ribs, 74-99 (mean 89.6) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial and finer spiral microriblets, four to seven between each pair of major ribs, with a secondary sculpture of prominent spiral cording, especially noticeable on base of shell. Sutures shallow, whorls strongly rounded to prominent supraperipheral sulcus, periphery protruded into a threadlike keel. Aperture flatly ovate, internally showing protrusion of periphery, inclined about 25° from shell axis. Parietal barriers 5, extending posteriorly beyond line of vision, with seven to eight accessory traces: major parietals threadlike for first quarter whorl, weakly and almost evenly expanded posteriorly at edge of vision. Accessory traces very slender, anteriorly indistinguishable from major barriers. Columellar wall with single, high, bladelike barrier, parallel to plane of coiling, reaching anterior margin, usually with one or two very small accessory traces. Palatal barriers 4, deeply recessed, extending about three-sixteenths of a whorl, with six to eight accessory traces: lower palatal a greatly reduced ridge; 2nd and 3rd high lamellar blades, with gradual anterior descension; 4th palatal supraperipheral, reduced in height, a V-shaped ridge lying opposite expanded portion of upper parietal. Palatal traces as in *G. pilsbryi aukenensis.*

The average size, relatively flattened shell, 5 major parietals, protruding carina, and fine ribs are diagnostic and prevent confusion of *G. pilsbryi* with any other *Gambiodonta.* The large *G. mirabilis* has the three keels, while the smaller *G. mangarevana* has only 4 parietals and is much, much higher. The subspecies *G. pilsbryi aukenensis* is characterized by a more prominent sulcus, the carina extended into a knife-edge keel and in having slightly fewer and more widely spaced radial ribs on the body whorl.

Description. – Shell of average size, with 6⅝ rather loosely coiled whorls. Spire elevated, depressedly dome shaped in outline, last whorl deflected below periphery, H/D ratio 0.575. Embryonic whorls 1⅝, eroded, only remnants of heavy radial ribbing left. Postnuclear whorls with moderately wide, protractively sinuated radial ribs, 95 on the body whorl, whose interstices are usually 2-3 times their width. Microsculpture of extremely fine radial riblets and finer spiral riblets, with very strong secondary spiral cording developed on the shell base. Sutures very shallow, whorls rounded above shallow supraperipheral sulcus, a protruded threadlike carina which is beaded where radial ribs cross. Umbilicus with narrow oval opening, expanded into brood chamber internally. Umbilical margin sharp with an expanded inner portion. Color mainly leached from shell, with regularly spaced, retractive, reddish flammulations remaining. Aperture subtriangular with evenly rounded margins. Parietal wall with 13 threadlike barriers anteriorly, 5 of which become slightly and almost equally elevated posteriorly. Columellar barrier a very high lamellar ridge, parallel to the plane of coiling, with small recessed accessory denticles. Major palatal barriers 4, with eight accessory traces: lower palatal a very short low thread; palatals 2 and 3 relatively low lamellar ridges; upper palatal a thin, high, V-shaped ridge slanted upward to point toward the upper expanded parietal. Height of holotype 3.01 mm., diameter 5.23 mm.

Holotype. – Gambier Islands: Mangareva, Station 277, Mangareva Islet, vicinity of Ganhutu. Collected on open ground by Donald Anderson on June 26, 1934. BPBM 138979.

Range. – Mangareva Islet, Mangareva, Gambier Islands.

Paratypes. – Same as list of material.

Material. – Mangareva: Mangareva Islet (Stations 142, 277) vicinity of Ganhutu (88 specimens, BPBM 138948-50, BPBM 138979-80).

Remarks. – The ribbing of *Gambiodonta pilsbryi* is intermediate in size between that of *G. tumida* and *G. mangarevana.* It is easily separated from both on the basis of its flatter spire, more rostrate periphery, and 5 parietal barriers. The type is unusual in that the columellar barrier ends at, and not near, the apertural edge.

At Station 277, Cooke and Kondo found only 1 specimen of *G. tumida,* 28 of *G. mirabilis,* and 62 of *G. pilsbryi pilsbryi;* but at Station 142, Donald Anderson collected 23 *G. tumida,* 7 *G. mirabilis,* and 26 *G. pilsbryi pilsbryi.* The two stations could not be distinguished on a large scale map, yet obviously are separated by at least 100-200 ft. in relation to the shore line and by an unknown distance parallel to the shore. Hence the difference in species abundance at the two stations almost certainly represents differential accumulation in the two deposits.

Great pleasure is taken in naming this species after the late H. A. Pilsbry, dean of American malacologists, and the foremost student of non-marine mollusks.

Gambiodonta pilsbryi aukenensis, new subspecies (Cooke & Solem). Figures 185; 187d-f.

Diagnosis. – Shell of average size, diameter 4.64-5.36 mm. (mean 5.07 mm.), with 6-6⅝ normally coiled whorls. Apex and spire moderately elevated, slightly flattened above, last part of body whorl only slightly deflected below periphery, H/D ratio 0.519-0.605 (mean 0.559). Umbilical opening irregularly oval, modified internally to form brood chamber. Postnuclear sculpture of narrow, prominent, strongly protractively sinuated radial ribs, 69-85 (mean 77.5) on the body whorl, whose interstices are usually slightly more than twice their width. Microsculpture typical, secondary spiral cording strongest on shell base. Sutures shallow, whorls strongly rounded above prominent supraperipheral sulcus, periphery of body whorl strongly protruded into a threadlike keel. Aperture compressedly ovate, strongly marked internally by peripheral protrusion, inclined about 25° from shell axis. Parietal barriers 5, extending well beyond line of vision, with five to eight accessory traces: 5 major barriers low and threadlike for anterior one-quarter whorl, subequally and only moderately elevated posteriorly, with 4th and 5th slightly lower than upper three. Accessory traces very slender, scarcely distinguishable anteriorly from terminal portions of major barriers. Columellar barrier a high lamellar blade, with gradual anterior descension to edge of columellar callus, lying parallel to plane of coiling, with at most one deeply recessed columellar trace. Major palatal barriers 4, deeply recessed, extending about three-sixteenths of a whorl, with six to eight very inconspicuous accessory traces: lower palatal greatly reduced in height, barely distinguishable from accessory trace: 2nd and 3rd high and bladelike, with gradual anterior descension; 4th supraperipheral in position, reduced in height, a V-shaped ridge lying opposite upper parietal. Accessory palatal traces in normal position.

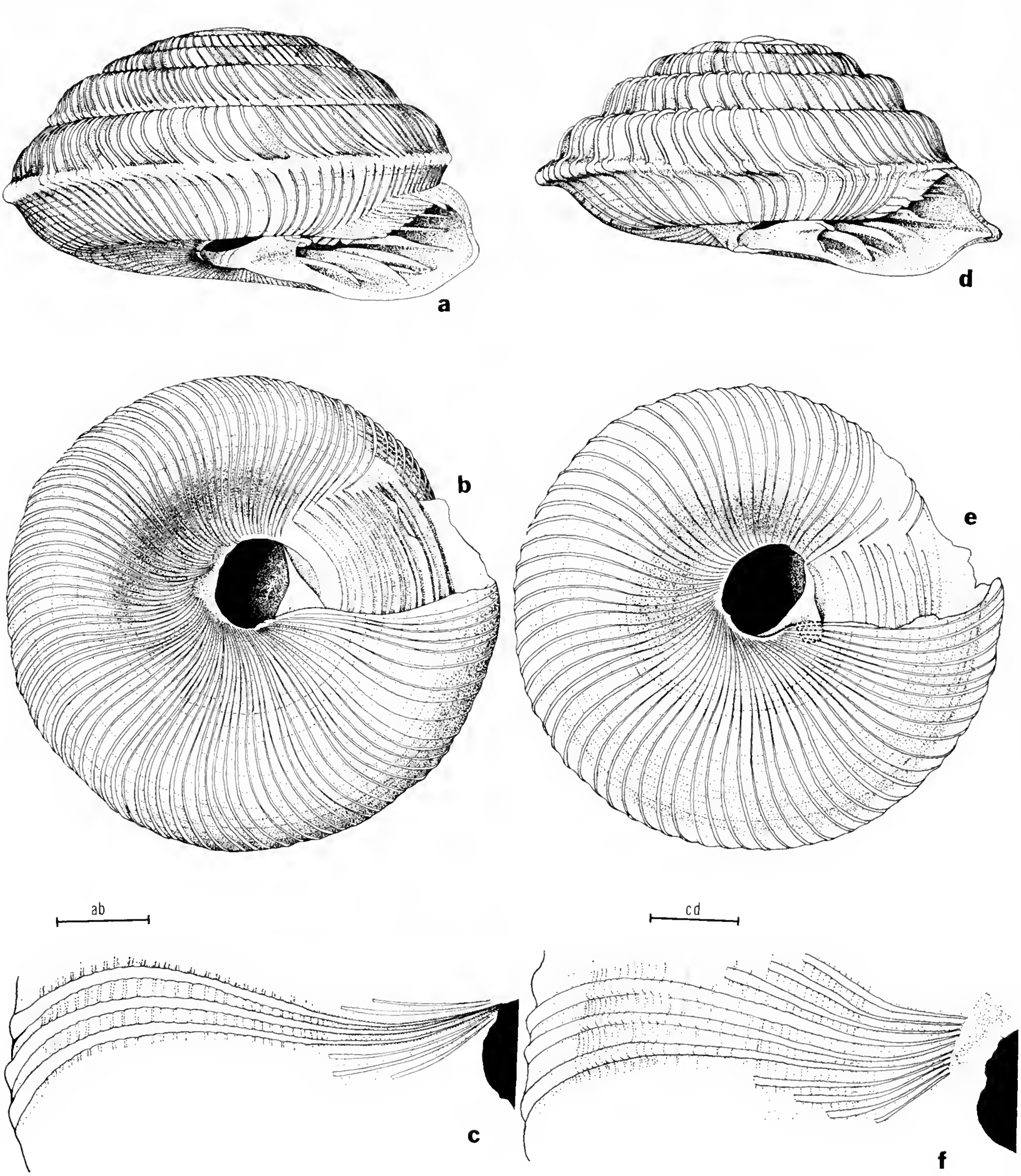

FIG. 187. **a-c**, *Gambiodonta pilsbryi pilsbryi*, new species. Station 277, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 138979; **d-f**, *Gambiodonta pilsbryi aukenensis*, new subspecies. Station 88, Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 138711. Sculpture as shown in fig. *f* is normal, in fig. *c* with characteristic surface erosion on rib tops, both figures with microspirals and microradials omitted. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

Gambiodonta pilsbryi aukenensis differs from the nominate subspecies found on Mangareva Islet in several features: the peripheral keel is much more strongly protruded, the ribbing on the body whorl is more widely spaced and, on the average, fewer in number; the diameter is very slightly greater (caused by the greater protrusion of the peripheral keel) and the H/D ratio is slightly lower (caused by the same factor).

Description. — Shell of average size, with 6⅛ normally coiled whorls. Apex and spire moderately elevated, slightly flattened above, last whorl not deflected below periphery, H/D ratio 0.519. Apical whorls 1½, sculpture partly eroded, with traces of broadly rounded radial ribs remaining. Postnuclear sculpture of narrow, prominent, strongly protractively sinuated radial ribs, 70 on the body whorl, whose interstices are slightly more than twice their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by barely visible and extremely crowded spiral riblets, with a secondary sculpture of low rounded spiral cords, becoming stronger on base of shell. Sutures shallow, whorls strongly rounded above prominent supraperipheral sulcus, periphery strongly protruded into a threadlike keel. Color mainly leached from shell, with traces of irregular, broad, reddish flammulations remaining. Umbilicus modified to form a brood chamber, closed by inward growth of last whorl and a half, remaining opening irregularly ovate. Aperture compressedly ovate, strongly marked internally by peripheral protrusion, inclined about 25° from shell axis. Parietal barriers 5, extending posteriorly beyond line of vision, with four accessory traces: major parietals threadlike for anterior quarter whorl, weakly elevated and expanded posteriorly. Columellar barrier a high bladelike ridge, parallel to plane of coiling, gradually descending to edge of columellar callus, with a single deeply recessed accessory trace. Major palatal barriers 4, deeply recessed, extending posteriorly about three-sixteenths of a whorl, with six accessory traces: lower palatal greatly reduced in height, scarcely larger than neighboring accessory traces; 2nd and 3rd palatals high and bladelike, with gradual anterior descension; 4th palatal supraperipheral in position, reduced in height, a V-shaped ridge, lying opposite upper parietal. Five palatal traces low and inconspicuous, trace located between 2nd and 3rd palatals almost equal to them in height and much larger than 1st palatal. Height of holotype 2.74 mm., diameter 5.36 mm.

Holotype. — Gambier Islands: Mangareva, Aukena Islet, Station 88, near the gap. Collected along the trail by Donald Anderson and C. M. Cooke, Jr., on May 28, 1934. BPBM 138711.

Range. — Aukena Islet, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Aukena Islet (Stations 82, 88, 102, 103) in the vicinity of the gap (79 specimens, BPBM 138686, BPBM 138711-2, BPBM 138760, BPBM 138801).

Remarks. — While the heights of *G. pilsbryi pilsbryi* and *G. p. aukenensis* are essentially identical (table CVIII) the differences in diameter (with 53 df, "*t*" = 4.6707) and H/D ratio ("*t*" = 3.0188) are highly significant. The greater protrusion of the peripheral keel noticeably increased the diameter and thus lowered the H/D ratio in shells of the same height.

Specimens of *G. pilsbryi aukenensis* were taken in quantity only at Station 88, where 96 examples were found together with 197 *Gambiodonta grandis* and two examples of *G. mirabilis.* The difference in sculpture size is such that no confusion of juveniles is possible. Single specimens of *G. p. aukenensis* were found among the limited *Gambiodonta* material taken at Stations 82, 102, and 103.

Gambiodonta mangarevana, new species (Solem & Cooke). Figure 186c.

Diagnosis. — Shell small, diameter 4.38-4.58 mm. (mean 4.51 mm.), with 6⅝ normally coiled whorls. Apex and spire strongly elevated, somewhat rounded above, last whorl deflected strongly below periphery, H/D ratio 0.657-0.715 (mean 0.686). Umbilical opening irregularly oval, modified internally to form brood chamber. Postnuclear whorls with high, narrow, prominent, strongly protractively sinuated radial ribs, 67-77 (mean 70.7) on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, crossed by finer and much more crowded spiral riblets, with prominent secondary spiral cording visible on base of shell and near sutures. Sutures shallow, whorls strongly rounded above very shallow supraperipheral sulcus, periphery slightly protruded into a weak threadlike keel. Aperture ovate, without internal indication of peripheral protrusion, inclined about 25° from shell axis. Parietal barriers 4, extending posteriorly beyond line of vision, with six or seven accessory traces: major parietals low and threadlike for anterior quarter whorl, becoming strongly elevated and bulbously expanded posteriorly, 3rd and 4th with elevated portion extending further anteriorly. Normally traces located above 1st parietal, two between 1st and 2nd, one between 2nd and 3rd, and one between 3rd and 4th. Columellar barrier a high lamellar blade, parallel to plane of coiling, with gradual anterior descension. A single columellar trace located just above baso-columellar margin. Palatal barriers 4, extending nearly one-quarter whorl, with five to seven accessory traces: lower palatal greatly reduced in height, scarcely larger than accessory traces; 2nd and 3rd palatals very high, bladelike, with gradual anterior descension; 4th palatal supraperipheral, reduced in height, a large V-shaped ridge lying opposite upper parietal. Generally three palatal traces above 4th palatal, one between 3rd and 4th, two between 2nd and 3rd, and one between 1st and 2nd.

The small size, quite narrow and regularly spaced radial ribs, plus presence of basal radial ribs immediately separate *Gambiodonta mangarevana* from its larger relative, *G. tumida.* The higher dome-shaped spire, presence of spiral cording above the periphery, 4 (instead of 5) major parietals, and relatively prominent supraperipheral sulcus distinguish it from *G. pilsbryi. G. agakauitaiana* is smaller, higher, with a much deeper sulcus, and has only 3 major parietals.

Description. — Shell small, with 6⅝ normally coiled whorls. Apex and spire strongly elevated, apical portion somewhat flattened, last part of body whorl strongly deflected below periphery, H/D ratio 0.715. Embryonic whorls 1⅝, with strong, broadly rounded radial ribs, whose interstices are narrower than their width. Remaining whorls with regularly spaced, relatively narrow, protractively sinuated radial ribs, 77 on the body whorl, whose interstices are 2-3 times their width. Ribbing only slightly reduced on base of shell. Microsculpture of numerous, fine, radial riblets, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of low but regular rounded spiral cords. Spiral sculpture most prominent on base of shell and in supraperipheral sulcus. Sutures shallow, whorls strongly rounded above with very shallow supraperipheral sulcus. Color mainly eroded from shell with a few irregular, reddish-yellow flammulations remaining. Periphery of body whorl with a very low rounded keel. Aperture subtriangular with rounded margins. Parietal wall with 4 major barriers and seven accessory traces, all extending beyond line of vision. Major barriers

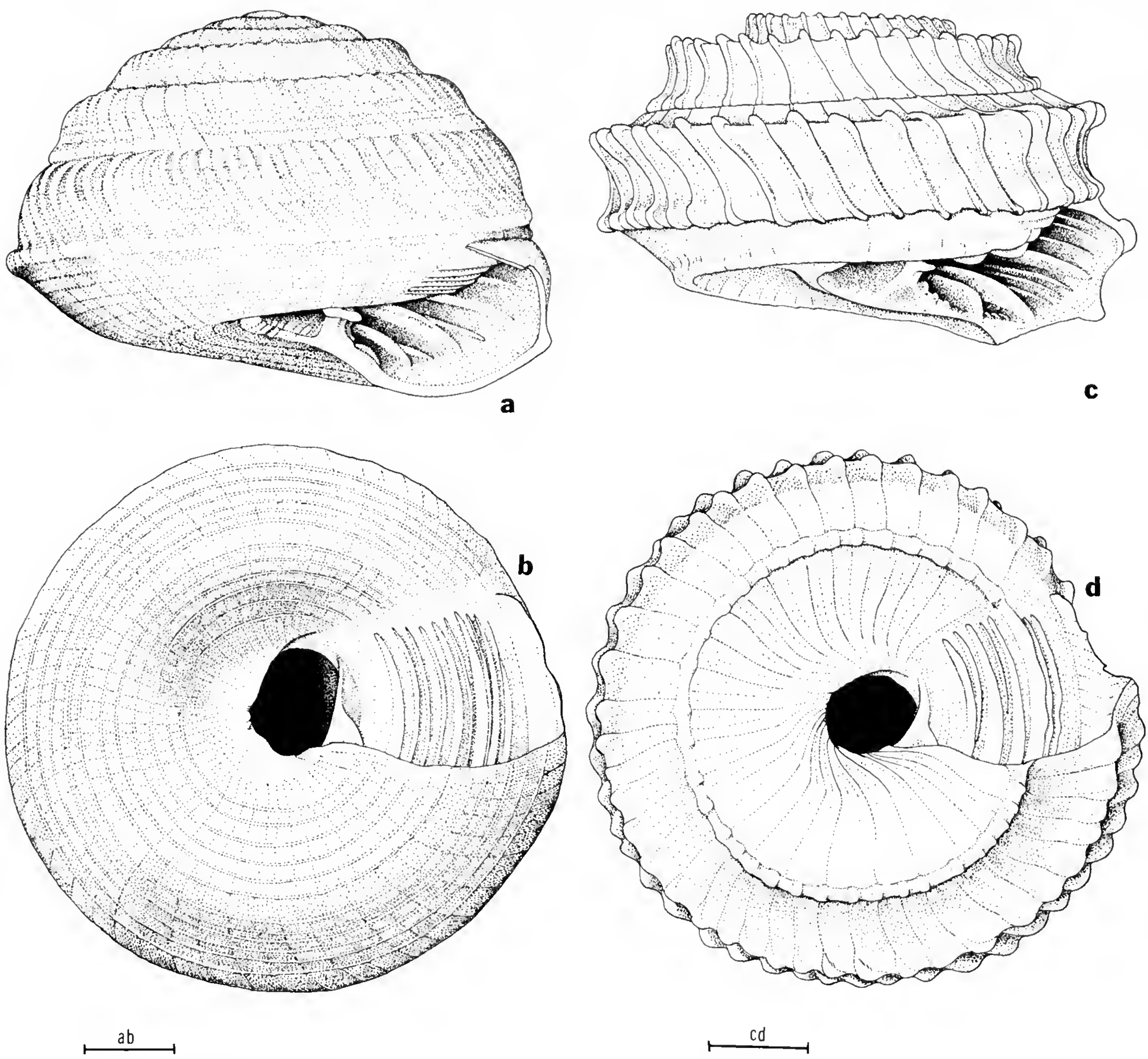

FIG. 188. **a-b**, *Gambiodonta tumida*, new species. Station 142, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 138978; **c-d**, *Gambiodonta mirabilis*, new species. Station 277, Mangareva Islet, Mangareva, Gambier Islands. Holotype. BPBM 138981. Scale lines equal 1 mm. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

identical in structure to those of *G. tumida*. Columellar barrier a high lamellate ridge, parallel to the plane of coiling, reaching the apertural margin, with a small accessory trace below. Major palatal barriers 4, with seven accessory denticles. Lower palatal reduced to a small ridge; numbers 2 and 3 high and lamellate, broadly rounded above; number 4 a deeply recessed, V-shaped ridge lying opposite the upper parietal. Height of holotype 3.27 mm., diameter 4.57 mm.

Holotype. – Gambier Islands: Mangareva, Station 189, Mangareva Islet, north end of Rikitea. Collected on open ground by Yoshio Kondo and C. M. Cooke, Jr., on June 8, 1934. BPBM 141695.

Range. – Mangareva Islet, Mangareva, Gambier Islands.

Paratypes. – Same as list of material.

Material. – Mangareva: Mangareva Islet (Stations 155, 182, 189) vicinity of Rikitea (5 specimens, BPBM 9632, BPBM 139005, BPBM 141669, BPBM 141695).

Remarks. – Only two adults and four juveniles were taken of this species. At first glance it appears to be a miniature form of *Gambiodonta tumida*, but the character of the ribbing is quite different in the two species (figs. 188a; 186c). The holotype is subcarinate on the body whorl, but the other adults and the juveniles are almost as strongly rostrate as in *G. pilsbryi pilsbryi*. The height of the major parietal barriers is intermediate between that of *G. mirabilis* and the much lower *G. pilsbryi*.

Only scattered individuals were collected, three specimens from Station 155, one from Station 187, and two from Station 189. No other *Gambiodonta* were collected at these stations, which are well removed geographically from the area where other Mangareva Islet *Gambiodonta* were obtained.

Gambiodonta mirabilis, new species (Cooke & Solem). Figures 22a-b; 188c-d.

Diagnosis. — Shell larger than average, diameter 5.03-5.75 mm. (mean 5.54 mm.), with 5-5⅞ normally coiled whorls. Apex and early spire flat or slightly depressed below level of antepenultimate whorl, later whorls descending sharply, H/D ratio 0.552-0.694 (mean 0.612). Umbilical opening irregularly ovate, modified internally to form brood chamber. Postnuclear whorls with prominent, narrow, rather widely spaced, strongly protractively sinuated radial ribs, 38-56 (mean 45.5) on the body whorl, whose interstices are 3-4 times their width, and which denticulate the supraperipheral keel, are reduced in height before denticulating peripheral keel, and are reduced to irregularity and very small size on the base of shell. Microsculpture of fine radial riblets crossed by much finer and more crowded spiral riblets, combined with irregular growth wrinkles. No secondary spiral cording. Sutures very shallow, whorls flattened or slightly concave in areas between three prominent keels: supraperipheral most protruded, slightly above midpoint between periphery and suture; peripheral keel strongly but narrowly protruded, also denticulated by crossing of major radial ribs; subperipheral keel located little less than halfway between periphery and edge of umbilical opening, much lower and more threadlike than preceeding two keels. Aperture pentagonal, strongly marked internally by protrusion of keels, inclined about 25° from shell axis. Major parietal barriers 2, extending posteriorly beyond line of vision, usually with six to eight accessory traces: upper parietal situated on top of subperipheral keel, low and threadlike for anterior three-sixteenths of a whorl, very strongly elevated and expanded above posteriorly to beyond line of vision; 2nd parietal similar in height, posterior portion slightly shorter and more recessed than 1st; parietal traces located normally three above upper parietal, two between the major parietals and one to three below major parietals. The 3rd parietal found in other species only a threadlike trace in *G. mirabilis*. Columellar barrier a high bladelike ridge, expanded and serrated above, parallel to plane of coiling, with one lower accessory denticle. Major palatal barriers 3, moderately recessed, extending posteriorly almost one-quarter whorl, with seven to twelve accessory traces; lower palatal of other *Gambiodonta* absent; "2nd" palatal high and bladelike with gradually curved anterior descension; "3rd" palatal higher with lower gradual anterior descension, more prominently flattened and expanded on top; "4th" palatal reduced in height, supraperipheral in position, a highly elevated V-shaped ridge. Palatal traces very inconspicuous, normal in position.

The triple keels of *Gambiodonta mirabilis* are unique in the Endodontidae and immediately separate this species from all Polynesian taxa. In having only 2 elevated parietals, a flat or depressed apex and less than six whorls, *G. mirabilis* is clearly separated from the other *Gambiodonta*.

Description. — Shell of slightly larger than average size with 5⅜ whorls. Spire flat above, rapidly descending from third whorl on, H/D ratio 0.588. Embryonic whorls 1½, sculpture of quite wide, irregularly rounded radial ribs, a few fine radial riblets visible between. Remaining whorls with widely spaced, relatively prominent, protractively sinuated radial ribs, 41 on the body whorl, whose interstices are about three or four times their width and that denticulate the upper two keels upon crossing them. Microsculpture of fine radial riblets, crossed by finer spiral riblets, no secondary cording. Sculpture prominent above keels, reduced in central sulcus and greatly reduced to absent on the base. Sutures very shallow, whorls flattened above, concave between keels. All whorls with a very high ridgelike supraperipheral keel, strongly beaded by radial ribs crossing; a slightly less prominent and less beaded subperipheral keel with the area between flattened; and a much lower threadlike basal keel with the whorls flattened both above and below it. Umbilicus with small ovate opening greatly expanded inside to form brood chamber. Color mainly absent from shell although some sinuate, reddish-brown flammulations remain. Aperture pentagonal, interiorly strongly marked by keel protrusion, inclined about 20° from shell axis. Parietal wall with 2 major barriers and four accessory traces: uppermost 2 parietals with threadlike traces extending beyond line of vision; major 2 parietals threadlike for anterior half, becoming quite high and lamellate after first three-sixteenths whorl, 1st parietal arising from thread of subperipheral keel; two lower parietal traces slightly elevated posteriorly. Columellar barrier a high lamellate ridge, parallel to plane of coiling, reaching apertural margin with accessory denticle below. Major palatal barriers 3, with twelve accessory traces: lower 2 palatals relatively high and lamellate, gradually descending to apertural edge; 3rd palatal a V-shaped ridge lying opposite the upper major parietal, somewhat recessed within aperture. Height of holotype 3.27 mm., diameter 5.50 mm.

Holotype. — Gambier Islands: Mangareva, Station 277, vicinity of Ganhutu, Mangareva Islet. Collected on open ground by Donald Anderson on June 26, 1934. BPBM 138981.

Range. — Aukena and Mangareva Islets, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Mangareva Islet (Stations 142, 277) vicinity of Ganhutu (35 specimens, BPBM 138951-2, BPBM 138981); Mangareva Islet (Station 197) northeast of Vaituatai Bay (2 specimens, BPBM 139018); Aukena Islet (Stations 82, 88) vicinity of the gap (4 specimens, BPBM 138687, BPBM 138708).

Remarks. — The few specimens from Vaituatai Bay on Mangareva and near the gap on Aukena Islet do not differ in any significant respects from the Ganhutu types. Once seen, the shape of the whorls of *Gambiodonta mirabilis* is unforgettable. No other Pacific Island endodontid can be confused with it.

Apparently, the great alterations in whorl contours produced by the addition of two keels had marked effects on the apertural barriers. The 2 major parietals are elevated at least twice the height found in other *Gambiodonta,* while the parietal trace occupying the position of the 3rd parietal shows a very slight posterior elevation and unquestionably is homologous with the lower parietal in other *Gambiodonta.* No posterior elevation was detected in either of the upper parietal traces. The basal portion of the palatal wall is obviously modified in contour and the lower palatal barrier of other *Gambiodonta* cannot be detected in *G. mirabilis.* The 3 major palatals present correspond exactly in position to the 2nd, 3rd, and 4th palatals of other species.

The startling appearance of *G. mirabilis* is not indicative of any great phylogenetic distance, since the barrier changes seem to be results of the two keel addition and could be thus a relatively minor genetic shift.

Only four specimens were found on Aukena (Stations 82, 88) and two from Vaituatai Bay, Mangareva Islet (Station 197). At the latter locality nine *G. tumida* were collected. At Station 277, *G. mirabilis* was second in number to *G. pilsbryi pilsbryi,* but at Station 142 was represented by much fewer individuals than either *G. tumida* or *G. pilsbryi pilsbryi.*

Gambiodonta tumida, new species (Cooke & Solem). Figure 188a-b.

Diagnosis. — Shell relatively large, diameter 5.88-6.41 mm. (mean 6.18 mm.), with 6-6¾ tightly coiled whorls. Apex and spire very strongly elevated, broadly rounded above, last portion of body whorl deflected slightly below periphery, H/D ratio 0.604-0.758 (mean 0.702). Umbilicus irregular in outline, internally modified to form brood chamber. Postnuclear sculpture of prominent, low, broadly rounded, strongly protractively sinuated radial ribs, 53-66 (mean 60.6) on the body whorl, whose interstices are much less than twice their width, and which are absent from base of shell. Microsculpture occasionally visible as low, broadly rounded radial riblets, four to six between each pair of major ribs, with exceedingly fine spiral ribbing barely visible under 96× magnification. Strong secondary spiral cording primarily visible on base of shell and above shallow supraperipheral sulcus. Sutures shallow, whorls strongly rounded above the broad and shallow supraperipheral sulcus, periphery slightly protruded into a threadlike keel. Aperture subovate, peripheral protrusion weakly reflected internally, inclined about 25° from shell axis. Parietal barriers 4, extending well beyond line of vision, with six to eight threadlike accessory traces: major 4 parietals with anterior one-quarter whorl low and threadlike, becoming suddenly elevated almost beyond line of vision, elevated portions high and bladelike, weakly expanded above, lower with elevated portion longer and reaching further anteriorly than upper parietals; one or two parietal traces located between each pair of major barriers with two or three above upper parietal and occasionally one below 4th parietal. Columellar barrier a high bladelike ridge, parallel to plane of coiling, with gradual anterior descension, a single accessory trace just above baso-columellar margin. Palatal barriers 4, extending three-sixteenths of a whorl, rather deeply recessed, with four to six accessory traces: lower palatal greatly reduced in height, a little larger than accessory traces, only slightly recessed; 2nd and 3rd palatal barriers high lamellar blades, with very gradual anterior descension; 4th palatal supraperipheral in position, a high V-shaped ridge with very gradual anterior descension, posterior portion lying opposite elevated 1st parietal. Accessory traces normally located between 1st and 2nd, 2nd and 3rd, 3rd and 4th, with two above 4th palatal.

The comparatively large size, very high spire, wide ribs, 4 parietals, and weak supraperipheral sulcus separate *Gambiodonta tumida* from the other species. *G. pilsbryi* has 5 weakly elevated parietals and a sharply protruded periphery, while *G. mangarevana* and *G. agakauitaiana* are more than 1 mm. smaller and differ in many details of sculpture and barrier characteristics.

Description. — Shell quite large, dome shaped, with 6½ tightly coiled whorls. Apex and spire greatly elevated, rounded above, last whorl strongly deflected below periphery, H/D ratio 0.717. Embryonic whorls 1½, partially eroded, with some traces of the heavy radial ribs remaining. Postnuclear whorls with low, broad, somewhat vague, strongly protractively sinuated radial ribs, about 62 on the body whorl, which are absent from the shell base. Microsculpture of low, broad, rounded radial riblets, extremely fine spiral riblets and a secondary sculpture of high and prominent spiral cords, which are most developed on shell base. Sutures shallow, whorls strongly rounded above broad and shallow supraperipheral sulcus. Periphery of body whorl with a slightly protruded threadlike carination, with the ribs continuing over and forming slight knobs on the keel. Umbilicus with a relatively narrow, oval opening, broadly expanded internally to form a brood chamber. Color partially eroded from shell, with large, irregular, reddish-yellow flammulations remaining. Aperture triangular, somewhat rounded above and below periphery, no internal evidence of peripheral keel. Parietal wall with 4 major barriers, extending well beyond line of vision, and six accessory traces: major parietals posteriorly elevated, 3rd and 4th with posterior elevation longer and extending further anteriorly. Accessory traces very narrow and low, anteriorly not separable from major barriers. Columellar barrier a broad lamellate ridge, crossing umbilical callus and reaching apertural margin. Junction of columellar and basal lips marked by broad groove, dipping down to the ridged umbilical margin. A small, recessed barrier (columellar) is located slightly above the middle of groove. Palatal barriers 4, deeply recessed, extending three-sixteenths of a whorl: lower a much reduced threadlike ridge. Middle 2 moderately high, elongate; upper a narrow V-shaped ridge situated opposite the upper expanded parietal. Palatal traces 5, low and inconspicuous, between 2nd and 3rd, 3rd and 4th palatals, with three above 4th palatal. Height of holotype 4.31 mm., diameter 6.02 mm.

Holotype. — Mangareva: Station 142, Mangareva Islet, vicinity of Ganhutu. Collected on open ground by Donald Anderson on June 26, 1934. BPBM 138978.

Range. — Mangareva Islet, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Mangareva Islet (Stations 142, 277) vicinity of Ganhutu (24 specimens, BPBM 9706, BPBM 138947-8, BPBM 138978, ex BPBM 138979); Mangareva Islet (Station 197) northeast of Vaituitai Bay (9 specimens, BPBM 139016-7).

Remarks. — Only adult specimens of *G. tumida* were found. *Gambiodonta pilsbryi* was collected in quantity at Stations 142 and 277, but all young specimens were referable to the latter. There is no problem in separating the two species (table CVII), since in *G. pilsbryi* the radial ribs are very narrow and regularly spaced while in *G. tumida* they are low and very broadly rounded. The absence of young *G. tumida* is puzzling, as is the difference in abundance (one specimen at Station 277 and 23 at Station 142). *Gambiodonta tumida* seems to be most closely related to *G. mangarevana* from the Rikitea area, which differs in its much smaller size (mean diameter 4.51 mm.) and its narrow and regular ribbing.

Gambiodonta grandis, new species (Cooke & Solem). Figure 189a-e.

Diagnosis. — Shell extremely large, diameter 10.9-13.4 mm. (mean 12.26 mm.), with 6¼-8 relatively tightly coiled whorls. Apex and spire very strongly and almost evenly elevated, slightly rounded above, last whorl not descending more rapidly, H/D ratio 0.509-0.721 (mean 0.591). Umbilical opening very narrow, irregularly ovate, modified internally to form brood chamber. Postnuclear sculpture of wide, very prominent, rounded, somewhat irregular radial ribs, 46-65 (mean 56.7) on the body whorl, whose interstices are less than twice

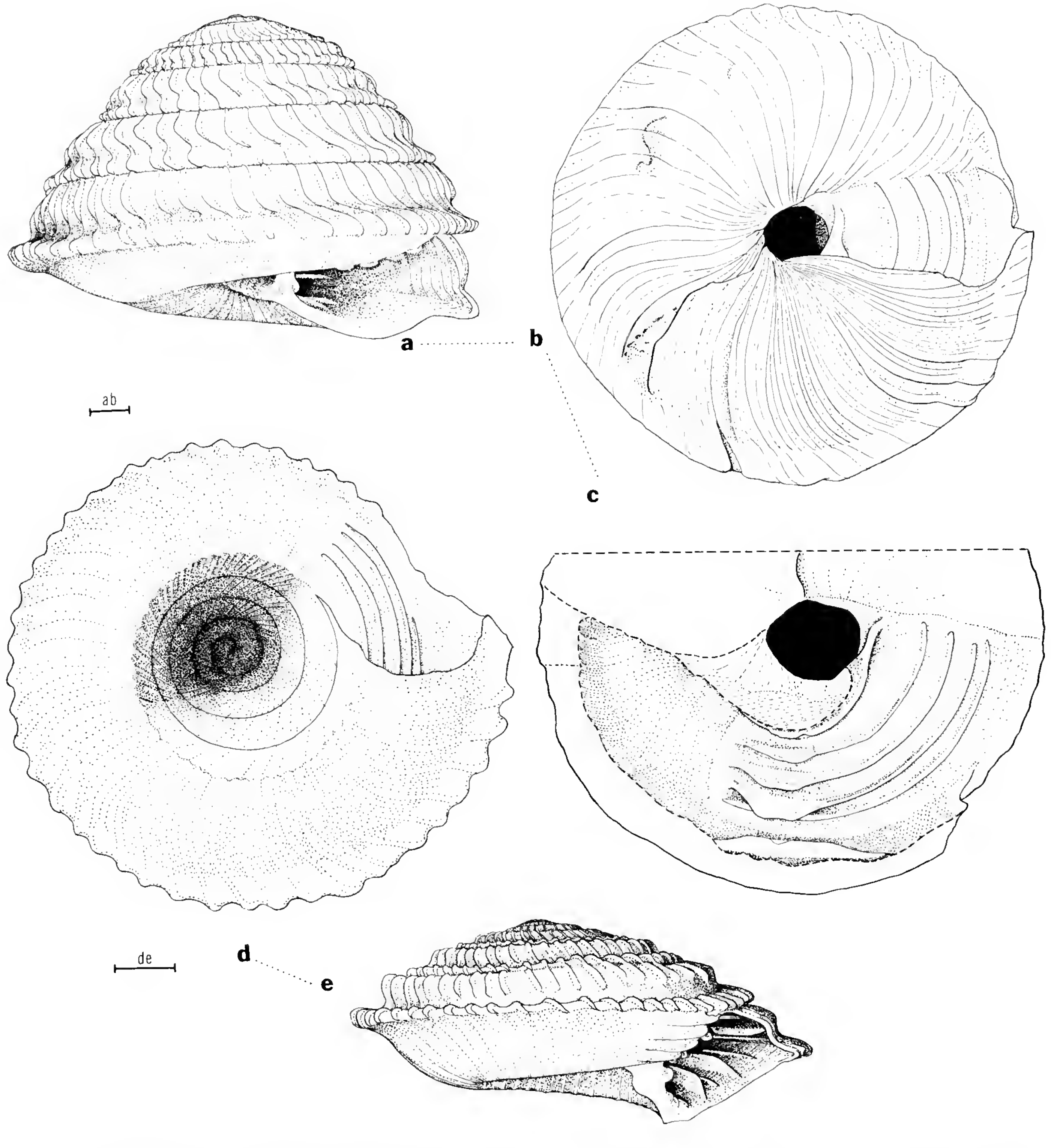

FIG. 189. *Gambiodonta grandis*, new species: **a-b**, Station 88, Aukena Islet, Mangareva, Gambier Islands. Holotype. BPBM 138709; **c**, paratype from Station 88, showing length and form of parietal lamellae. BPBM 138709; **d-e**, juvenile paratype from Station 88 showing form of young shell. BPBM 138710. Scale lines equal 1 mm. Fig. *c* greatly enlarged. Drawings by YK reproduced through the courtesy of Bernice P. Bishop Museum.

their width, and which are absent from base of shell. Radial and spiral microsculpture typical, no secondary cording developed. Sutures shallow, whorls strongly rounded down to supraperipheral sulcus, periphery protruded into a strong threadlike keel. Aperture ovate, strongly marked internally by peripheral protrusion, inclined about 25° from shell axis. Major parietal barriers 4, extending posteriorly beyond line of vision, occasionally with one accessory trace: upper parietal a raised threadlike ridge for entire length; 2nd, 3rd, and 4th parietals have anterior portions raised threadlike ridges, becoming strongly elevated and slightly expanded above posteriorly (fig. 189c). Columellar barrier high and bladelike, parallel to plane of coiling, with gradual anterior descension to edge of columellar callus, plus one very deeply recessed accessory denticle. Major palatal barriers 3, deeply recessed, extending about one-eighth whorl, with two to four very inconspicuous accessory traces: normal lower palatal often not detectable as such, at largest smaller than upper

TABLE CVIII. - LOCAL VARIATION IN GAMBIODONTA

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls
agakauitaiana BPBM 138903	6	2.70±0.050 (2.52-2.85)	4.01±0.021 (3.94-4.07)	0.675±0.0139 (0.633-0.716)	6 1/8+ (6-6 3/8)
pilsbryi pilsbryi BPBM 138979, -48, -50	37	2.83±0.026 (2.35-3.14)	4.86±0.026 (4.51-5.29)	0.582±0.0046 (0.514-0.652)	6 3/4- (6 1/8-7 1/8)
pilsbryi aukenensis BPBM 138711	18	2.81±0.027 (2.61-3.01)	5.04±0.008 (4.64-5.40)	0.559±0.0052 (0.519-0.605)	6 3/8- (6-6 5/8)
mangarevana BPBM 141695, BPBM 139005	2	3.07±0.196 (2.88-3.27)	4.48±0.098 (4.38-4.58)	0.686±0.0290 (0.657-0.715)	6 5/8
mirabilis BPBM 138981, -51, -52	18	3.37±0.059 (3.07-3.86)	5.50±0.047 (5.03-5.75)	0.612±0.0085 (0.552-0.694)	5 3/8- (5-5 7/8)
tumida BPBM 138947, -78	16	4.31±0.073 (3.59-4.71)	6.14±0.054 (5.88-6.60)	0.702±0.0103 (0.604-0.758)	6 1/2- (6-6 3/4)
grandis BPBM 138709	73	7.36±0.069 (5.90-8.70)	12.30±0.067 (10.90-13.40)	0.597±0.0052 (0.511-0.721)	7 3/8+ (6 1/2-8)
BPBM 138904	8	6.24±0.152 (5.60-6.80)	11.65±0.198 (11.00-12.50)	0.535±0.0057 (0.509-0.558)	6 5/8+ (6 1/4-7 1/8)

traces; "2nd" and "3rd" palatals high lamellar blades, weakly expanded above, with less gradual anterior descension; "4th" supraperipheral, reduced in height, a V-shaped lamellar ridge. Palatal traces usually one between each pair of major palatal barriers, trace between 3rd and 4th palatal sometimes equal in size to 3rd palatal.

The very great size, many whorls, wide radial ribs, very deeply recessed palatal barriers, and almost total absence of accessory traces separate *Gambiodonta grandis* from the other species of the genus. Two extralimital species of similar size might be confused with it: *Pseudolibera lillianae* from Makatea has only a single parietal and no palatal barriers, while *Nesodiscus magnificus* from Borabora has a broadly open umbilicus, no radial sculpture, and only a single parietal.

Description. — Shell very large, with 8 tightly coiled whorls. Apex and spire very strongly and almost evenly elevated, slightly rounded above, last whorl deflected slightly below periphery, H/D ratio 0.721. Embryonic whorls 1½, with very wide, prominent radial ribs, microsculpture eroded. Postnuclear whorls with heavy, rounded, protractively sinuated radial ribs, about 85 on the body whorl, whose interstices are slightly wider than their width, and which are absent from shell base. Microsculpture of irregular growth lines between major ribs, continued as irregular wrinkles on base of shell. No secondary spiral cording. Sutures shallow, whorls slanting down to prominent supraperipheral sulcus, periphery strongly protruded into threadlike keel. No color pattern present. Umbilical opening irregularly ovate, expanded internally to form brood chamber. Aperture compressedly ovate, strongly marked internally by peripheral protrusion, inclined about 25° from shell axis. Major parietal barriers 4, extending posteriorly beyond line of vision, with one short anterior accessory trace: upper parietal threadlike for entire length; 2nd and 3rd threadlike for first quarter whorl, becoming strongly elevated posteriorly and slightly expanded above (as in fig. 189c); 4th with posterior elevated portion slightly lower and shorter than in 3rd. Accessory trace located above upper parietal at anterior end, very short. Columellar barrier a high, bladelike ridge with gradual anterior descension, lying parallel to plane of coiling, twisted slightly upward at apertural margin. Major palatal barriers 3, extending about one-eighth whorl, very deeply recessed, with three very inconspicuous accessory traces: lower palatal of normal *Gambiodonta* absent; "2nd" and "3rd" moderately elevated barriers with gradual anterior descension; "4th" supraperipheral, reduced in height. One palatal trace below lower palatal, one between each pair of palatals. Height of holotype 8.5 mm., diameter 11.8 mm.

Holotype. — Gambier Islands: Mangareva, Station 88, Aukena Islet along trail near gap. Collected on open ground by D. Anderson and C. M. Cooke, Jr., on May 28, 1934. BPBM 138709.

Range. — Aukena and Agakauitai Islets, Mangareva, Gambier Islands.

Paratypes. — Same as list of material.

Material. — Mangareva: Aukena Islet (Stations 82, 88, 102, 103) in vicinity of gap (227 specimens, BPBM 138685, BPBM 138709-10, BPBM 138758-9); Agakauitai Islet (Station 195) on northwest side (32 specimens, BPBM 138800, BPBM 138904).

Remarks. — This magnificent species was quite common on Aukena Islet at the gap. Specimens were lying in the open and many had been partially crushed or abraded by rain and the feet of passing natives.

The specimens from Agakauitai were mainly subadult, but the few adult shells fall within the range of variation of the type set although averaging smaller in size and lower in H/D ratio (table CVIII). With 79 df, "*t*" equals 3.0668 for diameter and 3.9362 for H/D ratio, indicating highly significant differences. They are indistinguishable in sculpture and dentition. The figured type is the highest specimen examined, but is in magnificent condition. Although atypical, it can best represent this species. More than in most *Gambiodonta,* the lower palatal is reduced to the identical size of neighboring traces, and the palatal traces between the 2nd and 4th palatals often become greatly enlarged, occasionally equalling in size and shape the major barriers themselves. Time did not permit cleaning of most apertures and a study of palatal barrier variation in *G. grandis* would be an interesting minor project.

The general appearance of *G. grandis* is most similar to *Libera jacquinoti,* which differs very obviously in barriers and size (fig. 179d-f).

Genus **Thaumatodon** Pilsbry, 1893

Man. Conchol., (2), **9**, p. 26.

Endodontidae with typical apical sculpture and microsculpture, secondary spiral cording developed only in *decemplicata* and *corrugata.* Postnuclear sculpture of narrow to very wide (*hystricelloides, vavauensis, euaensis*) radial ribs, with a pronounced tendency toward great reduction of ribbing on body whorl (*hystricelloides, euaensis*) or over entire spire (*subdaedalea, corrugata*). Apex and spire flat or slightly elevated (*laddi, corrugata, spirrhymatum, decemplicata*) to markedly elevated (*hystricelloides, subdaedalea, vavauensis, euaensis*), body whorl descending slightly to moderately, mean H/D ratio 0.494-0.535 (except 0.600-0.670 in *hystricelloides, vavauensis, euaensis*). Body whorl usually rounded or laterally compressed, bikeeled in *spirrhymatum.* Whorls 5-5½, except *laddi* (4+) and *multilamellata* (6⅜). Umbilicus rather widely open, slightly narrowed (*hystricelloides*), or secondarily narrowed (*euaensis*). Major parietals 3 or 4, with straight or twisted (*hystricelloides*), small (*subdaedalea*) to large (*hystricelloides*) serrated beads above, or crystalline barbs (*multilamellata*). Several accessory traces present except in *multilamellata* and *decemplicata.* Columellar barriers 1 or 2, parallel to or slanting downwards from plane of coiling. Palatal barriers 3 to 6, normally 4, (except 5 in *multilamellata* and *decemplicata*; 3 in *vavauensis*), regularly beaded above (hooks in *multilamellata*), accessory traces present only in *spirrhymatum, hystricelloides, vavauensis,* and *euaensis.* Pallial region typically endodontid, except for greater development of rectal kidney arm. Hermaphroditic duct convoluted for quarter to half of length, except in *spirrhymatum.* Talon a short, untapered to tapered nub on carrefour. Uterus with clear division into four zones. Vas deferens entering epiphallus through a valve. Epiphallus about one-quarter to one-half length of penis, internally with two pilasters that continue into penis, variously splitting. Penial retractor originating on diaphragm, inserting directly onto penis-epiphallus junction. Spermatheca inserting on penial side of penioviducal angle.

Type species. — *Pitys multilamellata* Garrett, 1872 (original designation).

Originally described as a subgenus of *Endodonta,* by inertia *Thaumatodon* has been applied, usually in a subgeneric sense, to any non-carinated endodontid with apertural barriers from Polynesia, Micronesia, or Hawaii that was not referred to *Endodonta, Nesodiscus, Nesophila,* or *Libera.* Its type species has not been dissected. For the reasons outlined below under the discussion of *Thaumatodon multilamellata,* I have no hesitation in using this generic name for what seems to be an anatomically compact and highly distinctive group of species from the southwestern fringes of Polynesia.

Both anatomical and conchological structures ally *Thaumatodon* to the Palau Island *Aaadonta,* while the Lau Archipelago monotypic genera *Zyzzyxdonta* and *Priceconcha* are obvious derivatives, most probably from the *subdaedalea* group of *Thaumatodon.* In ornamentation of the apertural barriers and structures of the terminal male genitalia, so far as is known, these genera are highly specialized in comparison with the remaining Endodontidae. The major anatomical differences are development of an epiphallic zone, with valvular entrance of the vas deferens, found only in *Aaadonta, Priceconcha,* and *Thaumatodon,* compared with the apical or subapical direct entrance of the vas deferens into the penis found in all other Endodontidae. This is the largest morphologic change in the genitalia found in the subfamily. I consider these three genera, plus *Zyzzyxdonta,* to be the most advanced Pacific Island Endodontidae. The insertion of the spermathecal shaft on the penis has occurred elsewhere as a secondary modification (*Rhysoconcha*), but is almost as unique an event.

While obviously more closely interrelated than related to other genera, *Aaadonta* and *Thaumatodon* show numerous differences. *Thaumatodon* has typical endodontid apical sculpture; *Aaadonta* has only the spiral sculpture. *Thaumatodon* has the shell periphery laterally compressed or compressed above and below a rounded periphery except in *T. spirrhymatum*; *Aaadonta,* a periphery with protruded threadlike keel (except *A. pelewana*). *Thaumatodon* has major radial sculpture on at least part of the shell, with only *T. subdaedalea* and *T. corrugata* showing marked reduction; *Aaadonta* has all major ribbing lost, with only microradials remaining. *Thaumatodon* has a widely open umbilicus (secondarily narrowed in *T. euaensis*); *Aaadonta,* a much narrower umbilicus (secondarily widened in *A. angaurana* and *A. kinlochi*). *Thaumatodon* has the spire slightly to moderately elevated (only in *T. euaensis* does the height of spire approach half

TABLE CIX. - RANGE OF VARIATION IN THAUMATODON AND ZYZZYXDONTA

Name		Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
Thaumatodon										
multilamellata	18	115.4(94-143)	1.81(1.46-2.09)	3.37(2.85-3.77)	0.535(0.496-0.562)	6 3/8(6-6 3/4)	3.98(3.58-4.54)	4+0-$\underline{1}$	$\underline{1}$-2	5-6
decemplicata	46	103.2(85-122)	1.40(1.24-1.54)	2.64(2.37-2.93)	0.533(0.482-0.582)	5 1/8(4 7/8-5 1/2)	3.92(3.27-4.48)	4	1	5
hystricelloides	176	70.6(53-93)	2.42(1.69-2.85)	3.66(2.95-4.14)	0.663(0.573-0.752)	5 3/8+(5 1/8-6)	5.11(3.89-7.60)	4+2	1-2	4+$\underline{4}$-8-11
vavauensis	10	57.5(48-67)	1.65(1.45-1.99)	2.70(2.40-3.14)	0.610(0.568-0.634)	5 1/4(4 3/4-6)	3.85(3.37-4.44)	3+$\underline{2}$-4	$\underline{1}$-2	3-$\underline{4}$+2-$\underline{3}$
euaensis	47	REDUCED (48-65)	1.69(1.53-2.11)	2.54(2.35-3.03)	0.666(0.632-0.713)	5-(4 3/4-5 5/8)	9.83(7.22-13.3)	3-4+8-14	2+0-$\underline{1}$	4+3-4-$\underline{5}$
subdaedalea	21	REDUCED (44-55)	1.65(1.50-1.81)	3.24(2.96-3.59)	0.509(0.489-0.544)	5 1/8(4 3/4-5 1/2)	3.09(2.66-3.58)	3+$\underline{3}$-5	1+$\underline{0}$-1	4
corrugata	5	VERY REDUCED	1.54(1.46-1.59)	2.97(2.81-3.05)	0.518(0.500-0.540)	5-(4 3/4-5 1/8)	3.30(3.07-3.54)	3+4-5	1	4
laddi	18	195(180-210)	1.10(0.96-1.26)	2.15(1.99-2.38)	0.513(0.483-0.538)	4+(3 7/8-4 1/4)	3.35(3.13-3.61)	4+3-$\underline{4}$	1	4
Zyzzyxdonta										
alata	7	21-27 "WINGS"	1.53(1.39-1.66)	4.03(3.77-4.34)	0.379(0.368-0.387)	4 3/4-(4 1/2-5)	3.72(3.28-4.37)	3+$\underline{0}$-1	1	3

the body whorl width); *Aaadonta* has the spire markedly elevated, except for the secondarily altered *A. kinlochi* and *A. fuscozonata depressa*. *Thaumatodon* generally has 4 major parietals, with a tendency toward reduction or loss of the 2nd, and (usually) accessory traces; *Aaadonta* has 3 parietals, reduced to 2 in *A. irregularis,* and rarely has accessory traces. *Thaumatodon,* in the retracted specimens dissected, has a much greater development of the rectal kidney arm than does *Aaadonta*. *Thaumatodon* has a somewhat shorter epiphallus than *Aaadonta,* and *Thaumatodon* has the talon very short and blunt-tipped, while in *Aaadonta* it is long and tapering. In *Thaumatodon* the atrium is distinctly shorter than in *Aaadonta*.

Despite the recitation of differences, mostly concerning normally variable characters, the development of the beading on the apertural barriers and division of the penis into an epiphallus and penis, structures unique to the Pacific Island Endodontidae, indicate a monophyletic origin for *Aaadonta* and *Thaumatodon*.

Within *Thaumatodon,* patterns of variation are correlated with geography in a classical radiating pattern. The distribution (fig. 190) of individual species is limited: one in the Ellice Islands living on Vaitupu and Nukufetau (*decemplicata*); one on Rarotonga in the Cook Islands (*multilamellata*); one on Upolu, Western Samoa (*hystricelloides*); two in Tonga – *T. euaensis* on Eua Island and *T. vavauensis* on Vavau; and four in the Lau Archipelago of Fiji – *T. subdaedalea* on Mango, Vanua Mblavu, and Kimbombo Islands, *T. corrugata* on Mango Island, *T. spirrhymatum* on Thithia, and *T. laddi* on Wangava.

The species at the northern and eastern limits of distribution (*decemplicata* and *multilamellata*) are, in most respects, the least specialized. Both species retain major radial ribs of typical shape and size over the entire body whorl, but are slightly unusual in that the ribs are quite crowded with 12.44 and 10.90 ribs/mm., respectively. They both have 4 parietals, 5 palatals, and lack accessory traces. The spire height is only one-fifth to one-quarter the body whorl width, while the umbilicus is widely open with typical decoiling patterns. *T. decemplicata* is specialized only in developing weak secondary spiral cording; *T. multilamellata* shows the dramatic change of developing hooked denticles or pointed barbs (fig. 192d-e) on the palatal barriers. Otherwise, both species are very similar in appearance to the less specialized *Mautodontha* (*Garrettoconcha*), such as *M. consobrina* or *M. maupiensis*.

Species from the middle part of the range, Tonga and Samoa, are modified in several aspects that form a unitary pattern, but each species shows a few individual peculiarities. They agree in having quite elevated spires and correspondingly large H/D ratios (table CIX) with major ribbing that is very wide and prominent on the spire and early part of the body whorl. Only in *T. vavauensis* does the ribbing continue at full size to the apertural edge, while in *T. hystricelloides* it is partly reduced and in *T. euaensis* it is greatly reduced on the last part of the body whorl. Parietal barriers number 4 in *T. hystricelloides,* with two accessory traces and peculiarly (fig. 194d) twisted superior beading; the 2nd parietal is greatly reduced or absent in *T. euaensis* with many accessory traces and simple, rather prominent beading; and there are only 3 major parietals in *T. vavauensis* (2nd of other species reduced to a threadlike trace), with up to four accessory traces and simple beading. Palatal barriers either number 4, with either a few (*euaensis*) or many (*hystricelloides*) accessory traces, or vary from 3 to 4 with usually two accessory traces (*vavauensis*). The umbilicus is about as widely open in *vavauensis* as in the more generalized species, but fairly narrow in *T. hystricelloides,* and secondarily greatly narrowed in *T. euaensis*. Despite the twisted beading of *hystricelloides* and the wide umbilicus of *vavauensis,* the common pattern of spire elevation, unusual ribbing and proliferation of accessory apertural traces provides a marked contrast to the structures seen in the other species.

The four species from the Lau Archipelago of Fiji, *T. laddi, T. spirrhymatum, T. corrugata,* and *T. subdaedalea,* are more specialized and have a different pattern of specialization than those previously discussed. The spire is relatively low, with the umbilicus wider and the H/D ratio lessened (table CIX); the major sculpture is very fine and crowded (*laddi*), enlarged and crowded (*spirrhymatum*), or very widely spaced on the spire and drastically reduced on the body whorl (*corrugata* and *subdaedalea*); the columellar barrier is slanted downward from the plane of coiling (*corrugata* and *subdaedalea*), parallel to the plane of coiling (*spirrhymatum*), or parallel to the plane of coiling with the 1st palatal moved to the baso-columellar margin (*laddi*). In general appearance, they are closer to *decemplicata* and *multilamellata,* but the presence of numerous parietal traces and distinct sculptural modifications readily separate the two patterns of modification. *T. laddi* is much more similar to *T. decemplicata* than the other three, has 4 parietals as does *decemplicata,* but in shape and umbilical width is more allied to *subdaedalea* and *corrugata*. Since Wangava Island, the only known locality for *laddi,* is in a quite different part of the Lau Archipelago from the localities for *corrugata* and *subdaedalea,* I am not surprised at the differences.

Collecting efforts in the Lau Archipelago and the Ha'apai Group of Tonga, in particular, might yield additional species of *Thaumatodon*. The Bishop Museum collections made in the Lau Archipelago in the middle of 1938 apparently were during drought conditions and many islands were not visited. No material has been taken in the Ha'apai Group of Tonga since a few specimens found by Graeffe in the middle 1800's.

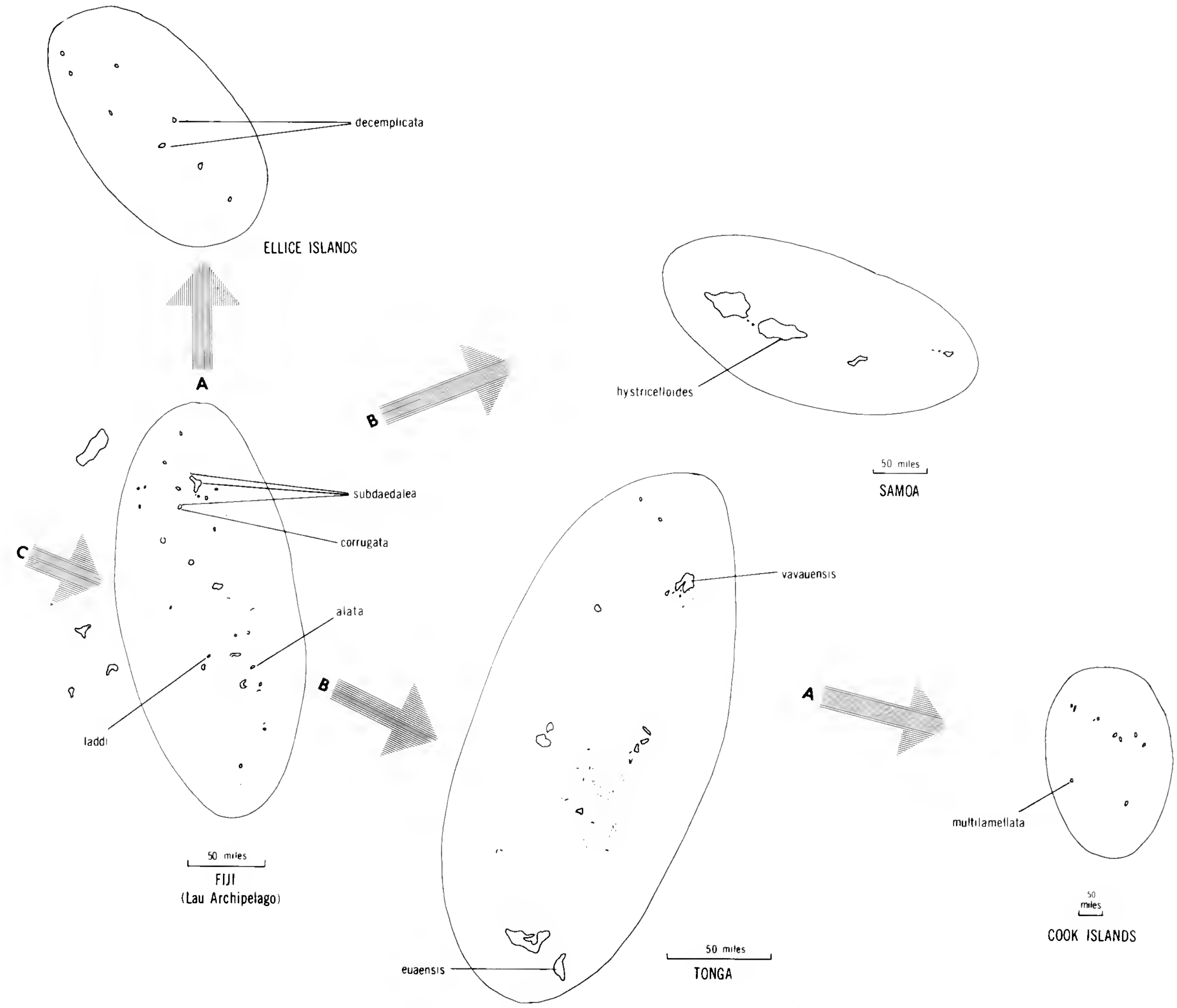

FIG. 190. Distribution of *Thaumatodon* and *Zyzzyxdonta* and hypothesized directions and waves of dispersal. *T. spirrhymatum* from Thithia not shown.

Presently known specimens thus offer a clear pattern of the most generalized species in the outer areas of distribution (Ellice Islands and Rarotonga) and a rather closely allied, strikingly modified complex in a middle zone (Samoa and Tonga). A very differently modified complex that produced two generically distinct derivatives (*Zyzzyxdonta* and *Priceconcha*) are found in a narrow "core" region (Lau Archipelago). While it is extremely doubtful that *Thaumatodon* originated in the Lau Archipelago, I consider it probable that Lau represents the last remaining segment of the central primitive *Thaumatodon* range. The major islands of Fiji and possibly the Bismarck-New Guinea area represent regions in which *Thaumatodon* or *Thaumatodon*-derivative groups have been replaced by Charopidae or helicarionid taxa. The Ellice and Cook Islands represent the furthest and probably latest expansion of *Thaumatodon*, with Tonga and Samoa containing a unitary, more advanced stock than the outer fringe areas. Present data are insufficient to determihe whether the Lau Archipelago *Thaumatodon* are either more or less advanced or more or less specialized than the Samoa-Tonga species. The probable directional movements of colonization are shown in Figure 190.

Anatomical variation between the four dissected species, *T. hystricelloides, T. euaensis, T. spirrhymatum,* and fragments of *T. decemplicata* was minor, concerning primarily the proportionate lengths of the penis and epiphallus. In *T. euaensis,* the epiphallus is about half the penis length; in the other three species it is only one-quarter to one-third. *T. decemplicata, T. spirrhymatum,* and *T. hystricelloides* agree in pilaster pattern, *T. euaensis* has one pilaster grossly enlarged to form a stimulatory pad.

KEY TO THE GENUS *Thaumatodon*

1. Body whorl not keeled..........2
   Body whorl with a very strong peripheral and prominent supraperipheral keel; Lau Archipelago, Fiji. *Thaumatodon spirrhymatum* Solem, 1973
2. H/D ratio of adults usually much more than 0.575, spire markedly elevated; ribs heavy and wide..........3
   H/D ratio of adults usually substantially less than 0.575, spire flat or barely emergent; ribs fine and numerous, very widely spaced, or greatly reduced on part of last whorl..........5
3. Mean diameter less than 3.0 mm.; ribs greatly reduced or absent on most of body whorl; Tonga..........4
   Mean diameter more than 3.55 mm.; ribs normally present on entire body whorl; Samoa. *Thaumatodon hystricelloides* (Mousson, 1865)
4. Mean D/U ratio about 10.0; Eua Island. *Thaumatodon euaensis,* new species
   Mean D/U ratio about 4.00; Vavau Island. *Thaumatodon vavauensis,* new species
5. Mean D/U ratio more than 3.70, umbilical margin not shouldered (fig. 193c); major ribs distinct but numerous (85-160); Ellice and Cook Islands..........6
   Mean D/U ratio less than 3.45, umbilical margins weakly to strongly shouldered (fig. 193f); major ribs very numerous or reduced to irregularity; Lau Archipelago, Fiji..........7
6. Mean diameter about 2.65 mm.; whorls 4⅞-5½; beading on apertural barriers restricted to posterior portion, never any hooked denticles on teeth; Ellice Islands. *Thaumatodon decemplicata* (Mousson, 1873)
   Mean diameter about 3.40 mm.; whorls 6¼-6¾; apertural barriers almost always with macroscopic spines or hooked denticles over entire length (fig. 192d-e); Rarotonga, Cook Islands..........*Thaumatodon multilamellata* (Garrett, 1872)
7. Adult with more than 4½ whorls; major parietal barriers 3; sculpture greatly reduced and irregular; mean diameter more than 2.8 mm...........8
   Adult with less than 4½ whorls; major parietal barriers 4, although 2nd greatly reduced in prominence; ribbing fine, but regular, 180 - 210 ribs on body whorl; mean diameter about 2.15 mm..........*Thaumatodon laddi,* new species
8. Body whorl with prominent spiral cording (fig. 196e). *Thaumatodon corrugata,* new species
   Body whorl without prominent spiral cording. *Thaumatodon subdaedalea* (Mousson, 1870)

GROUP OF *Thaumatodon decemplicata*

Thaumatodon multilamellata (Garrett, 1872). Figure 192a-e.

Pitys multilamellata Garrett, 1872, Amer. Jour. Conchol., **7**, (4), p. 320, pl. 19, fig. 25 – Rarotonga, Cook Islands; Garrett, 1881, Jour. Acad. Nat. Sci., Philadelphia, 8, (4), p. 389.

Patula multilamellata (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, **5**, p. 94.

Helix (*Pitys*) *multilamellata* (Garrett), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 569.

Helix (*Endodonta*) *multilamellata* (Garrett), Tryon, 1887, Man. Conchol., (2), 3, pp. 63-64, pl. 12, figs. 14-16.

Endodonta (*Thaumatodon*) *multilamellata* (Garrett), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26, pl. 4, figs. 35-38.

Diagnosis. – Shell larger than average, diameter 3.09-3.75 mm. (mean 3.39 mm.), with 6¼-6¾ quite tightly coiled whorls. Apex flat, spire slightly and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.496-0.562 (mean 0.533). Umbilicus U-shaped, regularly decoiling, contained 3.48-4.54 times (mean 3.99) in the diameter. Sculpture of fine, moderately closely spaced, almost vertical radial ribs, 98-160 (mean 122.0) on the body whorl, whose interstices are 2-3 times their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above, compressed laterally, with evenly rounded basal margin. Aperture sub-ovate, compressed laterally, inclined less than 5° from shell axis. Parietal barriers 4, extending posteriorly less than one-quarter whorl, sometimes (11 per cent) with an accessory threadlike trace between 2nd and 3rd parietals: upper parietal moderately high, expanded above with unusually sharp, rather widely spaced crystalline barbs, with gradual descension over anterior third; 2nd, 3rd and 4th parietals slightly reduced in height, moderately expanded above on posterior three-quarters, with gradual anterior descension. Columellar barriers 2, rarely 1, lying parallel or barely slanted down from plane of coiling; upper, when present, narrow, weakly expanded above with sharp anterior descension midway across columellar callus; lower slightly higher, thicker, moderately expanded above, with more gradual anterior descension midway across callus. Palatal barriers 5 (67 per cent) or 6 (33 per cent), extending posteriorly to line of vision, moderately recessed within aperture, equal in height, with gradual anterior descension, relatively low, surmounted either by recurved hooked structures (fig. 192d) or sharp barbs (fig. 192e).

In size and general appearance, *Thaumatodon multilamellata* is quite similar to *Mautodontha consobrina* from the Society Islands. The latter, however, has a fatter body whorl, much larger umbilicus and smaller, shorter, palatal barriers. The development of

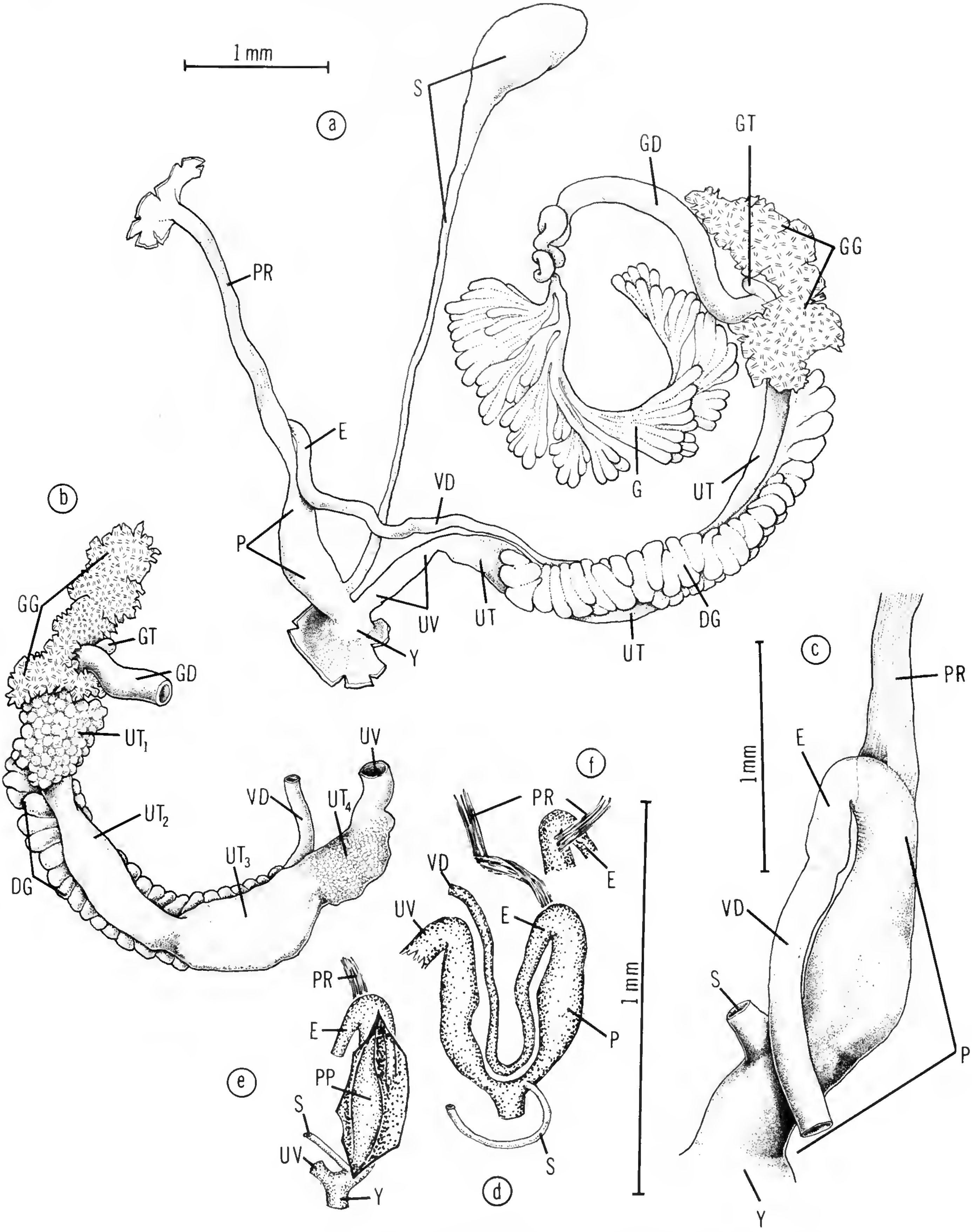

FIG. 191. Anatomy of *Thaumatodon*: **a-c**, *Thaumatodon hystricelloides*. Upolu, Samoa. FMNH 153423. *a*, genitalia, *b*, detail of uterine structure, *c*, penial complex; **d-f**, *Thaumatodon decemplicata*. Vaitupu, Ellice Islands. BPBM 189680. *d*, terminal genitalia, *e*, interior of penis, *f*, insertion of penial retractor. Scale lines equal 1 mm.

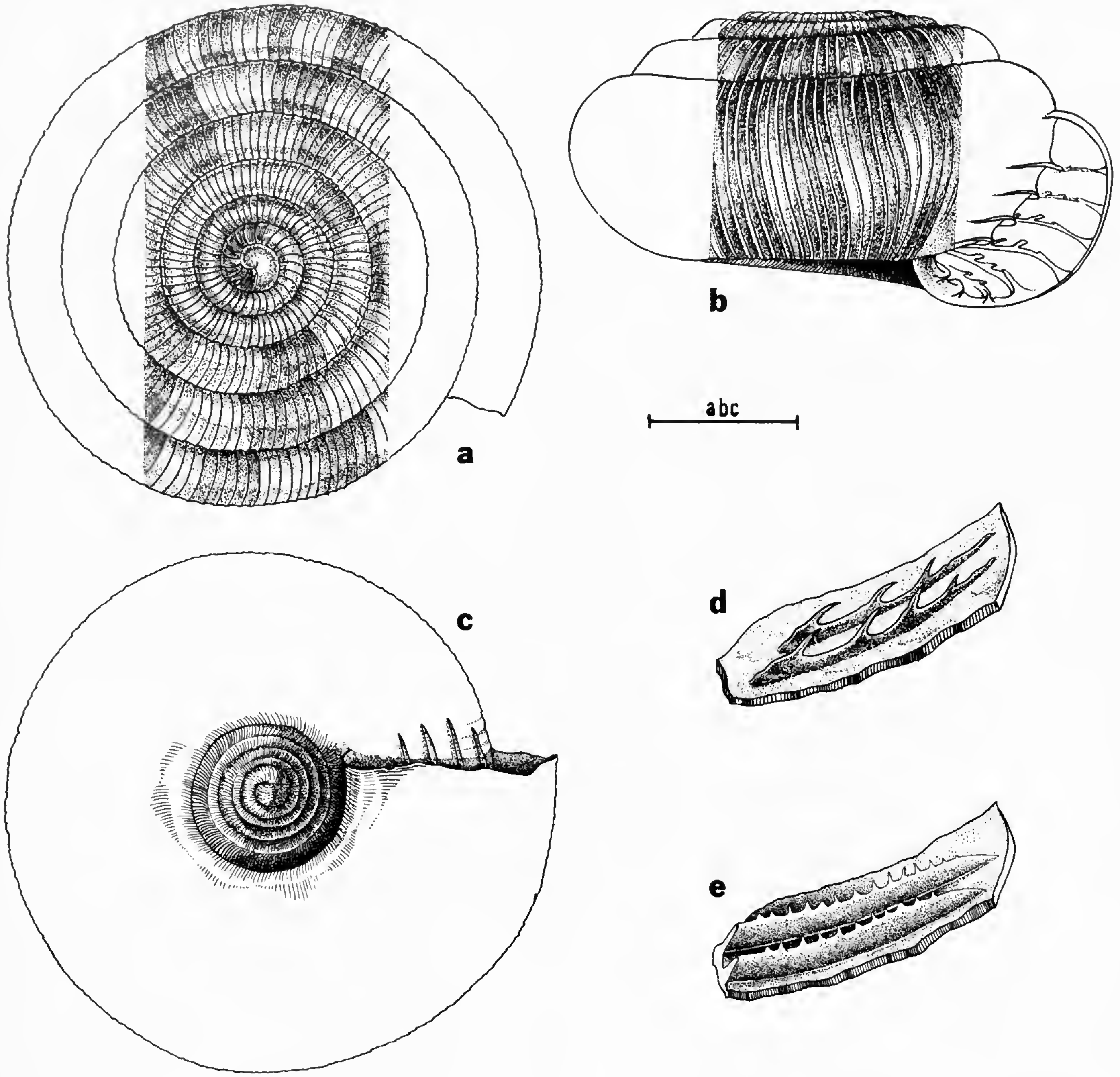

Fig. 192. **a-e**, *Thaumatodon multilamellata* (Garrett). Rarotonga, Cook Islands; **a-b**, paratype. BPBM 2316; **e**, FMNH 46268. Scale line equals 1 mm. *d-e* greatly enlarged (*a-d*, SG; *e*, MM).

distinct high hooks on the palatals is unique to *T. multilamellata,* and immediately separates it from all other endodontids. The much larger and much more elevated Tongan and Samoan species have heavy beading on the barriers, many accessory traces, and fewer, coarser ribs. *T. decemplicata* is nearly identical in shape and sculpture, but is much smaller and has shorter barriers with prominent beading on the parietals. All other *Thaumatodon* have only 4 major palatals.

Description. — Shell relatively large, with 6¾ tightly coiled whorls. Apex and early whorls of spire flatly coiled, last 3 whorls descending moderately rapidly, H/D ratio 0.496. Apical whorls 1½, sculpture mostly eroded with only traces of radial ribbing persisting in the sutures. Postnuclear whorls with prominent, V-shaped, vertically sinuated radial ribs, 124 on the body whorl, whose interstices are about twice their width. Microsculpture of relatively strong radial riblets, three to five between each pair of major ribs, with barely visible traces of very fine and crowded spiral riblets. Sutures deep, whorls strongly rounded above, somewhat compressed laterally with evenly rounded outer margin. Color light yellow horn with broad, regularly spaced reddish flammulations that become narrow on shell base. Umbilicus narrowly U-shaped, slightly and regularly decoiling, contained 4.11 times in the diameter. Apical sculpture of very fine, crowded radial riblets clearly visible in umbilicus. Aperture sub-ovate, compressed laterally, with evenly rounded outer margin, inclined less than 5° from shell axis. Parietal barriers, 4, extending almost one-quarter whorl: 1st parietal high, narrow, bladelike, with moderately sharp anterior descension; 2nd, 3rd, and 4th parietals differing primarily in more gradual anterior descension and extending slightly further anteriorly. Columellar barriers 2, moderately recessed within aperture: upper columellar thin, bladelike, with gradual anterior descension; lower columellar higher, thickened basally with sharp anterior descension. Palatal barriers 5, high, bladelike, extending posteriorly three-sixteenths of a whorl, with four to six crystalline hooks on upper edge which point toward the aperture; palatals gradually less recessed within aperture from bottom to top, equal in size and prominence. Height of lectotype 1.81 mm., diameter 3.75 mm.

Lectotype. — Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47792.

Range. — Rarotonga, Cook Islands.

Paratypes. — BPBM 2316, ANSP 290108.

Material. — Cook Islands: Rarotonga (18 specimens, AMS, Zurich, SMF 158296, FMNH 46268, BPBM 2316, ANSP 47792, ANSP 290108).

Remarks. — While most species of endodontids have the apertural barriers expanded above and minutely serrated with crystalline extensions (fig. 37a-c), *Thaumatodon multilamellata* is the only known species which has developed actual hooks that point toward the aperture or high pointed barbs. Somewhat similar hooks are also known in the totally unrelated Strobilopsidae from the holarctic region (see Pilsbry, 1931, pl. 11, fig. 7 of *Enteroplax boholensis*) and New Zealand taxa (Solem, 1970b, pl. 60).

T. multilamellata was reported by Garrett (1881, p. 389) as "Not uncommon, and obtained in two separate valleys on Rarotonga." During two trips to Rarotonga in 1964 and 1965, Mr. Laurie Price was unable to locate any of the Endodontidae described or reported by Garrett, except for the supralittoral *Libera fratercula. T. multilamellata* probably is extinct.

Available material, 18 specimens, suggested that there was subspecific differentiation between the two sampled colonies. Two specimens (FMNH 46268) had only 1 columellar barrier and quite minute, nearly vertical barbs on the palatal barriers (fig. 192e). All other specimens had the large hooks (fig. 192d), and 2 columellar barriers found in the type. Sometimes (11 per cent) an accessory parietal lamellar trace was present between the 2nd and 3rd parietals, and 33 per cent of the specimens had a 6th palatal.

In the absence of any anatomical evidence, association of this species with the other *Thaumatodon* is based upon a set of three specimens (Zurich), one of which has the barriers beaded instead of being "hooked." Possibly, only a single genetic mutation is involved in the transition from "beaded" to "hooked."

Thaumatodon decemplicata (Mousson, 1873). Figures 191d-f; 193a-c.

Pithys decemplicata Mousson, 1873, Jour. de Conchyl., **21**, p. 105 — Nukufetau and Vaitupu, Ellice Islands.

Helix (Pithys) decemplicata (Mousson), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 259.

Helix (Endodonta) decemplicata (Mousson), Tryon, 1887, Man. Conchol., (2), **3**, p. 63.

Endodonta (Thaumatodon) decemplicata (Mousson), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Diagnosis. — Shell smaller than average, diameter 2.44-2.76 mm. (mean 2.64 mm.), with 4⅞-5½ relatively tightly coiled whorls. Apex and spire slightly elevated, rounded above, last whorl descending much more rapidly, H/D ratio 0.513-0.562 (mean 0.533). Umbilicus V-shaped, of average width, regularly decoiling, contained 3.61-4.35 times (mean 3.92) in the diameter. Sculpture of closely set, protractively sinuated radial ribs, 85-110 (mean 94.1) on the body whorl, whose interstices are about twice their width. Microsculpture of fine radial riblets, three to five between each pair of major ribs, crossed by extremely fine and crowded spiral riblets, with a secondary spiral sculpture of narrow, rather widely spaced spiral cords. Sutures impressed, whorls strongly rounded above, slightly compressed laterally, with evenly rounded basal margin. Aperture subcircular, compressed laterally, inclined about 5° from shell axis. Parietal barriers 4, extending posteriorly less than one-quarter whorl: upper a high, thin blade, expanded above posteriorly, two or three, weak, widely spaced beads on posterior half, with gradual descension over anterior third; 2nd parietal slightly lower, with two larger beads on posterior three-eighths, anterior half a raised threadlike ridge terminating beyond edge of upper parietal; 3rd parietal slightly higher than 2nd, identical in shape, beading slightly larger and with anterior portion more elevated; 4th parietal greatly reduced in height posteriorly, with two or three very indistinct beads, anterior threadlike portion terminating slightly behind edge of 3rd parietal. Columellar barrier a low lamella, slightly twisted downwards from plane of coiling, with rather sharp descension almost to lip edge. Palatal barriers 5, extending posteriorly less than three-sixteenths of a whorl: lower moderately elevated, with three weak beads on posterior half, with sharp anterior descension to lip edge; 2nd slightly reduced in height, 3rd equal in height to 1st, 4th slightly lower than 2nd, all with same beading and with progressively more gradual anterior descension; 5th palatal supraperipheral, greatly reduced in height and length, beading reduced to three narrow, only weakly bulbous irregularities, moderately recessed within aperture.

Thaumatodon decemplicata is characterized by its small size, narrow ribbing, restriction of the simple beading to the posterior portion of the barriers, single columellar and 5 palatals. The much larger *T. multilamellata* (mean diameter 3.39 mm.) has "hooked" projections on the entire length of the palatal barriers and more whorls (6¼-6¾), but is essentially identical in shape and ribbing. The Tongan and Samoan species are much higher with very strong ribbing, although similar in size, while the *subdaedalea* complex has reduced sculpture and only 3 or 4 palatals.

Description. — Shell of less than average size, with a little more than 5⅛ tightly coiled whorls. Apex flat, whorls of spire descending gradually, H/D ratio 0.497. Embryonic whorls 1⅜, sculpture of fine crowded radial riblets, crossed by finer slightly more widely spaced spiral riblets. Postnuclear whorls with prominent, rounded, crowded, somewhat protractively sinuated radial ribs, 93 on the body whorl, whose interstices are usually less than twice their width. Microsculpture of prominent, rather widely spaced radial riblets, crossed by extremely fine and crowded spiral riblets with a secondary sculpture of strong, widely spaced spiral cording. Sutures moderately deep, whorls strongly rounded above, slightly compressed laterally with evenly rounded outer and basal margins. Umbilicus V-shaped, regularly decoiling, contained 3.66 times in the diameter. Color light reddish yellow-orange with narrow, zigzag, radial reddish markings, more prominent on body whorl, very faint above. Aperture ovate, with evenly rounded margins, inclined about 5° from shell axis. Parietal barriers 4, extending slightly less than one-quarter whorl:

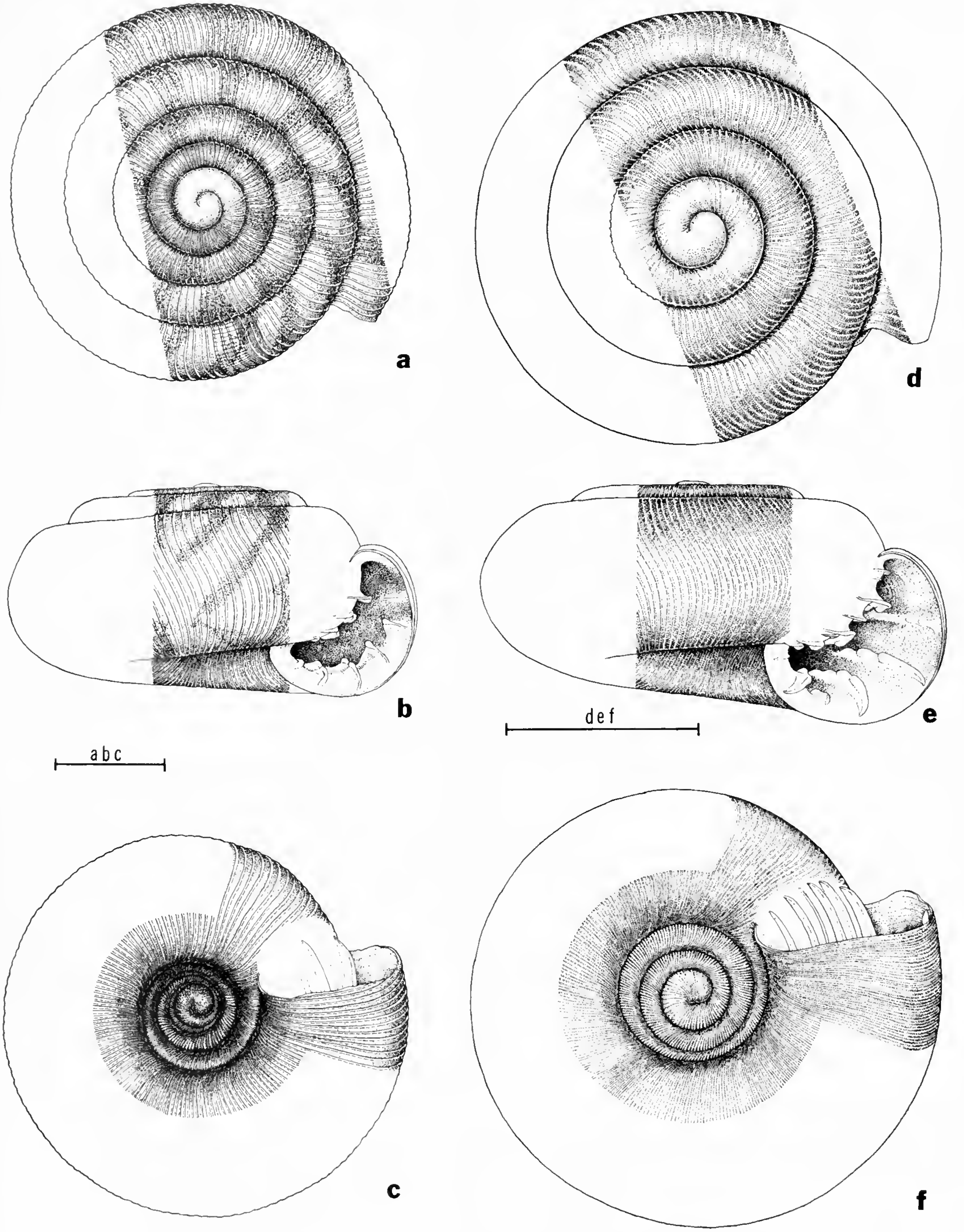

FIG. 193. **a-c**, *Thaumatodon decemplicata* (Mousson). Nukufetau, Ellice Islands. Paratype. FMNH 116990; **d-f**, *Thaumatodon laddi,* new species. Station 27, Wangava Island, Lau Archipelago, Fiji. Holotype. BPBM 166966. Scale lines equal 1 mm. (MM).

1st and 3rd moderately high with two strong posterior beads, 1st descending rather sharply and 3rd more gradually; 2nd and 4th reduced in prominence with anterior half threadlike, weakly expanded and beaded posteriorly. Columella with single, ridgelike barrier located near basal margin and slanting slightly downwards. Palatal barriers 5: lower 4 extending three-sixteenths of a whorl, moderately elevated, approximately co-equal and reaching lip margin, each with 2 beads above; upper palatal reduced in prominence, low, ridgelike, slightly supraperipheral in position. Basal and palatal lips with moderately heavy translucent callus. Height of lectotype 1.32 mm., diameter 2.65 mm.

Lectotype. — Ellice Islands: Nukufetau. Collected by Dr. E. Graeffe. Zurich 502969.

Range. — Ellice Islands: Nukufetau and Vaitupu Island.

Paratypes. — Nukufetau (Zurich 502969, FMNH 116990); Vaitupu (Zurich 502970, FMNH 116987).

Material. — Ellice Islands (5 specimens, FMNH 117004): Vaitupu (11 specimens, BPBM 189680); Nukufetau (19 specimens, BPBM 189673, FMNH 118394).

Remarks. — This species is known only from the original collections of Mousson on Nukufetau and Vaitupu, four specimens collected in rotting wood on Vaitupu by L. Isaacs in May, 1941 (BPBM 189680), and seven specimens collected by Isaacs on Nukufetau during the same period (BPBM 189673). Material from Vaitupu and Nukufetau do not differ significantly (table CX), nor do specimens from Graeffe's collecting in the 1860's and Isaacs' material taken in 1941. With 9-10 df, "*t*" was only 0.54-1.11 for all parameters.

Beading on the parietal barriers is restricted to the posterior portion, although present over the entire length on the lower palatals. Compared with *T. multilamellata* and *T. hystricelloides*, the barriers are much shorter and smaller.

The similarity in sculpture, shape, and form to *T. multilamellata* is quite marked, the major differences being in shell size, and the length and sculpture of the apertural barriers. The very small *T. laddi* from Wangava, Fiji, has a more open umbilicus with slight shouldering and very fine, crowded radial sculpture.

Description of soft parts. — Only the anterior parts of one animal were available. Terminal genitalia (fig. 191e, f) as follows: Vas deferens (VD) slender to penioviducal angle, thickened to point about three-quarters of way up penis where it enters a weakly expanded epiphallus (E). Latter not demarcated from penis proper (P), but probably functionally set off by insertion of penial retractor (PR, fig. 191d). Penis about 0.5 mm. long, expanded above, strongly tapered for anterior third to junction with spermatheca and atrium. Penis internally (fig. 191e) with two pilasters (PP), one greatly enlarged, both continuing to epiphallic head apically, the smaller fading out on lower portion of penis wall. Opening from vas deferens to epiphallus of same type found in *Aaadonta* (fig. 199d). Spermathecal stalk (S) same diameter as vas deferens, entering penis base just above junction of latter with atrium. Free oviduct (UV) almost equal in diameter to penis, narrowing abruptly just before joining penis to form atrium (Y). Length of latter not observed.

Radula lost in processing.

(Based on BPBM 189680.)

GROUP OF *Thaumatodon hystricelloides*

Thaumatodon hystricelloides (Mousson, 1865). Figures 191a-c; 194d-e; 197d-f; 208e.

Patula (Endodonta) hystricelloides Mousson, 1865, Jour. de Conchyl., **13**, pp. 169-170, 431, pl. 14, fig. 6 — Upolu, Samoa; Mousson, 1869, *op. cit.*, **17**, pp. 331-332.

Helix hystricelloides (Mousson), Pfeiffer, 1868, Monog. helic. viv., **5**, p. 221.

Pitys hystricelloides (Mousson), Pease, 1871, Proc. Zool. Soc. London, **1871**, p. 474; Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, **1887**, p. 130.

Helix (Endodonta) hystricelloides (Mousson), Tryon, 1887, Man. Conchol., (2), **3**, p. 65, pl. 12, fig. 30.

Endodonta (Thaumatodon) hystricelloides (Mousson), Pilsbry, 1893, *op. cit.*, (2), **9**, p. 27.

Partula (sic) *hystricelloides* Mousson, Fischer-Piette, 1950, Jour. de Conchyl., **90**, (2), p. 66 — location of figured specimens.

Diagnosis. — Shell large, diameter 3.42-4.11 mm. (mean 3.70 mm.), with 5⅛-5¾ moderately tightly coiled whorls. Apex somewhat flattened, spire strongly elevated, shape globose, last whorl descending slightly more rapidly, H/D ratio 0.576-0.752 (mean 0.663). Umbilicus narrowly U-shaped, regularly decoiling, contained 3.89-7.60 times (mean 5.11 times) in the diameter. Postnuclear sculpture of strong, protractively sinuated radial ribs, 59-93 (mean 70.9) on the body whorl, whose interstices are slightly less than twice their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above and on basal margin, slightly compressed laterally with evenly rounded outer margin. Aperture subcircular, compressed laterally, inclined about 5-10° from shell axis. Parietal barriers 4, extending posteriorly less than one-quarter whorl, with two accessory traces: upper a high, thin blade, expanded above with three to four large beads that twist downward and backward and are covered with minute barbs (fig. 195d), anterior three-eighths simple with sharp anterior descension; 2nd greatly reduced in height, a low lamellar blade, with two to three simple elongated beads (fig. 195d) on posterior two-thirds, anteriorly with more gradual descension to point just beyond end of upper parietal; 3rd slightly lower than 1st, strongly expanded and beaded above on posterior two-thirds, with rather gradual anterior descension; 4th a very low, threadlike trace, weakly elevated and beaded above. Accessory traces located above upper and below 4th palatal, both small threadlike ridges, upper only slightly, lower moderately recessed within aperture. Columellar barriers 1 or 2, upper, when present, a low threadlike trace, weakly elevated and beaded above posteriorly beyond callus; lower high and bladelike, expanded and beaded above posteriorly, lying parallel to plane of coiling, with sharp anterior descension to lip edge. Palatal barriers 4, extending posteriorly less than three-sixteenths of a whorl, with five to eleven accessory traces: lower at baso-columellar margin, very high, strongly expanded and beaded above posteriorly, with abrupt descension to lip edge; 2nd and 3rd equal to 1st in height and beading, with progressively more gradual anterior descension; 4th supraperipheral, scarcely larger than adjoining traces, a short, thin, low ridge with two very large beads above, with very gradual anterior descension. Accessory traces normally two or three between 1st and 2nd; two between 2nd and 3rd; two between 3rd and 4th; two to four above 4th palatal. Larger traces may show small beads above or consist just of small beads on the palatal wall with the lamellar blade absent.

The large size, markedly elevated spire, coarse ribs that normally continue to the aperture, and huge beaded barriers characterize *Thaumatodon hystricelloides*. Of the Tongan species, *T. vavauensis* is much smaller, has 3 major parietals, although very similar in shape and sculpture, while *T. euaensis* has a much narrower umbilicus, many more parietal traces,

TABLE CX. - LOCAL VARIATION IN THAUMATODON AND ZYZZYXDONTA

Name	Number of Specimens	Ribs	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
multilamellata BPBM 2316, BPBM 167424	7		1.89±0.049 (1.72-2.05)	3.50±0.087 (3.15-3.77)	0.539±0.0061 (0.515-0.562)	6 3/8+ (5 7/8-6 3/4+)	4.01±0.106 (3.62-4.32)
decemplicata BPBM 2284, BPBM 167436, BPBM 189680 (Ellice Islands)	5		1.43±0.046 (1.26-1.52)	2.62±0.049 (2.45-2.75)	0.546±0.0085 (0.514-0.562)	5 1/4+ (4 7/8-5 1/2)	3.94±0.130 (3.61-4.35)
Zurich (Vaitupu)	7	93.6±3.25 (85-106)	1.43±0.025 (1.32-1.51)	2.64±0.025 (2.53-2.73)	0.541±0.0087 (0.503-0.576)	5 1/4+ (5 1/4-5 1/2)	3.88±0.132 (3.51-4.39)
BPBM 189673 (Nukufetau)	3	92.7±2.03 (89-96)	1.42±0.051 (1.36-1.52)	2.64±0.086 (2.48-2.78)	0.540±0.0139 (0.513-0.560)	5 1/4+ (5 1/8-5 1/2)	3.94±0.156 (3.64-4.17)
Zurich (Nukufetau)	8	92.8±2.06 (86-99)	1.41±0.032 (1.26-1.54)	2.68±0.064 (2.43-2.93)	0.526±0.0110 (0.482-0.582)	5 1/4+ (4 5/8-5 1/2)	3.93±0.141 (3.27-4.48)
hystricelloides BPBM 106240, BPBM 167431, BPBM 115370	7	69.8±4.76 (58-86)	2.44±0.056 (2.28-2.68)	3.68±0.033 (3.51-3.77)	0.663±0.0132 (0.628-0.730)	5 1/2- 5 1/4-5 3/4)	5.64±0.435 (4.82-7.60)
Zurich (Upolu)	22	72.6±1.72 (64-93)	2.50±0.039 (2.15-2.85)	3.73±0.036 3.48-4.14)	0.670±0.0070 (0.600-0.727)	5 1/2+ (5 - 6)	5.06±0.156 (3.89-7.12)
Sydney (Upolu)	7	70.1±2.96 (59-78)	2.37±0.036 (2.24-2.53)	3.66±0.044 (3.45-3.78)	0.659±0.0047 (0.626-0.713)	5 1/2- (5 1/4-5 3/4)	4.94±0.205 (4.35-6.05)
subdaedalea BPBM 179839 BPBM 179911, BPBM 179912	5		1.68±0.038 (1.61-1.82)	3.39±0.071 (3.16-3.61)	0.495±0.0092 (0.477-0.524)	5 1/4- (5-5 1/2)	2.95±0.106 (2.66-3.20)
corrugata BPBM 179940, BPBM 179987, BPBM 180066	5		1.54±0.027 (1.46-1.59)	2.97±0.043 (2.81-3.05)	0.518±0.0067 (0.500-0.540)	5- (4 3/4-5 1/8)	3.30±0.081 (3.07-3.54)
laddi BPBM 166966	9		1.10±0.029 (0.96-1.26)	2.15±0.036 (1.99-2.38)	0.513±0.0063 (0.483-0.538)	4+ (3.7/8-4 1/4)	3.35±0.050 (3.13-3.61)
alata BPBM 167018, BPBM 167054	4		1.53±0.058 (1.39-1.66)	4.03±0.123 (3.77-4.34)	0.379±0.0041 (0.368-0.387)	4 5/8+ (4 1/2-5)	3.72±0.255 (3.28-4.37)
euaensis FMNH 152377	29		1.69±0.022 (1.53-2.11)	2.54±0.024 (2.35-3.03)	0.666±0.0039 (0.632-0.713)	5+ (4 3/4-5 5/8)	9.83±0.310 (7.80-13.29)

and is much smaller. All other *Thaumatodon* have much finer sculpture and are much more depressed.

Description. — Shell large, with 5⅜+ tightly coiled whorls. Spire distinctly elevated, apex barely protruding, whorls of spire descending progressively more rapidly, H/D ratio 0.619. Embryonic whorls 1½, sculpture mostly eroded with only faint traces of radial ribbing remaining. Postnuclear whorls with very prominent, rounded, slightly protractively sinuated radial ribs, 79 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of moderately strong, crowded radial riblets, five to eight between each pair of major ribs, with extremely fine, barely visible spiral riblets. Sutures moderately impressed, whorls slightly shouldered above, somewhat flattened laterally with evenly rounded basal margin. Color light yellowish-brown with occasional darker reddish flammulations visible. Umbilicus narrowly open, U-shaped, not decoiling, contained 3.89 times in the diameter. Aperture ovate, compressed laterally, inclined about 5° from the shell axis. Parietal barriers 4, extending slightly less than one-quarter whorl, with two accessory traces: upper parietal high, bladelike with laterally slanting beads above posteriorly and sharp anterior descension; 2nd parietal much lower, long, bladelike, with three irregular beads above; 3rd parietal equal in height to the 1st, broadly expanded above with four irregular beads visible; 4th parietal low, threadlike, relatively broad above with faint, irregular, posterior beading. Parietal traces located between upper parietal and upper parietal margin, and between lower parietal and columellar margin: upper, long, threadlike, very narrow; lower short, threadlike, deeply recessed within aperture. Columellar barriers 2: upper a low, recessed, threadlike trace; lower a high, threadlike ridge, parallel to plane of coiling and reaching lip edge. Major palatal barriers 4, with twelve accessory traces: lower palatal at baso-columellar margin, very high, crescentic, with broadly expanded posterior beading and sharp descension to lip edge; 2nd palatal slightly lower, broadly rounded above with large posterior beads; 3rd palatal slightly subperipheral, very high, with two broad posterior beads and gradual anterior descension, moderately recessed within aperture; upper major palatal low, threadlike, faintly beaded above, lying opposite upper parietal, almost peripheral in position. All palatal barriers extending a little more than one-eighth whorl. Palatal traces located between lower columellar and 1st palatal, 1st palatal and 2nd palatal, two between 2nd and 3rd palatals, three between 3rd and 4th palatals, and four between 4th palatal and upper palatal margin. All traces narrow, threadlike, occasionally faintly beaded above. Height of lectotype 2.14 mm., diameter 3.40 mm.

Lectotype. — Samoa: Upolu. Collected by E. Graeffe. Zurich 502959.

Range. — Formerly over much of Upolu, now restricted to upland forest areas, probably in most areas only over 2,600 ft. elevation.

Paratypes. — Zurich 502958, FMNH 116984 (43 specimens).

Material. — Samoa (17 specimens, FMNH 46420, BPBM 159, BPBM 106240, BPBM 115370, BPBM 167431, SMF 165383); Upolu (17 specimens, FMNH 91112, FMNH 116989, FMNH 116694, FMNH 117266, SMF 165382, Sydney, Zurich 502959, Paris, Brussels, Brit. Mus.); Lake Lanuto'o, ridge at 2,380 ft. elevation (1 specimen, BPBM 186395); Mt. Siga'ele at 2,675 ft. elevation, Station 24 (5 specimens, FMNH 153618); below crater rim of Lake Lanuto'o at 2,500 ft. elevation, Station 19 (90 specimens, FMNH 153038, FMNH 153061, FMNH 153130-1, FMNH 153423, FMNH 153542); Tapatapao — Lake Lanuto'o trail, Station 20, at 1,800 ft. elevation (2 specimens, FMNH 153412).

Remarks. — Cited by Garrett (1887b, p. 131) as "Not uncommon under rotten wood and beneath decaying leaves," in 1965 *T. hystricelloides* was only found below the crater rim of Lake Lanuto'o at 2,500 ft., on the trail up to the lake at 1,800 ft. elevation and near the summit of Mt. Siga'ele at 2,675 ft. elevation. Although numerous stations at lower elevations were visited, no trace of this species was found except in the upland forest remnants. At the one station it was quite common, but elsewhere seems to have become extinct. The observed habitat was under dead *Pandanus* leaves near Lake Lanuto'o and under rotting leaves on Mt. Siga'ele.

Previous material was taken by Graeffe (1860's), Garrett (1870's), and a single specimen by E. C. Zimmerman (1940). The Graeffe and Garrett specimens are widely, although sparsely, represented in collections throughout the world. Mousson's collection (Zurich) contained some 39 examples received from Graeffe in 1864, 1868, and 1872. Unfortunately, these specimens had been mixed together. The single example collected by Zimmerman in 1940 near Lake Lanuto'o (BPBM 186395) was the most elevated specimen examined (H/D ratio 0.752). Specimens collected by Solem and Price in 1965 did not differ in general appearance or barriers from those in older collections.

Apertural barrier variation consisted primarily in the number of palatal traces. As few as four, as many as eleven were observed, with eight to ten the most prevalent numbers. No differences between sets were observed.

Mousson's record of this species from Vavau, Tonga (Mousson, 1871, pp. 10-11) was based on *T. vavauensis*, new species.

Description of soft parts. — Foot slender, length about equal to shell diameter, truncated anteriorly, with head projecting in front of foot. Tail variable, rounded to slightly tapered behind. Sole undivided, smooth. Pedal grooves rather high on foot, suprapedal much weaker, both united above tail. No caudal horn or middorsal groove visible. Slime network very faint, no marked pattern. Ommatophores long, eyespots very small, black. Retractor muscles brown for first part of length. Gonopore a large slit directly behind right rhinophore, almost directly below right ommatophore.

Body color in life and preservative faint yellow-white.

Mantle collar (MC) with thickened, protruded edge, no distinct lappets developed, but a very large triangular, glandular extension onto pallial roof. Pneumostome in parietal-palatal angle, without any distinct mantle lobes. Anus (A) opening just inside edge of mantle collar, a distinct groove continuing to outer edge of collar.

Pallial region extending apically one-half whorl, of normal width, about 4.8 mm. long. Lung roof with bands of white granules flanking principal pulmonary vein, continuing apically along ureter and kidney. Kidney (K) about 1.8 mm. long, 1.7 times length of heart, tapering anteriorly, rounded basally, with small hooked portion abutting hindgut, and intestinal loop reaching base. Ureter (KD) starting at apex of kidney, following lower margin and opening just anterior of pericardial kidney termination, no secondary ureter present. Heart (H) nearly parallel to hindgut, rather slender and elongated. Principal pulmonary vein (HV) slender, angling towards pneumostome, unbranched until just before invasion of shell glands onto lung roof, then heavily invading area. Hindgut (HG) starting at reflexion of intestine 1.65 mm. above kidney base, passing normally forward to anus.

Ovotestis (fig. 191a, G) extending two-thirds whorl apically above stomach, composed of palmately clavate alveoli along a simple collecting tubule. Hermaphroditic duct (GD) slender at first, expanded into a very short contorted section, then grossly expanded to a long straight tube that turns and narrows slightly before entering carrefour. Albumen gland (GG) typical. Talon (GT) a fingerlike tube lateral to junction of hermaphroditic duct and carrefour. Prostate (DG) of two rows large acini opening into a separate tube, slightly shorter than uterus. Uterus (fig. 191a, b, UT) with a peculiar glandular head (UT_1), a slender section (UT_2), typically expanded lower chamber (UT_3), and then a terminal, more glandular portion (UT_4) before narrowing to enter free oviduct.

Vas deferens (VD) a continuation of prostate duct, loosely bound to penioviducal angle, entering through a lip arrangement into epiphallus. Epiphallus (E) less than one-third length of penis, opening of vas deferens as in *Aaadonta* (fig. 199d), with two pilasters continuing into penis. Penial retractor (PR) originating on diaphragm, inserting on penis-epiphallus junction. Penis (fig. 191c, P) enervated from right cerebral ganglion, about 1.5 mm. long, moderately bulbous on lower half, internally with weak crenulated pilasters continuing from epiphallus, then each bifurcating medially in penis, one uniting again just before atrium, the other pair gradually diminishing. Pattern very similar to that seen in *Aaadonta* (fig. 199d). Atrium (Y) short, not strongly sculptured.

Free oviduct (UV) narrow, internally with longitudinal pilasters, rather sharply delineated from thin-walled uterus. Spermatheca (S) with oval expanded head lying partly next to head of prostate and uterus, partly next to albumen gland base. Vagina absent.

Free muscle system typical of subfamily. Right ommatophoral retractor passing through penioviducal angle. Right rhinophoral retractor passing outside penioviducal angle, uniting with right ommatophoral retractor about two-thirds of way to point where tentacular retractors unite laterally with tail fan anterior to point where buccal retractors join tail fan to form columellar muscle.

Buccal mass normal, hump shaped. Buccal retractors split, two fine lateral bands uniting much posterior of main band junction. Esophagus arising just behind midpoint of stomach, esophagus opening into stomach just above apex of pallial cavity. Latter extends one-half whorl apically, before reflexing just short of ovotestis. Intestine with normal pattern of looping, lower loop abutting kidney base as in *Endodonta fricki*. Hindgut starting 1.5 mm. above apex of pallial cavity, following parietal-palatal angle forward to anus.

Digestive glands extending 1¼ whorls past ovotestis to apex of soft parts, in narrow strip along stomach, expanding in region of intestinal loops, touching apical wall of pallial cavity. Salivary glands uniting above esophagus for posterior half of length, with several digitiform extensions pointing downwards.

Jaw very delicate, composed of many elongated, separate but overlapping plates, weakly attached by a membrane.

Radula with more than 105 rows, central tooth about 8μ wide and 10μ long, laterals 7 or 8, with 11-12 marginals.

(Based on five adult specimens, FMNH 153423.)

Thaumatodon euaensis, new species. Figures 194a-c; 195.

Diagnosis. — Shell small, diameter 2.35-3.03 mm. (mean 2.54 mm.), with 4¾-5⅜ normally coiled whorls. Apex and spire rather strongly and evenly elevated, last whorl descending only slightly more rapidly, H/D ratio 0.632-0.713 (mean 0.666). Umbilicus very narrow, U-shaped, not decoiling, contained 7.22-13.3 times (mean 9.83) in the diameter. Postnuclear whorls with high, broadly rounded, protractively sinuated radial ribs, that fade out on last parts of body whorl, spaced so that there would be between 45 and 65 ribs on the body whorl if not absent on last parts. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures relatively shallow, whorls strongly rounded above and on basal margin, somewhat compressed laterally on lower palatal margin. Aperture subovate, somewhat compressed laterally, inclined about 15° from shell axis. Parietal barriers 3 (38.1 per cent) or 4 (61.9 per cent), 2nd greatly reduced in prominence or absent, extending posteriorly slightly more than three-sixteenths of a whorl, with eight to fourteen accessory traces: upper very high, slender, expanded and very weakly beaded on posterior two-thirds, with sharp anterior descension; 2nd, when not reduced to a threadlike trace, about one-third to one-half height of 1st parietal, expanded above with two distinct beads posteriorly, anterior half threadlike and extending to anterior end of upper parietal; 3rd parietal slightly lower at first, more prominently expanded and beaded above on posterior half, with anterior third a threadlike trace; 4th parietal almost equal in height to 3rd, usually with more gradual anterior descension and greater elevation of anterior portion. Parietal traces variable in number and position, generally two above upper parietal; one between 1st and 2nd; one between 2nd and 3rd; three between 3rd and 4th parietals; and three or four between 4th parietal and parietal-columellar margin. Columellar barriers 2, often (19 per cent) with slender trace present between upper columellar and columellar-parietal margin; upper columellar moderately elevated, bladelike, lying parallel to plane of coiling, somewhat expanded and serrated above posterior to apex of columellar callus, with gradual anterior descension to lip edge; 2nd columellar much higher, similar in position, with sharp anterior descension almost to lip edge. Palatal barriers 4, extending posteriorly more than one-eighth whorl, very large, generally with three (40 per cent) or four (45 per cent) accessory traces; lower palatal extremely high, slender, expanded and weakly but distinctly beaded posteriorly with sharp anterior descension to lip edge; 2nd and 3rd palatals equal in height, weakly beaded above, with progressively more gradual anterior descension, also nearly reaching lip edge; 4th palatal lying opposite upper parietal, greatly reduced in height and length, very slender and weakly expanded above, with abrupt anterior descension almost to lip margin. Accessory traces located between 1st and 2nd, 2nd and 3rd, 3rd and 4th, and often (45 per cent) above 4th palatal. Occasionally there will be a second accessory trace above the 4th palatal, or an accessory trace between the lower columellar and 1st palatal.

Thaumatodon euaensis differs from the obviously closely related Samoan species *T. hystricelloides* in being much smaller, having a distinctly narrower umbilicus, not having the 4th parietal barrier reduced in size, always possessing 2 columellar barriers, having the radial ribbing greatly reduced on the body whorl, and in having the body whorl distinctly compressed laterally. The other Tongan species, *Thaumatodon vavauensis*, is a more depressed, widely umbilicated shell, with very prominent radial ribbing on the body whorl and only three to five accessory parietal traces.

Description. — Shell small, with 5¼ normally coiled whorls. Apex and early spire moderately and almost evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.671. Apical whorls 1½, sculpture eroded. Postnuclear whorls with prominent, broadly rounded, protractively sinuated radial ribs, that are prominent until last two-thirds of body whorl, becoming indistinguishable on last quarter. If major ribbing continued normally, there would be about 65 ribs on body whorl. Microsculpture of extremely fine radial riblets, five to eight between each pair of major ribs on early body whorl, crossed by extremely fine and crowded spiral riblets. Suture shallow, whorls strongly rounded above and on

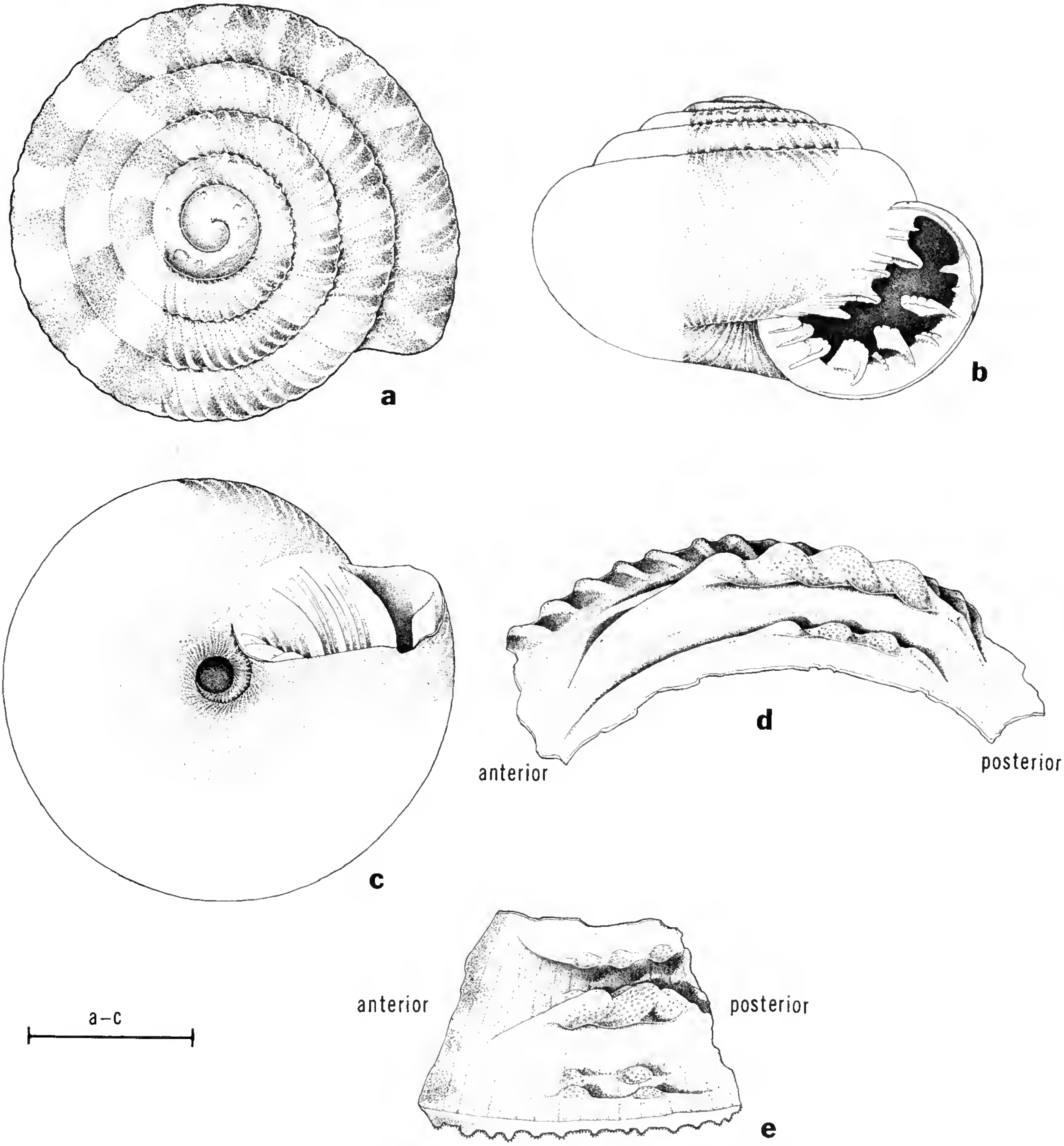

FIG. 194. **a-c**, *Thaumatodon euaensis*, new species. Station T-22, Eua Island, Tonga. Holotype. FMNH 154784; **d-e**, *Thaumatodon hystricelloides* (Mousson). *d*, parietal lamellae, *e*, 3rd and 4th palatal lamellae. Scale line equals 1 mm. Figures *d* and *e* greatly enlarged. (MM).

umbilical margin, distinctly compressed laterally on lower palatal margin, walls of umbilicus very strongly rounded. Color light yellow-brown, with irregular, dark red flammulations, that become narrow and strongly zigzagged on shell base, much more prominent on body whorl than upper spire. Umbilicus quite narrow, distinctly wider at apex than on last whorl, contained 9.11 times in the diameter. Aperture subovate, distinctly compressed laterally, inclined about 15° from shell axis. Parietal barriers 4, extending posteriorly slightly more than three-sixteenths of a whorl, with eleven accessory traces: upper parietal quite high, slender, expanded above, weakly beaded on posterior third, with very sharp anterior descension; 2nd parietal about one-third height of 1st, weakly expanded and prominently beaded above posteriorly, with gradual descension to anterior threadlike five-eighths, that terminates opposite anterior end of upper parietal; 3rd parietal two-thirds height of 1st, expanded above and weakly beaded posteriorly, with gradual descension to anterior threadlike third; 4th parietal equal in height to 3rd, with more gradual descension anteriorly and much more elevated anterior portion. Parietal traces located two above upper parietal, one between 1st and 2nd, one between 2nd and 3rd, three between 3rd and 4th, and four between 4th and columellar-parietal margin. Upper parietal trace a slender, bladelike ridge, only slightly lower than 2nd parietal. Columellar barriers 2, lying parallel to plane of coiling and reaching lip edge, with one threadlike superior trace: 1st columellar moderately elevated, distinctly expanded and serrated above behind columellar callus, with gradual anterior descension; 2nd columellar much higher, equally expanded and serrated above posteriorly, with sharp anterior descension. Palatal barriers 4, extending posteriorly more than one-eighth whorl, with three accessory traces: 1st very high, expanded, weakly beaded above posteriorly with very sharp anterior descension to lip edge; 2nd and 3rd equal in height to 1st, expanded and weakly beaded above posteriorly, with progressively more gradual anterior descension; 4th palatal lying opposite parietal, greatly reduced in height, weakly expanded above, with sharp anterior descension almost to lip edge, much shorter than 3rd parietal, with very gradual posterior descension. Palatal traces located between 1st and 2nd, 2nd and 3rd, and 3rd and 4th palatals, with the first accessory trace being much lower and smaller than the upper two which are elevated V-shaped ridges. Height of holotype 1.81 mm., diameter 2.70 mm.

Holotype. — Tonga Islands: Eua Island, Station T-22, main ridge on east side at 1,000 ft. elevation in heavy primary forest. Collected by Laurie Price on January 31, 1966. FMNH 154784.

Range. — Eua Island, Tonga.

Paratypes. — FMNH 152377, BPBM

Material. — Tonga: Eua Island (Station T-22) 1,000 ft. elevation in heavy primary forest on east side of main range (49 specimens, FMNH 152377, FMNH 154784).

Remarks. — Only 29 of the 49 examples collected were adult, but no very young specimens were obtained. The following ideas concerning umbilical form were reached solely by careful inspection of shells with adult umbilical form. It is evident that in very young shells the umbilicus is distinctly wider than in adults, and that umbilical narrowing takes the same form as in the Marquesan *Taipidon semimarsupialis*, by inward growth of the entire last whorl coiling. As a result, the D/U ratio of *Thaumatodon euaensis* is much, much greater than in any other species of *Thaumatodon* (table CIX).

In general appearance, as well as in many details of sculpture and structure, *T. euaensis* is an obvious, close relative of the Samoan *T. hystricelloides*. The most significant differences between the two are covered above in the diagnosis. *T. vavauensis*, from Vavau Island, Tonga, is somewhat similar in appearance but differs by a number of features, including strength of ribbing, width of umbilicus, height of spire, number and relative size and length of apertural barriers. Relationships to *T. hystricelloides* seem to be much closer than those to *T. vavauensis*.

One specimen had a single, oblong egg resting just inside the umbilicus. No other examples showed indications of the umbilicus being used as a brood chamber.

Description of soft parts. — Foot and tail retracted into pallial cavity, when dissected all external features as in *T. hystricelloides*.

Body color faint yellow-white, no darker markings.

Mantle collar (MC) with thickened edge, no distinct lobes, large glandular extensions onto pallial roof (ripped by palatal barriers during dissection). Pneumostome typical. Anus (A) opening just inside pneumostome in normal position.

Pallial region (fig. 195a) extending five-eighths whorl apically, lung roof with broad bands of white granules flanking principal pulmonary vein and kidney, extending to apex of soft parts. Kidney (K) about 1.5 mm. long, bilobed, rectal arm almost half length of pericardial, base of kidney lying above intestinal loop. Ureter (KD) opening just anterior to rectal kidney arm termination. Heart (H) more than half length of kidney, nearly parallel to hindgut. Principal pulmonary vein (HV) slender, extending to glandular mantle lobe intrusions, without obvious branching. Hindgut typical.

Ovotestis (G) composed of multiple clumps palmately clavate alveoli along a simple collecting tubule, occupying full whorl above stomach reflexion. Hermaphroditic duct (fig. 195c, GD) narrow at first, becoming abruptly expanded, convoluted for a distance, then becoming straight, finally reflexing into bulb of carrefour. Albumen gland typical, surface dented by intestinal loops, an artifact introduced by contraction. Talon (GT) with a short, stubby shaft inserting on a bulbous carrefour. Prostate typical. Uterus extending past end of prostate, with same structure found in *T. hystricelloides*.

Vas deferens (fig. 195b, VD) contorted in region of peniovidical angle, an artifact of contraction. Epiphallus (E) about half length of penis, structure as in *Aaadonta constricta constricta* (fig. 199d).

Penial retractor (PR) arising from diaphragm, inserting on penis-epiphallus junction. Penis (P) about 1.0 mm. long (fig. 191a, P), twisted from contraction in available material, internally with one epiphallic pilaster fading out, other becoming grossly enlarged to form a stimulatory pilaster submedially that extends nearly to atrium. Atrium (Y) short.

Free oviduct (UV) with weak pilasters internally, much thicker-walled than uterus. Spermatheca (S) with expanded head lying next to base of albumen gland just at level of pallial cavity apex, slender shaft inserting on penial side of peniovidical angle. Vagina absent.

Free muscle system typical. Right ommatophoral retractor passing through peniovidical angle, tentacular retractors fuse midway to union with tail fan and buccal retractor at columellar insertion.

Digestive system as in *T. hystricelloides*.

Radula with more than 92 rows, central tooth about 8μ square, laterals 7, marginals more than 8.

(Based on FMNH 152377, four adult specimens.)

Thaumatodon vavauensis, new species. Figure 196a-c.

Patula (Endodonta) hystricelloides Mousson, 1871 (not Mousson, 1865), Jour. de Conchyl., 19, pp. 10-11 — Vavao, Tonga Islands (error in identification).

Diagnosis. — Shell small, diameter 2.40-3.14 mm. (mean 2.70 mm.), with 4¾-6 rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.568-0.634 (mean 0.610). Umbilicus open, U-shaped, regularly decoiling, contained 3.37-4.44 times (mean 3.85) in the diameter. Postnuclear sculpture of high, prominent, protractively sinuated, broadly rounded radial ribs, 48-67 (mean 57.5) on the body whorl, whose interstices are 1½-2 times their width. Microsculpture a lattice of fine radial riblets, five to eight between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Sutures impressed, whorls strongly rounded above and one basal margin, distinctly compressed laterally, with gently rounded outer margin. Aperture subovate, distinctly compressed laterally, inclined about 15° from shell axis. Parietal barriers 3, extending posteriorly more than three-sixteenths of a whorl, generally with four, sometimes only two or three accessory traces: upper high, thin, weakly expanded above, with five to six weak beads on top, gradually descending from anterior quarter to just before termination when descension becomes

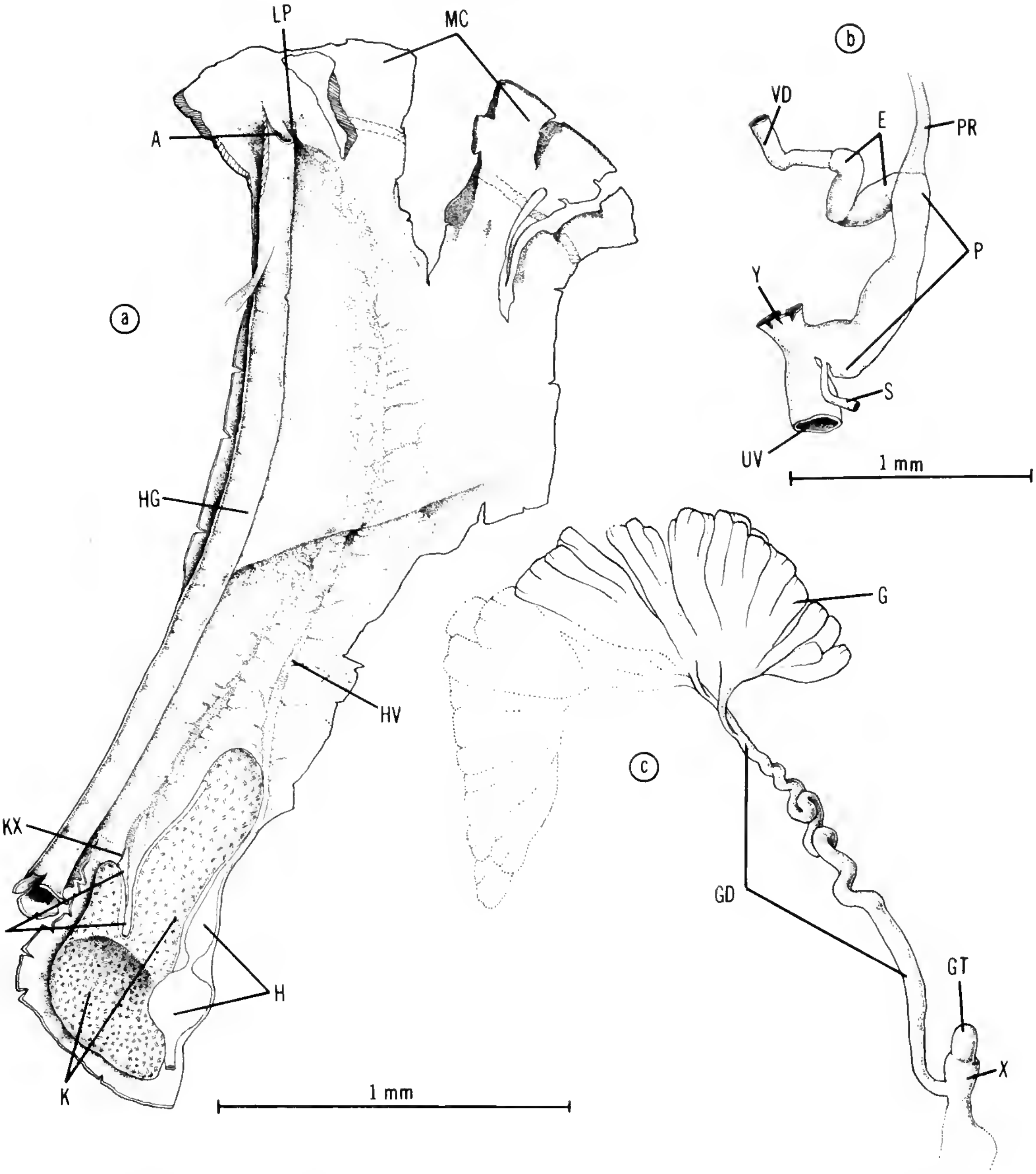

FIG. 195. Anatomy of *Thaumatodon euaensis*. Eua Island, Tonga. FMNH 152377: **a**, pallial region with mantle collar split by apertural lamellae during dissection; **b**, penial complex; **c**, detail of apical genitalia. Scale lines equal 1 mm.

sharp; 2nd slightly lower in height, beading even weaker, restricted to posterior half, with much more gradual anterior descension; 3rd slightly reduced in height from 2nd, beading on posterior half only, with gradual anterior descension to posterior of raised threadlike anterior quarter. Accessory traces generally located above upper, between each pair of major parietals, and between lower parietal and parietal-columellar margin. Columellar wall with 1 or 2 (usually) barriers: upper, when present, a small threadlike trace moderately to deeply recessed within aperture; lower varying from a raised threadlike ridge to moderately high barrier, lying parallel to plane of coiling, with sharp anterior descension to lip edge, rarely reduced and deeply recessed within aperture. Palatal barriers usually 3, sometimes more, extending posteriorly about three-sixteenths of a whorl, with two or three accessory traces: lower 2 high and bladelike, markedly expanded and beaded above, with sharp anterior descension to lip edge; 3rd supraperipheral in position, markedly reduced in height, weakly beaded above, with more gradual anterior descension; 4th palatal, when present, located between 1st and 2nd, equal in height; accessory traces normally between 1st and 2nd, 2nd and 3rd palatals, additional trace, when present, above upper palatal.

The greater H/D ratio, more projecting spire, much narrower umbilicus, and normal presence of 4 major parietal barriers at once distinguish *Thaumatodon euaensis* from the otherwise very similar *T. vavauensis*. The latter has a widely open umbilicus, rather depressed spire, and only 3 major parietals. The Samoan *T. hystricelloides* is much larger, more elevated, and always has 4 major parietals. All other *Thaumatodon* have very fine or reduced ribbing.

Description. — Shell small, with 4⅞ moderately tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.621. Embryonic whorls, 1⅜, with fine, rather widely spaced radial riblets and smaller, almost equally widely spaced spiral cords. Remaining whorls with heavy, protractively sinuated radial ribs, 64 on the body whorl, whose interstices are less than twice their width. Microsculpture of fine radial riblets, five to eight between each pair of major ribs, and much finer spiral riblets that are barely visible at 96× magnification.

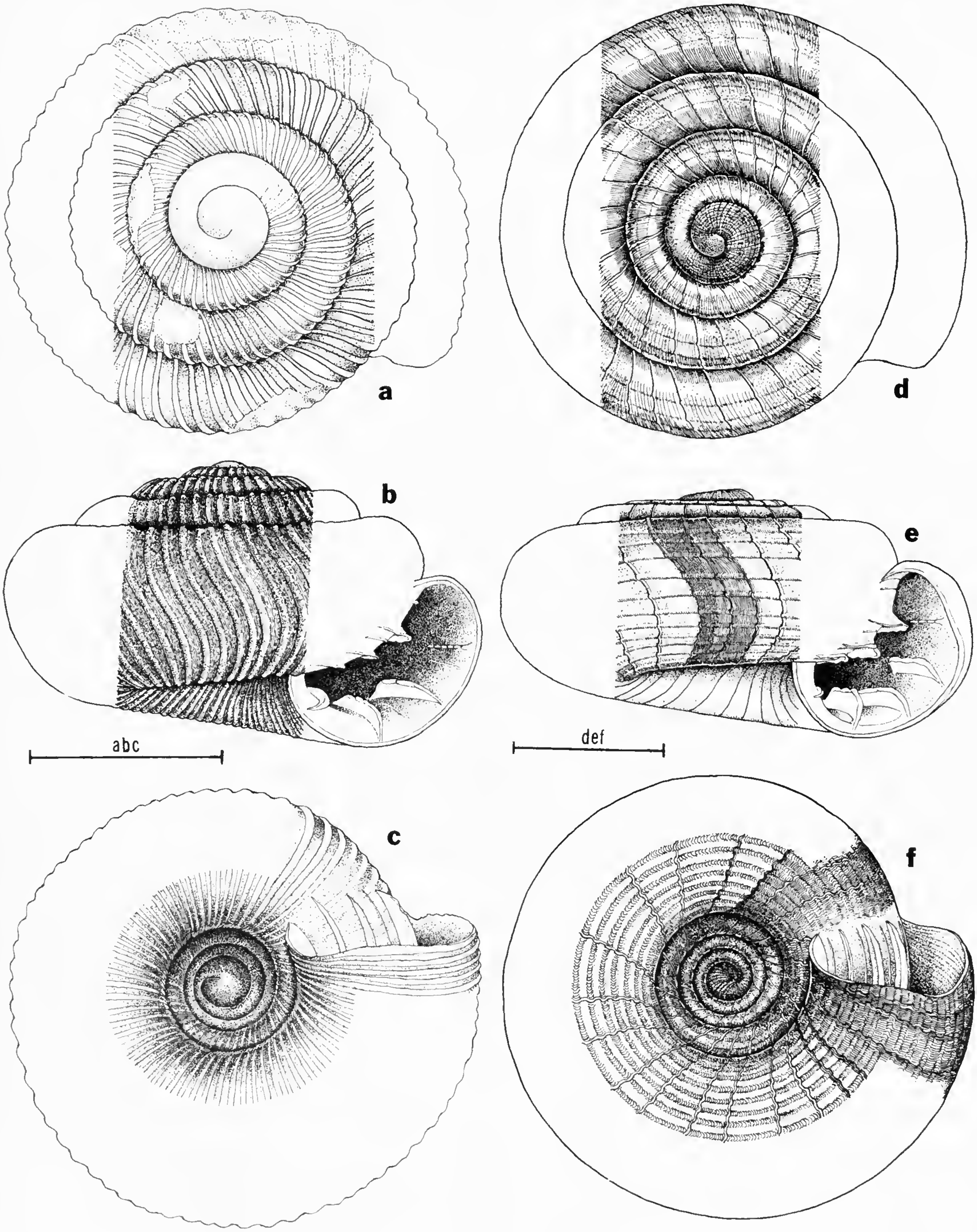

Fig. 196. **a-c,** *Thaumatodon vavauensis,* new species. Cliff near Holonga, Vavau Island, Tonga. Holotype. BPBM 87860; **d-f,** *Thaumatodon corrugata,* new species. Station 89, Mango Island, Lau Archipelago, Fiji. Holotype. BPBM 179940. Scale lines equal 1 mm. (MM).

Sutures moderately impressed, whorls strongly rounded above, flattened laterally. Umbilicus U-shaped, last whorl decoiling a little more rapidly, contained 4.11 times in the diameter. Aperture ovate, slightly compressed laterally, inclined about 15° from shell axis. Parietal barriers 3, extending posteriorly more than three-sixteenths of a whorl, plus two low accessory traces: upper high, bladelike, weakly expanded and beaded above on posterior two-thirds, with gradual anterior descension until just before termination; 2nd slightly reduced in height, more strongly expanded and beaded above on posterior half, with gradual anterior descension to termination just in front of upper parietal; 3rd parietal lower than 2nd, expanded and beaded above posteriorly, with anterior third a raised threadlike ridge. Accessory traces very low and inconspicuous, located above upper parietal, between 1st and 2nd parietals. Columellar barrier a high lamellar ridge, lying parallel to plane of coiling, expanded and beaded above posteriorly, with abrupt anterior descension to lip edge. Palatal barriers 3, extending posteriorly almost three-sixteenths of a whorl, with two accessory traces: lower palatal basal in position, very high, markedly beaded above on posterior half, with rather sharp anterior descension to lip edge; 2nd palatal equal in height to 1st, beaded above, with slightly more gradual anterior descension; 3rd palatal greatly reduced in height, weakly beaded above, with much more gradual anterior descension, situated almost opposite upper parietal. Accessory traces low and threadlike, located between 1st and 2nd, 2nd and 3rd palatals, deeply recessed. Height of holotype 1.51 mm., diameter 2.44 mm.

Holotype. — Tonga: Vavau, cliff on Liku or north side near Holonga at 200-350 ft. elevation. Collected by I. E. Hoffmeister on July 10, 1928. BPBM 87860.

Range. — Vavau, Tonga.

Paratypes. — Same as list of material.

Material. — Tonga: Vavau (1 specimen, Zurich 502971), near Toulo (Station T-8), 2 miles south of Neiafu (7 specimens, FMNH 152487); Leimatu'a (Station T-17), 9 miles north of Neiafu (1 specimen, FMNH 152329).

Remarks. — The single specimen reported by Mousson (1871, pp. 10-11) as *hystricelloides* was located in Zurich. It proved to be a somewhat abnormal specimen of the species described here, differing in possessing a 4th major palatal barrier and in having a much narrower umbilicus. In some respects it shows characters transitional to *Thaumatodon euaensis.*

Despite intensive collecting on Vavau Island in January of 1966, unfortunately during a period of drought, only eight subadult dead examples were obtained from leaf litter at two localities, north and south of Neiafu.

GROUP OF *Thaumatodon subdaedalea*

Thaumatodon subdaedalea (Mousson, 1870). Figure 197a-c.

Patula (Endodonta) subdaedalea Mousson, 1870, Jour. de Conchyl., **18**, pp. 117-118, pl. 7, fig. 6 — Mango Island, Fiji Islands.

Helix (Patula) subdaedalea (Mousson), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 258.

Pitys subdaedalea (Mousson), Garrett, 1887, Proc. Zool. Soc. London, **1887**, p. 179.

Helix (Endodonta) subdaedalea (Mousson), Tryon, 1887, Man. Conchol., (2), **3**, pp. 64-65, pl. 12, fig. 26.

Endodonta (Thaumatodon) subdaedalea (Mousson), Pilsbry, 1893, Man. Conchol., (2), **9**, p. 27; Gude, 1913, Proc. Malacol. Soc. London, **10**, (5), p. 330.

Endodonta (Thaumatodon) maupiensis (Garrett) var. *subdaedalea* (Mousson), Germain, 1932, Ann. Inst. Oceanol., **12**, (2), p. 45 (name only).

Diagnosis. — Shell larger than average, diameter 2.93-3.59 mm. (mean 3.20 mm.), with 4¾-5½ very tightly coiled whorls. Spire and apex moderately and evenly elevated, last whorl descending slightly, H/D ratio 0.489-0.544 (mean 0.509). Umbilicus broadly V-shaped, shouldered, slightly flattened inside, regularly decoiling, contained 2.66-3.58 times (mean 3.09) in the diameter. Sculpture usually of widely spaced, strongly protractively sinuated, fine radial ribs whose interstices are 3-8 times their width, often greatly reduced to indistinguishable on body whorl (about 44-55, if all were distinct). Microsculpture of fine radial riblets, crossed by much finer and more crowded spiral riblets, on spire eight to twelve radials between each pair of major ribs. Sutures deep, whorls strongly rounded above, flattened laterally and basally. Aperture subovate, flattened laterally and basally, inclined about 15° from shell axis. Parietal barriers 3, extending posteriorly slightly more than one-quarter whorl, usually with five, sometimes three or four, accessory traces: upper a high, bladelike ridge, expanded and with three widely spaced beads on posterior two-thirds, with gradual anterior descension; 2nd slightly reduced in height, beading larger and more widely spaced, with more gradual anterior descension, 3rd greatly reduced in height, beading widely spaced, with very gradual anterior descension. Accessory traces normally very low and thin, located above upper, one between each pair of barriers and two below 3rd parietal; lower trace intermediate in height between remaining traces and lowest parietal, not beaded above. Columellar barrier high and bladelike, slanting slightly downwards from plane of coiling, with gradual anterior descension to lip edge; plus a raised threadlike trace, weakly expanded and beaded above posteriorly, more deeply recessed within aperture. Palatal barriers 4, extending posteriorly three-sixteenths of a whorl, rarely with an accessory trace between 3rd and 4th palatals; lower basal in position, high, thin, expanded and with two or three large beads above, rather sharp descension to lip edge; 2nd and 3rd equal in height, usually with three beads above, with progressively more gradual anterior descension; 4th supraperipheral, greatly reduced in height, much longer, with more gradual anterior descension and deeper recession.

The large size, much finer and more widely spaced sculpture, and wide umbilicus readily separate *Thaumatodon subdaedalea* from *T. decemplicata. T. corrugata* from Mango Island differs slightly in size and proportion (table CIX), possesses strong spiral cording on the shell (fig. 196d) and has the microradial ribs much finer and more lamellate. The beading on the apertural barriers is much weaker in *T. subdaedalea* than in other species of *Thaumatodon.*

Description. — Shell slightly larger than average with 5½ very tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending a little more rapidly, H/D ratio 0.536. Embryonic whorls 1⅜, sculpture of narrow, widely spaced, rounded radial ribs, becoming more crowded near the end, crossed by fine, relatively crowded spiral riblets. Postnuclear whorls with low, gently rounded, broad, protractively sinuated radial ribs, whose interstices are 3-6 times their width, that become indistinguishable on latter part of body whorl. Microsculpture a lattice of very fine radial riblets crossed by even finer and much more crowded spiral riblets. Sutures deep, whorls strongly rounded above, somewhat compressed laterally and on basal margin. Umbilicus broadly V-shaped, regularly decoiling, margins weakly shouldered, whorls flattened inside, contained 3.26 times in the diameter. Color light reddish-yellow-brown, without darker maculations. Aperture elongately ovate, compressed laterally, with evenly rounded outer and basal margin, inclined about 15° from shell axis. Parietal barriers 3, extending

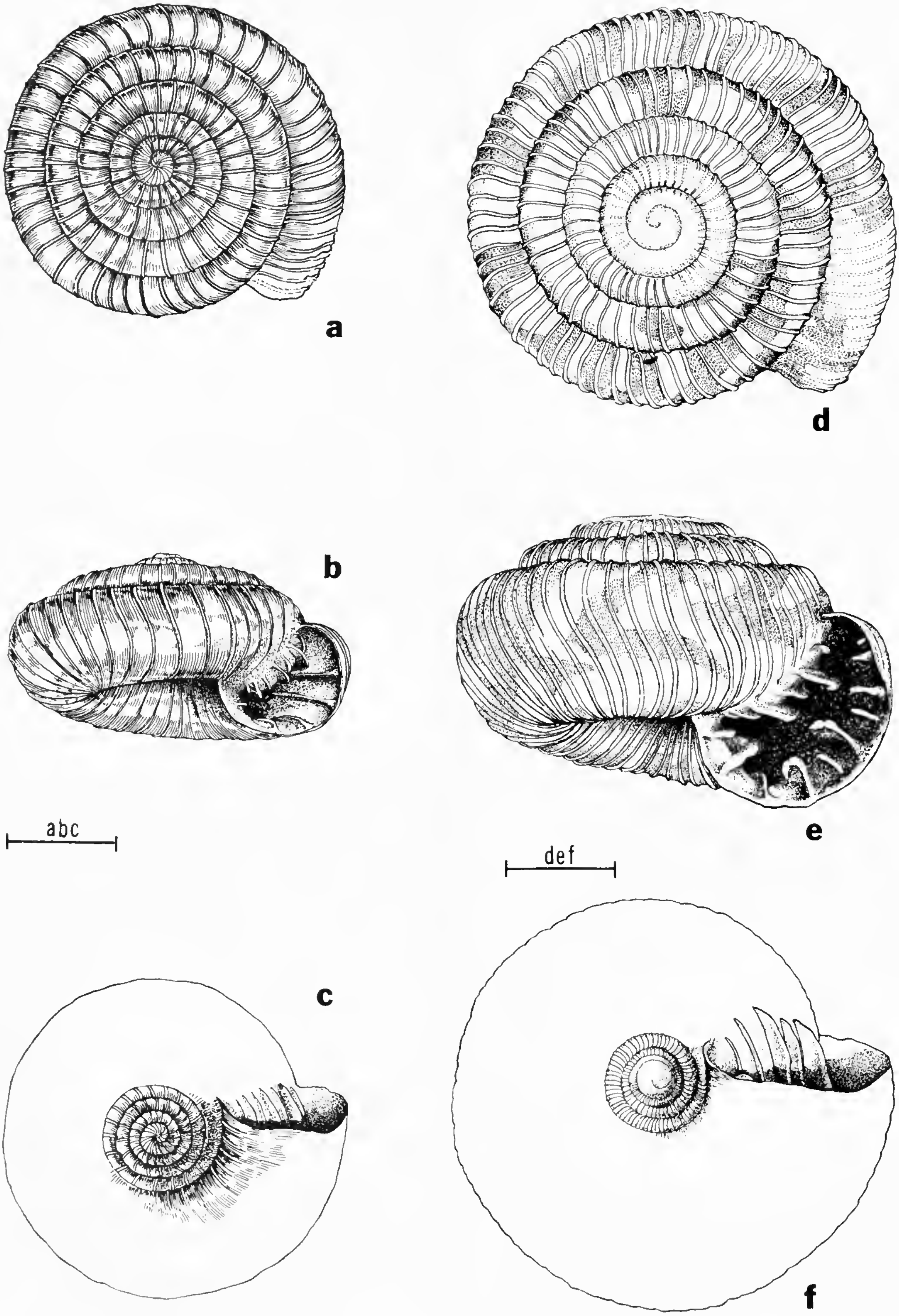

FIG. 197. **a-c**, *Thaumatodon subdaedalea* (Mousson). Mango Island, Lau Archipelago, Fiji. Lectotype. Zurich 502974; **d-f**, *Thaumatodon hystricelloides* (Mousson). Upolu, Western Samoa. Paratype. Zurich 502958. Scale lines equal 1 mm. (SG).

slightly over one-quarter whorl, with five accessory traces: major parietals high, bladelike, slightly expanded above, upper with four narrow beads on posterior two-thirds and relatively sharp anterior descension, middle with less distinct beading and more gradual anterior descension, lower much reduced in height with two weak beads above. Two accessory traces located below lowest parietal, one between 2nd and 3rd, another between 1st and 2nd, and one above 1st parietal. Columellar barrier a narrow, bladelike ridge, almost parallel to shell axis, reaching lip margin. Palatal barriers 4, extending almost one-quarter whorl posteriorly, first 3 almost equal in size, reaching lip margin, moderately expanded above with three very weak, regularly spaced beads. Upper parietal a lower V-shaped ridge, very weakly and irregularly beaded above posteriorly, slightly recessed from apertural margin. Height of lectotype 1.69 mm., diameter 3.16 mm.

Lectotype. — Fiji: Lau Group, Mango Island. Collected by E. Graeffe. Zurich 502974.

Range. — Mango, Vanua Mbalavu and Kimbombo Islands, Lau Archipelago, Fiji.

Paratypes. — Zurich (2 specimens, Zurich 502974).

Material. — Fiji: Mango Island (Zurich, 3 specimens), one-half mile southeast (Station 88) of Marona at 200 ft. elevation, one-half mile inland (5 specimens, BPBM 179912). Vanua Mbalavu (Station 95) at 1-200 ft. elevation (4 specimens, BPBM 179839); northwest coast (Station F-8) on limestone outcrops in heavy forest (2 specimens, FMNH 168144, collected October 3, 1970 by L. Price). Kimbombo, east islet, 100 yd. inland at 50-150 ft. elevation in leaf mold (9 specimens, BPBM 79102).

Remarks. — The specimens from Vanua Mbalavu cannot be distinguished from those found on Mango. Only two of the Kimbombo specimens were adult. They are distinctly, but slightly, higher spired than the Mango shells collected about the same time, although the lectotype of *T. subdaedalea* is higher than the Mango Island topotypes in the Bishop Museum. The differences are not large enough to be significant and the apertural barriers and ribbing are identical. One juvenile specimen from Kimbombo (BPBM 79078) had the radial sculpture reduced to microriblets only.

Development of a second, closely related species on Mango, *Thaumatodon corrugata*, was a surprising discovery since *T. subdaedalea* has been found on other islands of the Lau Group. *T. corrugata* differs most obviously in the possession of marked spiral cording on the body whorl (fig. 196d-e), but also is distinctly smaller, with slightly fewer whorls, a narrower umbilicus, and an insignificantly higher spire in adult shells (table CIX, CX). Since both species were collected on the same day and by the same collector (Yoshio Kondo, August 14, 1938), there is no question of yearly climatic conditions having produced a dwarf population. The differences in size and umbilical proportion undoubtedly are correlated, so these represent one factor rather than two in separating the species.

Thaumatodon corrugata, new species. Figure 196d-e.

Diagnosis. — Shell of average size, diameter 2.81-3.04 mm. (mean 2.97 mm.), with 4¾-5⅛ tightly coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.500-0.540 (mean 0.518). Umbilicus broadly V-shaped, regularly decoiling, contained 3.07-3.54 times (mean 3.30) in the diameter. Major sculpture of very widely spaced, protractively sinuated, low, irregular radial ribs crossed by evenly spaced, very strong spiral cords that become slightly reduced on the upper part of the whorls. Microsculpture of fine radial riblets crossed by much finer and more crowded spiral riblets, spacing obscured by irregularity of major radials. Sutures deeply impressed, whorls strongly rounded above, flattened laterally above periphery and basally. Aperture subovate, flattened laterally, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly more than one-quarter whorl, with four or five accessory traces: upper a very high, thin blade, expanded and with four or five prominent beads above on posterior two-thirds, with rather gradual anterior descension; 2nd equal in height posteriorly, usually with four beads above on posterior half, with more gradual anterior descension; 3rd greatly reduced in height, with very weak beading and quite gradual anterior descension. Accessory traces located above upper parietal, one between each pair and one or two below 3rd parietal. Columellar barrier a low lamellar blade, slanting slightly downward from plane of coiling, with gradual anterior descension almost to lip edge. Palatal barriers 4, extending posteriorly three-sixteenths of a whorl: lower basal in position, high, bladelike, expanded and with two beads above, with rather sharp descension to lip edge; 2nd and 3rd equal in height and beading to 1st, with progressively more gradual anterior descension; 4th supraperipheral, much lower, with narrow, elongated beads and very gradual anterior descension, more deeply recessed within aperture.

The strong spiral cording, more reduced sculpture, stronger beading, and small columellar barrier easily separate *T. corrugata* from its very close relative, *T. subdaedalea*. The Tongan species, *T. vavauensis* and *T. euaensis*, have much wider and stronger ribbing on the spire, are much higher and have narrower umbilici.

Description. — Shell of average size, with 5 very tightly coiled whorls. Apex and spire evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.511. Embryonic whorls 1⅜, sculpture of widely spaced microradial riblets with spiral sculpture of much lower and more closely spaced spiral riblets. Remaining whorls with irregularly lamellate, very widely spaced, protractive radial ribs, becoming greatly reduced to indistinguishable on body whorl with secondary sculpture of strong spiral cords that are very prominent on base and sides but slightly reduced above. Microsculpture of extremely fine, somewhat lamellate, irregularly sinuated radial riblets, about 15-20 between the major rib traces. Sutures deeply impressed, whorls strongly rounded above, slightly flattened laterally above the periphery and basally. Umbilicus broadly V-shaped, contained 3.07 times in the diameter, with slightly shouldered margin. Color light yellowish-red with irregular, slightly darker reddish markings. Aperture ovate, compressed above periphery and basally, inclined about 5° from shell axis. Parietal barriers 3, with five accessory threadlike traces, all extending more than one-quarter whorl. Upper 2 parietals high and lamellate for nearly entire length with three subequal swollen beads on top. The beads are minutely serrated. Lower parietal much reduced in height with two smaller beads above. Columellar barrier thin, low, nearly parallel to plane of coiling with very fine swollen beading above posteriorly. Palatal barriers 4, extending slightly less than three-sixteenths of a whorl: lower 3 high and bladelike, with three irregularly spaced, swollen and serrated beads above; upper palatal slightly recessed, a low V-shaped ridge with two slight beads evident above. Columellar and lower palatal barriers reaching apertural margin. Height of holotype 1.55 mm., diameter 3.13 mm.

Holotype. — Fiji: Lau Archipelago, Mango Island, Station 89, one-half to three-quarters mile south-southwest of Marona at 350-400 ft. elevation. Collected by Yoshio Kondo on August 14, 1938. BPBM 179940.

Range. — Known only from Mango Island, Lau Archipelago, Fiji.

Paratypes. — Same as list of material.

Material. — Mango Island, one-half to 1 mile south-southwest of Marona (Stations 89, 90, 94) at 200-400 ft. elevation (5 specimens, BPBM 179940, BPBM 179987, BPBM 180066).

Remarks. — No individuals at all intermediate in sculpture between *T. subdaedalea* and *T. corrugata* were seen. The former was collected southeast of Marona at 200 ft. elevation, while *corrugata* was found south-southwest of Marona at 200-400 ft. elevation. The difference in sculpturing is absolute, and the differences in proportion are significantly large. Comparing just the adult material of *T. subdaedalea* collected in 1934 from Vanua Mbalavu, Kimbombo, and Mango, 5 specimens, with the adults of *T. corrugata*, 5 specimens, there are 8 df (table CX). The samples are different at the 0.05 per cent probability level for diameter ("*t*" = 5.0676), the 2.5 per cent probability level for D/U ratio ("*t*" = 2.65689) and not significantly different ("*t*" = 1.7537) for H/D ratio.

I have chosen to consider *corrugata* a distinct species, rather than a subspecies.

Thaumatodon laddi, new species. Figure 193d-f.

Diagnosis. — Shell very small, diameter 1.99-2.38 mm. (mean 2.15 mm.), with 3⅞-4¼ moderately tightly coiled whorls. Apex flat, spire barely elevated, last whorl descending much more rapidly, H/D ratio 0.483-0.538 (mean 0.513). Umbilicus broadly open, V-shaped, only slightly decoiling, margins weakly shouldered, contained 3.13-3.61 times (mean 3.35) in the diameter. Postnuclear sculpture of very fine, protractively sinuated, broadly rounded radial ribs, about 180-210 on the body whorl, whose interstices are 1-3 times their width, coalescing partly on last portion of body whorl. Microsculpture of very fine radial riblets, one to two between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above and on basal margin, compressed laterally. Aperture ovate, slightly to moderately compressed laterally, inclined less than 10° from shell axis. Parietal barriers 4, extending posteriorly one-quarter whorl, usually with three, rarely four, accessory traces: upper high and thin, with three or four very large beads above on posterior half to two-thirds, weakly expanded, with sharp anterior descension; 2nd a very low trace with remnants of beading above, terminating anteriorly slightly in front of upper; 3rd parietal equal in height to 1st posteriorly, three large beads above, with rather gradual anterior descension; 4th parietal intermediate in height between 2nd and 3rd, strongly beaded above on posterior half, with anterior third a low, raised lamella. Accessory traces located above upper and below lower parietal, usually with one trace between 3rd and 4th, occasionally one between 1st and 2nd. Columellar barrier a raised lamellar ridge, lying parallel to plane of coiling, with gradual anterior descension midway across columellar callus. Palatal barriers 4, extending posteriorly three-sixteenths of a whorl, with zero to two accessory traces: lower at baso-columellar margin, high and thin, with three or four beads above on posterior four-fifths, with abrupt descension to lip edge; 2nd almost identical to 1st; 3rd with more gradual anterior descension; 4th lying almost opposite upper parietal, reduced in height and beading prominence, with rather sharp anterior descension. Occasionally, one accessory trace is present between the 1st and 2nd, then 2nd and 3rd palatals.

The very small size, prominent beading on the barriers and very crowded, rather irregular ribbing identify this species. *Thaumatodon corrugata* and *T. subdaedalea* have the 2nd parietal replaced by a threadlike trace, the 1st palatal not at the baso-columellar margin, very widely spaced ribbing on the spire and are much larger. All other *Thaumatodon* have much coarser ribbing and differ in barrier structure details.

Description. — Shell very small, with 4¼ relatively tightly coiled whorls. Apex flat, lower whorls of spire descending slightly, last whorl rather rapidly, H/D ratio 0.528. Apical whorls 1⅝, sculpture of widely spaced radial ribs with equally widely spaced spiral threads present. Lower whorls with vague, irregular, rounded, protractive radial ribs that sometimes coalesce, about 150 on first three-quarters of body whorl, irregular on remaining portion. Microsculpture a fine microlattice structure visible only under very high magnification, with one or two radial riblets between each pair of major ribs. Sutures moderately impressed, whorls rounded above, slightly flattened above periphery and on lower basal margin. Umbilicus broadly open, V-shaped, margins slightly shouldered, contained 3.13 times in the diameter. Color light reddish-yellow. Aperture ovate, slightly flattened above periphery and on lower basal margin, inclined less than 10° from shell axis. Major parietal barriers 4, extending one-quarter whorl, numbers 2 and 4 reduced in height, with four accessory threads. Upper parietal high and lamellate with four widely spaced, minute but bulbous beads above; 2nd parietal very much lower with two tiny beads posteriorly; 3rd parietal equal in height to 1st with three globosely swollen beads posteriorly; 4th parietal distinctly higher and with much more prominent beading than 2nd. One large and one very fine trace above 1st parietal, third trace between 3rd and 4th parietal, fourth trace below 4th parietal. Columellar barrier a low, threadlike trace, parallel to plane of coiling, reaching midway across columellar callus. Palatal barriers 4, extending posteriorly three-sixteenths of a whorl, with two accessory traces: lower at baso-columellar margin, weakly expanded above, with three prominent beads on posterior half, with abrupt anterior descension to lip edge; 2nd and 3rd equal in height to 1st, beading much more bulbous, with more gradual anterior descension; 4th supraperipheral, markedly reduced in height, with five slender beads on posterior four-fifths, with rather sharp anterior descension. Accessory trace located between 1st and 2nd palatals, large and faintly beaded posteriorly; trace between 2nd and 3rd very small (omitted from type figure). Height of holotype 1.25 mm., diameter 2.37 mm.

Holotype. — Fiji: Wangava Island, Station 27, northeast end, one-quarter mile inland at 75 ft. elevation. Collected by H. S. Ladd on July 22, 1934. BPBM 166966.

Range. — Wangava Island, Lau Archipelago, Fiji.

Paratypes. — BPBM 166966 (17 specimens), FMNH 168093 and FMNH 168095 (47 specimens).

Material. — Fiji: Wangava Island, northeast end, one-quarter mile inland (Station 27) at 75 ft. elevation (18 specimens, BPBM 166966); north end (Station F-4) at 100 ft. elevation (47 specimens, FMNH 168093, FMNH 168095, collected September 30, 1970 by L. Price).

Remarks. — The beading on the apertural barriers is proportionately more bulbous than in any other known species of *Thaumatodon*. All the 1934 specimens were collected dead among leaf mould in a pocket of coral rock. The 1970 specimens were collected alive under limestone blocks in heavy forest.

In possessing a slightly shouldered open umbilicus and in having reduced radial sculpture, *T. laddi* is very similar to *T. corrugata* and *T. subdaedalea*, also from the Lau Archipelago. In both of the latter species the 2nd parietal is represented by a low threadlike trace, and the "3rd" and "4th" parietals of typical *Thaumatodon* are the 2nd and 3rd in these species. *T. laddi* has the 2nd parietal retaining posterior beading (although greatly reduced in height) and the 1st palatal moved to the baso-columellar margin. The columellar barrier is reduced to a recessed, threadlike trace. The fine crowded sculpture and much smaller size of *T. laddi* also serve to differentiate it from the other Lau Archipelago species.

Great pleasure is taken in naming this species after Harry L. Ladd, long-time student of Pacific geology and discoverer and describer of the very important fossil endodontoids from the deep core drillings on Bikini, Eniwetok and Funafuti.

Thaumatodon spirrhymatum Solem, 1973

Thaumatodon spirrhymatum Solem, 1973, Veliger, **16**, (1), pp. 25-30, figs. 1, 10-15, 17,*b*, 18, 21 – Thithia Island, Lau Archipelago, Fiji.

Diagnosis. – Shell large for genus, diameter 2.96-3.45 mm. (mean 3.23 mm.), with 4½-5⅜ normally coiled whorls. H/D ratio 0.441-0.564 (mean 0.494), apex and early spire usually flat. Umbilicus broadly open, V-shaped, regularly decoiling, contained 3.17-3.92 times (mean 3.53) in the diameter. Sculpture typical, body whorl ribs thickened, becoming obsolete near aperture, major ribs 66-120 (mean 81.3) on body whorl. Periphery bikeeled, with both a sharply angled supraperipheral and protruded threadlike peripheral. Parietal barriers 4, extending posteriorly beyond line of vision, with four or five accessory traces. Columellar barriers 2, lying parallel to plane of coiling. Palatal barriers 4, extending posteriorly three-sixteenths of a whorl, with three or four accessory traces. All major barriers beaded above.

Thaumatodon spirrhymatum has a bikeeled body whorl, relatively flat spire, and somewhat enlarged sculpture. *T. subdaedalea* (Mousson, 1870) and *T. corrugata* are similar in general appearance, but lack the peripheral keeling and have very different sculpture. *T. laddi* has much finer sculpture and also a rounded periphery. Extralimital species differ in many and obvious features, except for the Hawaiian *Cookeconcha stellulus* (fig. 93), which differs in size, sculpture, and apertural barriers, although having very similar keeling pattern.

Holotype. – Fiji: Lau Archipelago, Thithia Island, Station F-9, under rotting wood in deep forest on limestone blocks, near Taruka Village on northwest part of island at 10-100 ft. elevation. FMNH 176001.

Paratypes. – FMNH 168221 (36 specimens).

Remarks. – Full descriptive information on shell and anatomy, plus illustrations are presented in Solem (1973d). The keeling is immediately diagnostic when combined with the retention of relatively normal ribbing. *Priceconcha* and *Zyzzyxdonta* also have keeled peripheries, but in the former the whorl count has increased dramatically and the sculpture is virtually absent, while in the latter, the peripheral ribs are extended into "winglike" structures. These are not duplicated elsewhere in the family.

Genus **Priceconcha** Solem, 1973

Veliger, **16**, (1), pp. 20-21.

Endodontidae in which the major radial sculpture has been lost, microsculpture absent on spire and greatly reduced on body whorl. Shell larger than average, whorl count increased to about 7⅜. Apex and spire strongly and almost evenly elevated, slightly rounded above, H/D ratio about 0.555. Umbilicus broadly V-shaped, regularly decoiling, contained about 2.90 times in the diameter, margins strongly rounded. Periphery with strong, threadlike keel. Parietal barriers 5, with ten or eleven accessory traces, extending more than one whorl posteriorly. Columellar barriers 2, with two accessory traces. Palatal barriers 5, with four or five accessory traces. All major barriers beaded above. Radular structure typical of family. Genitalia with penial insertion of spermathecal shaft, epiphallic zone in penis, and elongation of vas deferens-free oviduct zone. Pallial organs narrowed and elongated as adjustments to space problems.

Type species. – *Priceconcha tuvuthaensis* Solem, 1973.

Priceconcha was collected on tree trunks and thus represents at least a semi-arboreal taxon in a normally strictly terrestrial family. *Libera bursatella* has been found in the axils of *Freycinetia* on Tahiti, and some *Cookeconcha* occur in moss on tree trunks, but otherwise the family is terrestrial.

Conchologically, *Priceconcha* is distinguished by its great degree of sculpture reduction, drastically increased whorl count, extremely long parietal barriers, and peripheral keel. The sculpture reduction occurred despite the relatively small size of the shell and probably correlates with the habitat shift. In the field and during first sorting, this species was thought to be a very small trochomorphid, an indication of the atypical shell form and appearance. Anatomically, *Priceconcha* agrees with the *Thaumatodon-Aaadonta* pattern except for changes correlated with the greatly increased whorl count. Full discussion of these changes is given in Solem (1973d) and is not repeated here.

Priceconcha tuvuthaensis Solem, 1973

Priceconcha tuvuthaensis Solem, 1973, Veliger, **16**, (1), pp. 20-25, figs. 2-9, 16, 17, *a*, 19-20 – Tuvutha Island, Lau Archipelago, Fiji.

Diagnosis. – Shell larger than average, diameter 4.05-4.54 mm. (mean 4.29 mm.), with 7⅛+ to 7⅝ very tightly coiled whorls. Apex and spire strongly elevated, H/D ratio 0.528-0.587 (mean 0.558). Umbilicus broadly V-shaped, regularly and evenly decoiling, contained 2.73-3.07 times (mean 2.90) in the diameter. Shell surface smooth, except for traces of microreticulations on last two whorls and faint growth striae. Periphery with a strong protruding keel. Parietal barriers 4, extending posteriorly more than one whorl, with ten or eleven accessory traces. Columellar barriers 2, lying parallel to plane of coiling, with two accessory traces. Palatal barriers 5, extending posteriorly more than one whorl, with three or four accessory traces. All major barriers beaded above.

The high whorl count, lack of sculpture, high spire, peripheral keel, and very long beaded barriers separate *Priceconcha tuvuthaensis* from any *Thaumatodon* and the other Lau endemic, *Zyzzyxdonta*. The larger Society Islands *Nesodiscus* are quite similar in overall appearance, but differ in size, anatomy, reduction of apertural barriers, and origin.

Holotype. — Fiji: Lau Archipelago, Tuvutha Island, west coast in heavy forest at 100 ft. elevation. Collected on tree trunks during wet spell by Laurie Price on October 2, 1970. FMNH 168131.

Paratypes. — FMNH 168136 (2 specimens).

Remarks. — Illustrations of shell, radula, and anatomy were given in Solem (1973d) and are not repeated here. The large (5.6-7.6 mm.) *Nesodiscus* with equivalently reduced sculpture, *N. cretaceus,* and *N. fabrefactus,* are very similar in general appearance, but differ both in barrier features and much wider umbilici.

Genus **Zyzzyxdonta,** new genus

Endodontidae with typical apical sculpture, postnuclear whorls with widely spaced radial ribs protruded into hollow, winglike structures (fig. 198c) at the carinated periphery. Whorls about 5, rather loosely coiled, apex flat, spire slightly elevated. Body whorl with protruded, keeled periphery, not descending more rapidly, with distinct subperipheral sulcus. Umbilicus widely open, U-shaped, last whorl not decoiling as rapidly. Apertural barriers consisting of 3 parietals, a single columellar that slants downwards, and 3 long palatals. All barriers with large, swollen and serrated beads above. Anatomy unknown.

Type species. — *Zyzzyxdonta alata*, new species.

The beaded apertural barriers and general appearance of the microsculpture indicate affinity to *Thaumatodon* and *Aaadonta*. The extremely depressed form (table CIX), sharply protruded periphery, and peculiar development of the remaining radial ribs into winglike protrusions immediately separate *Zyzzyxdonta alata* from both genera. In the exact form of the barriers and umbilicus, *Z. alata* is much more similar to *Thaumatodon* than to *Aaadonta*. Unquestionably, it is a local derivative of *Thaumatodon,* but the morphological gap is large enough to demand generic separation. *Priceconcha* also is keeled, but in a different way and has very different sculpture.

Species of the genus *Aaadonta* represent the extreme development of fine sculpture and have the westernmost range of existing Endodontidae. The single known species of *Zyzzyxdonta* represents the extreme gross sculptural development within the family and is at the southwestern fringe of distribution. It was thought appropriate that their names be as widely separated as their sculpture.

Zyzzyxdonta alata, new species. Figure 198a-c.

Diagnosis. — Shell slightly larger than average, diameter 3.62-4.34 mm. (mean 4.03 mm.), with 4½-5 relatively loosely coiled whorls. Apex and spire flat, lower whorls descending moderately, last whorl not descending more rapidly, H/D ratio 0.368-0.427 (mean 0.379).

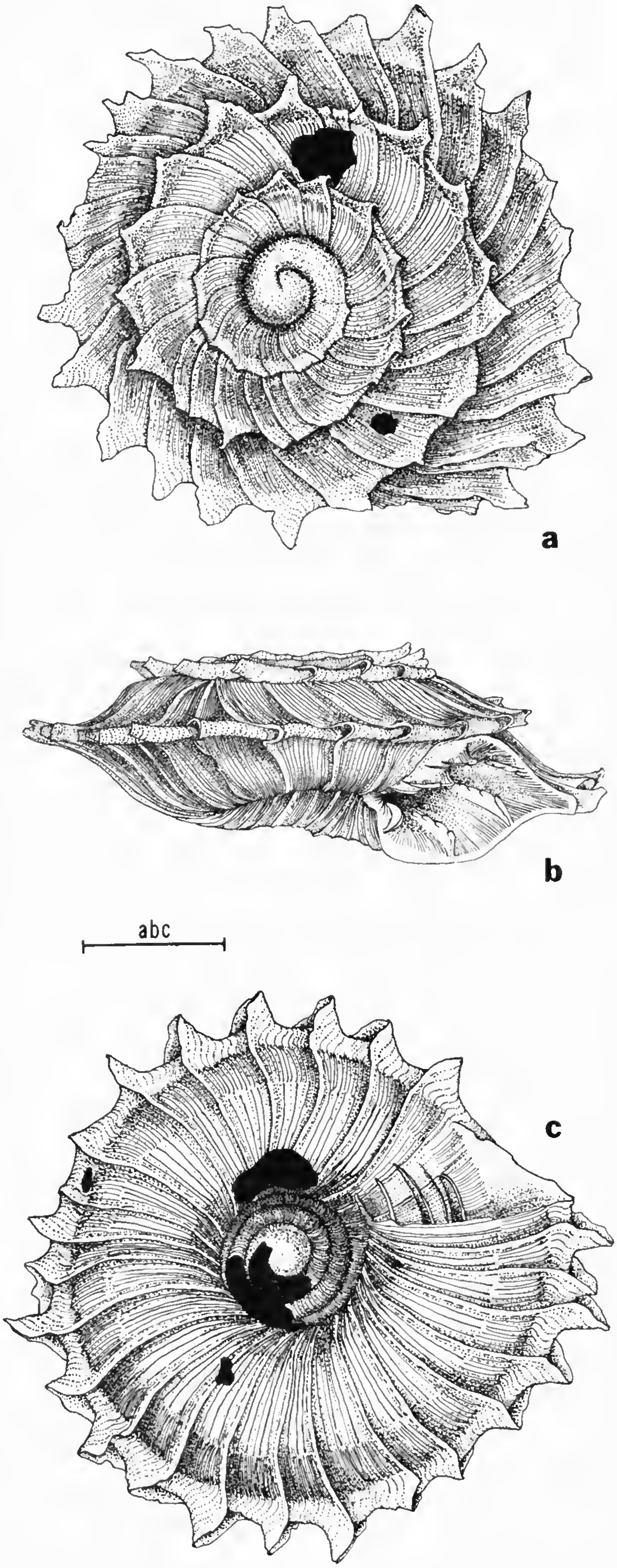

FIG. 198. **a-c**, *Zyzzyxdonta alata*, new species. Northeast quarter of Navutu-I-Loma, Yangasa Cluster, Lau Archipelago, Fiji. Holotype. BPBM 167018. Scale line equals 1 mm. (MM).

Umbilicus broadly open, U-shaped, somewhat contracted by tighter coiling of last whorl, contained 3.28-4.37 times (mean 3.72) in the diameter. Whorls sharply angulated, ribs on angulation protruding into hollow, winglike structures (fig. 198), varying in number from 21-27 on body whorl. Sculpture of fine radial riblets with a few stronger ribs becoming protruded into the hollow winglike structures at the periphery. Sutures hidden by extended wings, whorls flat down to strongly protruded periphery, with evenly rounded basal margin to shouldered umbilicus. Aperture subquadrangular, with strongly protruded periphery, inclined about 30° from shell axis. Parietal barriers 3, extending posteriorly to line of vision: upper high, thin, expanded and with five or six prominent beads above on posterior three-quarters, with gradual anterior descension from end of beaded portion; 2nd and 3rd progressively slightly lower, with finer beading, and more gradual anterior descension. Usually with an accessory trace, moderately recessed, between 1st and 2nd parietals. Columellar barrier moderately elevated, bladelike, expanded above and weakly beaded posteriorly, slanted down from plane of coiling, with gradual anterior descension almost to lip edge. Palatal barriers 3, extending posteriorly one-quarter whorl: lower 2 subperipheral, equal in height, with four or five prominent beads above, with sharp descension to lip edge; 3rd supraperipheral, greatly reduced in height and length, moderately recessed, with less conspicuous beading above.

Protrusion of the major ribs into winglike hollow extensions on the periphery is unique to *Zyzzyxdonta alata* among the known endodontids. The character of the apertural barriers, with the major ribs strongly beaded above, relates *Z. alata* to *Thaumatodon,* but the very depressed shape, carinated periphery, and peculiar rib structure are diagnostic.

Description. — Shell relatively large, with 4½ rather loosely coiled whorls. Apex flattened, slightly depressed below plane of winged rib extensions, lower whorls descending slightly, H/D ratio 0.382. Embryonic whorls 1½, sculpture reduced in prominence, consisting of very inconspicuous, quite widely spaced radial riblets with a few, even more widely spaced, much lower spiral cords. Lower whorls with very fine radial growth striae and a few widely spaced major ribs, 23 on the body whorl, that become protruded into winged, cuplike structures at the periphery. Under 96× magnification a vague microspiral sculpture is barely visible. Sutures shallow, margined above by peripheral keel surmounted by rib extensions. Umbilicus widely open, slightly contracted by coiling of last whorl, U-shaped, contained 4.37 times in diameter, with relatively sharply rounded margin. Aperture roughly subquadrangular, with rostrate lateral extension. Parietal barriers 3, extending posteriorly to line of vision: upper parietal quite high and lamellate with four large, regularly spaced, equal-size beads above; 2nd parietal almost equal in height, anterior portion slightly lower, with three regularly spaced and shaped beads above; 3rd parietal a moderately high threadlike ridge with only vague superior beading. Columellar barrier thin, high, slanting slightly downward across columellar callus, reaching apertural margin, with weak indications of posterior beading. Palatal barriers 3, long, extending one-quarter whorl: lower 2 high lamellae, relatively thin, with five regularly spaced beads above, reaching apertural margin with very rapid anterior descension, subperipheral in position; 3rd palatal a narrower, much lower ridge with five thin beads above, supraperipheral in position. Height of holotype 1.65 mm., diameter 4.31 mm.

Holotype. — Fiji: Lau Archipelago, Yangasa cluster, Navutu-i-Loma, Station 28, northeast quarter of island on a limestone outcrop, 150 yards inland at 100 ft. elevation. Collected by H. S. Ladd on July 24, 1934. BPBM 167018.

Range. — Navutu-i-Loma, Yangasa cluster, southeast Lau Archipelago, Fiji.

Paratypes. — Same as list of material.

Material. — Fiji: Lau Group, Navutu-i-Loma, northeast quarter of island (Station 28), 150 yd. inland, at 100 ft. elevation (7 specimens, BPBM 167018, USNM 664707, BPBM 167054); Station F-2 at 50-100 ft. elevation (1 specimen, FMNH 168061) collected September 28, 1970 by L. Price).

Remarks. — At first glance, the carinated body whorl and the very peculiar winged extensions of the major ribs would suggest that *Z. alata* is a very isolated species. The character of the apertural barriers, however, immediately related it to *Thaumatodon.* The parietal trace probably is a remnant of the 4th parietal found in many *Thaumatodon.* Barrier placement and umbilical shape are much as in the *subdaedalea* group, but the shell form and ribbing are so distinctive that generic separation is warranted. Unfortunately, no live material of this very unusual species was collected.

There is a superficial similarity to the much larger (diameter about 9 mm.) trochomorphid snail, *Kondoa asteriscus* (H. B. Baker, 1941, p. 272, pl. 65, figs. 13 - 15) from Truk, Caroline Islands. This species has the carinated periphery studded with solid triangular projections that do not originate from radial ribs, while in *T. alata* the winglike projections are hollow extensions of a few radial ribs.

Other Endodontidae with strongly protruded peripheries include the Austral Islands *Australdonta magnasulcata* (fig. 127a-c) and the Hawaiian *Cookeconcha stellulus* (Gould) (fig. 93a-c). The former does not have extraordinary rib enlargement, but in the latter species the major ribs are greatly reduced in number and very high.

Genus **Aaadonta,** new genus

Endodontidae in which the apical and postapical major radial sculpture is absent. Apex with about 20 fine and squiggly spiral cords, secondary radial irregularities near end of nuclear growth. Postnuclear sculpture of fine radial riblets with varyingly prominent lateral beads arranged in spiral series that represent continuations of the apical spirals and appear as secondary spiral cords. Apex and spire usually markedly elevated (flat in *kinlochi*), normally spire protrusion two-thirds to nine-tenths body whorl width, less in *fuscozonata depressa.* Body whorl with protruded keel, except *pelewana.* Whorls 5-6, tightly coiled. Umbilicus usually very narrow to closed, secondarily widened in *angaurana* and *kinlochi.* Major parietals 3 (reduced to 2 in *irregularis*), beaded above, sometimes (*constricta* and *irregularis*) with a single accessory trace. Columellar barrier absent (some *constricta*), normally 1, sometimes (*fuscozonata*) 2, usually parallel to plane of coiling, slightly declined in *pelewana* and *fuscozonata.* Major palatals 3, 4, or 5, all strongly beaded, accessory traces present in *pelewana, fuscozonata, irregularis.* Pallial region typical, with very short rectal kidney arm. Hermaphroditic duct convoluted for one-third of length, remaining portion normal. Talon elongated with head slightly to moderately bulbous, shaft tapered. Epiphallus about half length of penis, vas deferens entering through a valve, internally with two pilasters that variously expand, split or fade out in penis. Penial retractor arising from diaphragm, inserting on penis-epiphallus junction. Spermatheca inserting on penial side of peniovidical angle. Atrium relatively long. Radula without unusual features.

Type species. — *Endodonta constricta* Semper, 1874.

Under light microscope examination, the apical sculpture mimics the fine spiral cording seen in some Charopidae. At 1,000-3,000× magnification (figs. 28e; 29a) the typical spiral squiggles of the Endodontidae are evident. While many Charopidae have fine spiral cords which appear wavy near the end of the apex, this is a secondary phenomenon caused by low radial swellings underlying the spiral cords. These cords are never formed in the fashion seen in *Aaadonta*. Postnuclear sculpture of *Aaadonta* (figs. 28c-e; 29b) consists solely of microradial riblets with vague secondary spiral additives. Despite the quite different macroscopic appearance of this sculpture, it differs from the typical endodontid pattern only by the absence of any major radial ribbing on either the apex or the postnuclear whorls. Such a loss could be the result of a single mutation, since the major radial sculpture is additive to the basic microsculpture pattern (pp. 30-33).

While providing the most obvious differentiating feature, other characters are more significant in providing generic separation. The beaded apertural barriers, insertion of the spermatheca on the penial side of the penioviducal angle, and development of an epiphallic region with complex vas deferens entrance are characters shared with *Thaumatodon* from the Lau Archipelago of Fiji, Tonga, Ellice Islands, Western Samoa, and Rarotonga, and the *Thaumatodon* derivative genera in Lau, *Priceconcha* and *Zyzzyxdonta*. *Aaadonta* has a rostrate periphery, generally very elevated spire, narrow umbilicus, a shorter rectal kidney arm, longer atrium, longer epiphallus, and long tapering talon. A more comprehensive comparison has been given above (p. 444). *Thaumatodon* has normal apical sculpture and, at least on the upper spire, prominent postnuclear radial sculpture. Only in the *T. laddi-corrugata-subdaedalea* complex of Lau is there a clear tendency toward great reduction and loss of sculpture. In these cases both macro- and microsculpture are affected by the reduction. Since there is no loss or reduction in the microsculpture of *Aaadonta*, I consider it improbable that there was gradual loss of major radial sculpture. In genera such as *Nesodiscus* and *Endodonta*, gradual reduction in major sculpture is followed by gradual loss of the microsculpture before the apical and early spire major sculpture disappears. Only in the group of *Libera dubiosa* Ancey, *L. spuria* Ancey, and *L. garrettiana* is there progressive loss of major sculpture without concomitant loss of microsculpture. All three of these species retain major apical radials and an increase in prominence of secondary spiral cording is inversely correlated with decrease in major radial ribs. Under the circumstances, postulation of major radial rib loss by mutational change is an acceptable hypothesis.

Aaadonta is the only Micronesian genus of Endodontidae. While the Miocene *Cookeconcha subpacificus* (Ladd, 1958) and the Pleistocene-Pliocene *Minidonta inexpectans* (Ladd, 1958) are known from the deep-core drillings on Bikini, they belong to the anatomically and conchologically most generalized groups. Anatomical features and the denticle beading relate *Aaadonta* to *Thaumatodon*, which also is the geographically nearest extant endodontid genus. In general, the high spire of *Aaadonta* is otherwise characteristic of brood chamber taxa (*Libera, Pseudolibera, Gambiodonta*), where deflected growth is required to permit development of a sufficiently deep umbilicus. Of those Endodontidae with a SP/BWW ratio of 0.640 or greater, 18 have brood chambers [*Pseudolibera*, *Taipidon semimarsupialis,* four (of six) *Gambiodonta,* 12 (of 19) *Libera*], three are *Nesodiscus*, and only *Anceyodonta ganhutuensis* and *A. sexlamellata* (Pfeiffer) agree with the seven (of nine) *Aaadonta* in having high spires but tiny umbilici. Similarly, the rostrate periphery is unusual in forms that lack a brood chamber. Of 31 taxa with rostrate peripheries, there are seven *Libera,* three *Gambiodonta,* five *Endodonta,* five *Nesodiscus,* six *Aaadonta,* three *Thaumatodon* derivatives (*T. spirrhymatum, Zyzzyxdonta alata,* and *Priceconcha tuvuthaensis*), and two isolated species — *Cookeconcha stellulus* and *Australdonta magnasculcata*.

Median size of rostrate *Aaadonta* is 4.07 mm. in diameter compared with 5.85 mm. for the remaining 25 rostrate taxa.

Primarily because of the sculptural and shape alterations, *Aaadonta* seems to be quite distinctive conchologically, but the differences are relatively few.

Both in shell characters and penial anatomy, *Aaadonta* is the most advanced endodontid genus. Within the genus, no clear hierarchy can be recognized. *A. kinlochi* is specialized only in its flattened spire and relatively large size. The largest species, *A. irregularis*, has reduced barrier numbers with only 2 major parietal and 3 major palatals. *A. constricta* has the greatest development of a rostrate periphery and strongly rounded whorls, although having the most conservative barrier pattern. *A. angaurana* has quite laterally compressed whorls and only 4 palatal barriers. Variation in the recession and prominence of the columellar barrier is exceptionally large, only *A. fuscozonata* having a 2nd columellar, while in some races of *A. constricta* the barrier is so deeply recessed that it can be seen only by extreme tilting of the aperture.

A. fuscozonata depressa, A. f. fuscozonata, and *A. pelewana* form an obviously monophyletic series. The first two have weakly rostrate peripheries, the latter an obtusely rounded periphery. All other *Aaadonta* have a strongly rostrate periphery. Their size and shape also is quite distinctive. In both races of *A. fuscozonata*, the beading on the upper parietal barrier is distinctly finer and more widely spaced than on the lower 2. In *A. pelewana*, the beading is equal in

TABLE CXI. - RANGE OF VARIATION IN AAADONTA

Name	Number of Specimens Examined	Height	Diameter	H/D Ratio	Whorls	D/U Ratio	Pr	C	P
pelewana	10	1.96(1.91-2.01)	2.82(2.78-2.86)	0.694(0.676-0.704)	5 5/8(5 1/2-5 3/4)	8.42(7.22-9.40)	3	1	3-4+1-2
fuscozonata fuscozonata	36	2.27(2.09-2.52)	2.93(2.68-3.15)	0.767(0.662-0.820)	6+(5 5/8-6 1/2)	27.7 (17-46.5)	3	2	3+0-2
fuscozonata depressa	3	2.21(2.09-2.32)	3.15(2.95-3.31)	0.702(0.698-0.707)	5 1/2+(5 1/2-5 5/8)	16.8 (16-17.8)	3	2	5+2
constricta constricta	84	2.29(2.02-2.72)	4.02(3.81-4.27)	0.570(0.530-0.635)	5 3/8+(5 1/8-6)	5.58(4.91-6.63)	3+1	0-1	5
constricta babelthuapi	4	2.25(2.15 2.35)	3.47(3.44-3.54)	0.647(0.625-0.682)	5 1/8(5 1/8-5 1/4)	6.50(5.77 7.42)	3+1	0-1	5
constricta komakanensis	42	2.72(2.52-2.85)	4.12(3.97-4.27)	0.660(0.612-0.700)	5 5/8+(5 1/2-5 7/8)	6.59(5.77-8.00)	3+0-1	1	5
angaurana	128	2.01(1.82-2.19)	3.92(3.58-4.21)	0.511(0.471-0.565)	5 3/4+(5 3/8-6 1/8)	4.35(3.83-4.70)	3	1	4
irregularis	7	3.01(2.58-3.31)	5.10(4.64-5.60)	0.589(0.541-0.666)	5 7/8-(5 1/2-6 1/8)	5.57(4.30-7.15)	2+0-1	1	3+2-3
kinlochi	173	1.75(1.59-1.96)	4.68(4.27-5.03)	0.374(0.342-0.413)	5+(4 5/8-5 1/2)	3.81(3.07-4.44)	3	1	3-4

prominence on all parietals in the majority of specimens examined, but weaker in a few. *A. pelewana* and *A. f. fuscozonata* agree in having the 2nd palatal reduced in size, while in *A. f. depressa* the 2nd palatal is equal in size to the 1st and 3rd. The nominate race of *fuscozonata* has the palatals extending about one-half whorl, while in the other two taxa they extend less than one-quarter whorl. Ranking of *depressa* as a subspecies and *pelewana* as a species is arbitrary and may not be supported when more material is available. Probably all three should be considered species.

When specimens of several species are available for direct comparison, the differences are obvious and striking. Even without other material, *A. pelewana, A. fuscozonata,* and *A. kinlochi* are unmistakable. *A. pelewana* is the only species that lacks a prominent supraperipheral sulcus and does not have a rostrate periphery; *A. fuscozonata* is characterized by its diminutive size and tiny umbilicus (table CXI); while *A. kinlochi* is the only species with a flat or nearly flat spire. Differences between *A. constricta, A. angaurana,* and *A. irregularis* are less dramatic. The first two overlap in size, but when ratios are plotted (fig. 202) can readily be separated, while the very large *A. irregularis* has a reduced barrier complement. *A. pelewana* and *A. fuscozonata* also can be distinguished on the basis of plotted ratios (fig. 205).

There was considerable variation in the percentage of adult specimens present in each taxon collected by the Bishop Museum Micronesian Expedition (table CXII). Those forms taken at only a single station (*constricta komakanensis, angaurana,* and *kinlochi*) were 9.5-16.8 per cent adult while the three species taken only as scattered individuals (*constricta babelthuapi, fuscozonata depressa,* and *irregularis*) were nearly all adult. The two species taken in fair numbers at more than one station (*constricta constricta* and *fuscozonata fuscozonata*) ranged widely in intermediate percentages.

TABLE CXII. - PERCENTAGE OF ADULTS IN AAADONTA

Species known from: -	Total collected	Number of adults	Per cent adults
Single stations -			
constricta komakanensis	42	4	9.5
angaurana	128	14	10.9
kinlochi	173	29	16.8
Several stations -			
constricta constricta			
Total	82	21	25.6
Sta. 182	27	10	37.0
Sta. 201	51	11	21.6
fuscozonata fuscozonata			
Total	36	14	38.9
Sta. 219	20	3	15.0
Sta. 221	12	8	66.7
Sta. 222	3	3	100.0
Scattered individuals -			
constricta babelthuapi	4	3	75.0
fuscozonata depressa	3	3	100.0
irregularis	7	6	85.7

Anatomically, *Aaadonta* agrees with *Thaumatodon* and *Priceconcha* in having the spermatheca enter the base of the penis instead of merging into the free oviduct channel to form a vagina, and in having a reflexed epiphallic portion of the penis lying morphologically above (although topographically below) the penial retractor insertion. In *Aaadonta* the reflexed epiphallic portion is about one-half of the penis length, while in *Thaumatodon* it may be only one-quarter the length. All other Pacific Island endodontid genera have the vas deferens entering laterally on a straight penis at or markedly below the penial retractor insertion, and the spermatheca merges with the free oviduct to form a true vagina (except in *Rhysoconcha*).

In the only *Thaumatodon* dissected in entirety, *T. hystricelloides* and *T. euaensis*, there are peculiar glandular patches on the uterus apex and base (fig. 191b). They were not found in any other species dissected. *Priceconcha tuvuthaensis* was so heavily parasitized that this section of the genitalia could not be studied in detail.

Materials of *A. c. constricta, A. c. komakanensis, A. c. babelthuapi, A. kinlochi,* and *A. fuscozonata fuscozonata* were available for study. Presumed wet examples of *A. irregularis* in the Bishop Museum were not located, and only terminal fragments of *A. f. depressa* were seen. *A. angaurana* and *A. pelewana* were represented only by dead shells. Few differences were noted between the three species dissected in detail. The free oviduct is much longer in *A. fuscozonata,* which has 5⅝-6½ whorls, than in *A. kinlochi*, which has 4⅝-5½ whorls, and *A. constricta constricta* (5⅛-6 whorls) is intermediate in oviduct length. These differences were not quantified because of difficulties in handling the material, but are obvious through inspection of Figures 199b, e, and 200b. In *A. kinlochi* (fig. 200b) the hermaphroditic duct is more convoluted than in the other two species. Possibly this has resulted from the reduction in whorl count found in that species. Otherwise observed differences lie in penis size and pilaster patterns. *A. kinlochi* (fig. 200c) and *A. fuscozonata* have one pilaster splitting to form a weak pocket, while in *A. c. constricta* (fig. 199d) two pilasters merge to form a similar pocket. The relative size of the pilaster arms varies rather widely within each species. Data on penis length are as follows:

A. kinlochi	1.7 mm.
A. f. fuscozonata	1.6-1.8 mm.
A. c. constricta	1.4 mm.

Unfortunately, it was not possible to dissect two species using material taken at the same station. There

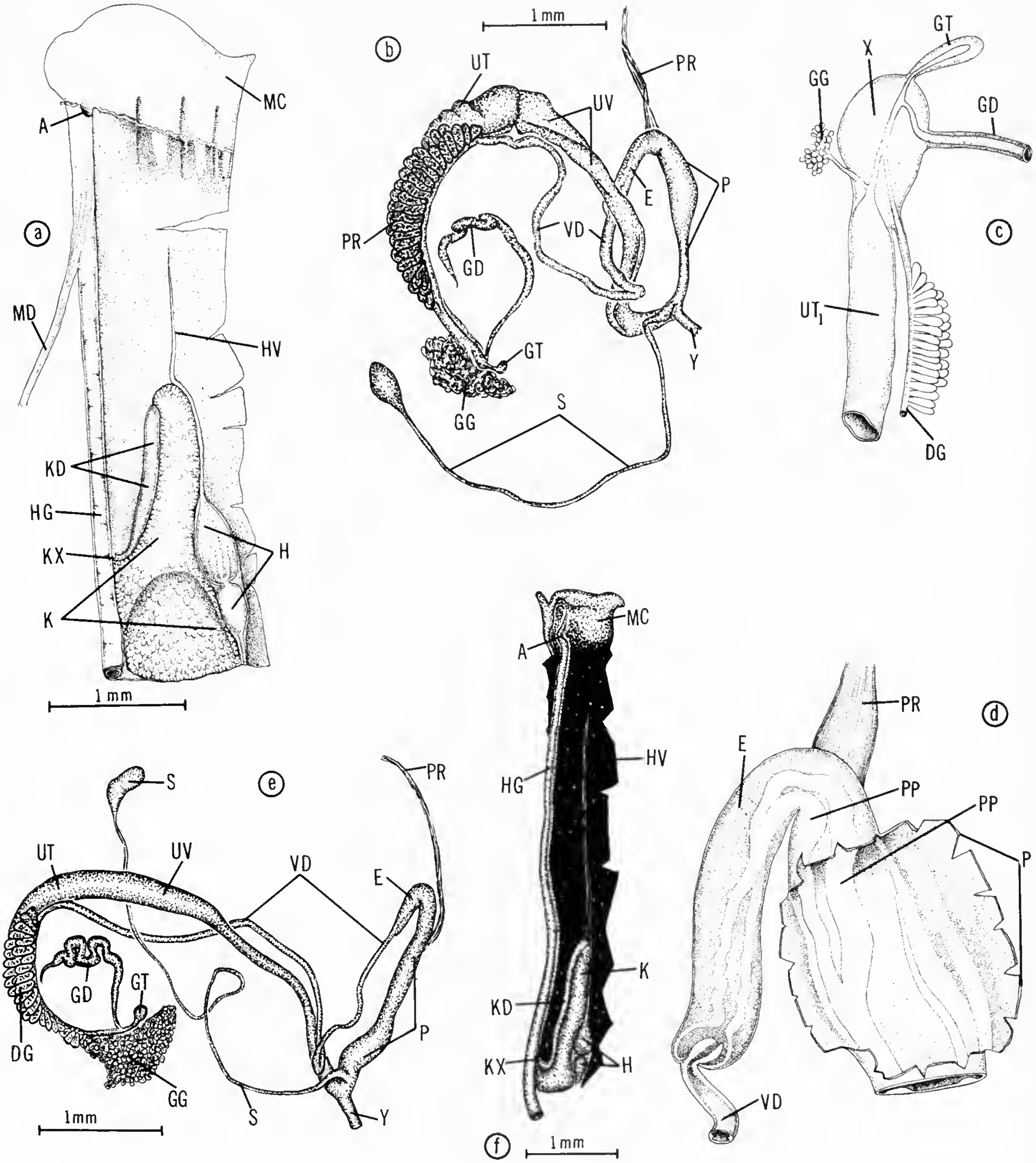

FIG. 199. Anatomy of *Aaadonta:* **a-d**, *Aaadonta constricta constricta,* BPBM 159938. *a,* pallial region; *b,* genitalia with ovotestis omitted, *c,* diagram of carrefour region, dotted lines indicating uncertain channel patterns, *d,* detail of epiphallus and apical part of penis; **e-f**, *Aaadonta fuscozonata fuscozonata,* BPBM 158778. *e,* genitalia with ovotestis omitted, *f,* pallial region.

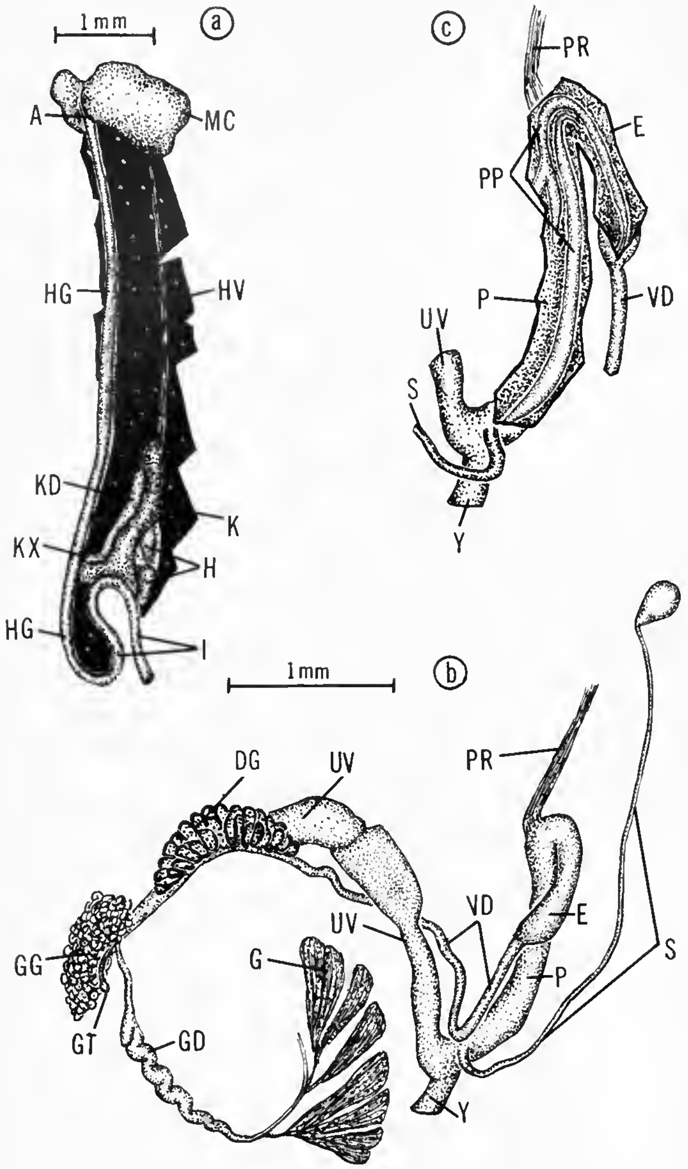

FIG. 200. Anatomy of *Aaadonta kinlochi*, BPBM 158778: **a**, pallial region and lower intestinal loops; **b**, genitalia; **c**, detail of penial complex.

were no obvious structural differences suggesting character displacement in penial pilaster pattern. Possibly the size difference is sufficient to isolate sympatric taxa.

Pallial region proportion also differed, *A. c. constricta* having a shorter and broader region (fig. 199a) than either *A. f. fuscozonata* (fig. 199f) or *A. kinlochi* (fig. 200a). The ratio of kidney length to total pallial cavity length was least in *A. constricta* (1.9-2.0), intermediate in *A. fuscozonata* (2.5-2.9), and greatest in *A. kinlochi* (3.1-3.4). The differences in cross-sectional whorl area between the tightly coiled *A. fuscozonata* and *A. kinlochi* with its fewer, more loosely coiled whorls undoubtedly are considerable. Hence a thicker kidney in *A. kinlochi* could result in equivalent kidney volume in a relatively shorter distance. Thus the higher pallial length/kidney length ratio of *A. kinlochi* does not conflict with the shortened pallial cavity that accompanies reduced whorl counts.

Aaadonta is restricted to the Palau Islands. Species distribution is summarized in Table CXIII. Only *A. constricta babelthuapi* has been collected on two islands, Ngemelis and Babelthuap, with the former record based on a single individual. Peleliu, which has been relatively well collected, yielded examples of *A. c. constricta, A. irregularis*, and *A. fuscozonata depressa*. Koror, the next best sampled island, has *A. c. komakanensis* and *A. f. fuscozonata*. Although only a single station on Angaur yielded endodontids, there are two endemics, *A. angaurana* and *A. kinlochi*. Single stations on Ngemelis and Babelthuap yielded the same race of *A. constricta*. More intensive collections are needed from both islands. An undescribed charopid was collected on Auluptagel, but no examples of *Aaadonta*. Quite probably additional species will be found.

Sympatric occurrence of *Aaadonta* species was found several times. Unfortunately, it was not possible to dissect these sympatric forms. On Koror, *A. constricta komakanensis* and *A. f. fuscozonata* were found at Station 221, with the former dominant and comprising 78 per cent of the sample. On Peleliu, *A. c. constricta* and *A. irregularis* were taken at Stations 182 and 201, with the former comprising 93-96 per cent of the samples. At Station 203 on Peleliu five *Aaadonta* specimens included one *A. c. constricta* and two each of *A. irregularis* and *A. fuscozonata depressa*. On Angaur, both *A. angaurana* and *A.*

TABLE CXIII. - DISTRIBUTION OF AAADONTA

	Palau Islands				
	Angaur	Peleliu	Ngemelis	Koror	Babelthuap
constricta					
c. constricta		X			
c. babelthuapi			X		X
c. komakanensis				X	
irregularis		X			
angaurana	X				
kinlochi	X				
fuscozonata					
f. fuscozonata				X	
f. depressa		X			
pelewana		X (?)		X (?)	

kinlochi were collected at the same station, with *A. kinlochi* (57.5 per cent) more plentiful. This was a thanatocoenosis, however, with no living *A. angaurana* and only 12 of 173 *A. kinlochi* (6.9 per cent) taken alive.

The above data suggest a few possibilities for field investigation. Is *A. irregularis* anywhere common and dominant in numbers over *A. constricta*? What are the ecological differences between the two species? Is *A. angaurana* extinct and stratigraphically separated from the material of *A. kinlochi*? Why were no examples of *A. c. komakanensis* present at Stations 217 and 219 and how does the ecology of that race and *A. f. fuscozonata* differ?

Key to the Genus *Aaadonta*

1. Spire strongly elevated, H/D ratio usually much more than 0.460........2
   Spire flat or only barely protruding above peripheral keel, H/D ratio less than 0.440........*Aaadonta kinlochi,* new species
2. Umbilicus minute, D/U ratio more than 13........3
   Umbilicus narrowly to moderately open, D/U ratio less than 11. 4
3. Major palatal barriers 3; Peleliu Island. *Aaadonta fuscozonata depressa,* new subspecies
   Major palatal barriers 5; Koror Island. *Aaadonta fuscozonata fuscozonata* (Beddome, 1889)
4. Shell diameter more than 3.25 mm.; periphery of aperture rostrate........5
   Shell diameter less than 3.00 mm.; periphery of aperture obtusely rounded........*Aaadonta pelewana,* new species
5. Shell diameter less than 4.5 mm........6
   Shell diameter more than 4.5 mm. *Aaadonta irregularis* (Semper, 1874)
6. Mean D/U ratio substantially more than 5.00........7
   Mean D/U ratio substantially less than 5.00. *Aaadonta angaurana,* new species
7. Mean diameter about 3.9-4.2 mm........8
   Mean diameter about 3.5 mm. *Aaadonta constricta babelthuapi,* new subspecies
8. Columellar barrier prominent (fig. 204a); mean H/D ratio near 0.660; mean D/U ratio near 7.5; Koror Island. *Aaadonta constricta komakanensis,* new subspecies
   Columellar barrier inconspicuous (fig. 203b); mean H/D ratio near 0.570; mean D/U ratio near 5.6; Peleliu Island. *Aaadonta constricta constricta* (Semper, 1874)

Aaadonta constricta (Semper, 1874)

The development of a supraperipheral sulcus and shouldering of the whorls is carried furthest in *A. constricta* of all *Aaadonta*. Intermediate in size between the very small *fuscozonata-pelewana* grouping and the large *irregularis-kinlochi* pair, only *A. angaurana* is apt to be confused on the basis of size (table CXI). It differs in having much flatter whorls, a more open umbilicus (D/U ratio 3.83-4.70) and only 4 palatal barriers. *A. constricta* is the most widely distributed species, having been collected on Koror, Peleliu, Babelthuap, and Ngemelis (table CXIII). Three subspecies are recognized:

A. constricta constricta (Semper, 1874) from Peleliu Island is more depressed (mean H/D ratio 0.570), has a wider umbilicus (mean D/U ratio 5.58), only a weak columellar barrier, and less strongly rounded whorls;

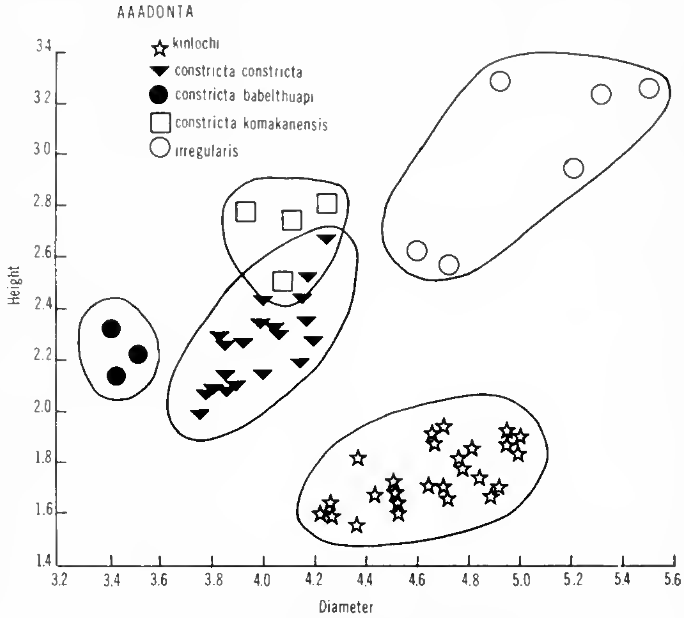

FIG. 201. Size and shape variation in *Aaadonta kinlochi, A. constricta,* and *A. irregularis.*

A. constricta komakanensis, new subspecies from Koror Island, is a high shell (mean H/D ratio 0.660), with narrow umbilicus (mean D/U ratio 7.47), prominent columellar barrier, a much less compressed lower palatal wall, and a greatly reduced 3rd parietal barrier;

A. constricta babelthuapi, new subspecies from Babelthuap and Ngemelis is a small, high shell (mean H/D ratio 0.647), with an umbilicus of intermediate size (mean D/U ratio 6.50), usually no columellar barrier visible, and very strongly rounded whorls.

The differences between these subspecies are of a lesser magnitude in terms of barrier complement than

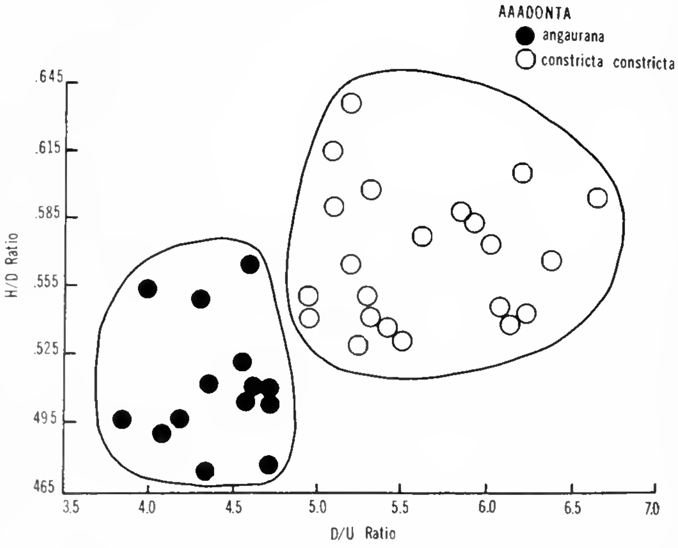

FIG. 202. Proportionate differences between *Aaadonta angaurana* and *A. c. constricta.*

are those between *A. f. fuscozonata* and *A. f. depressa*, but reach very high levels of significance in terms of size and proportions.

Populations of *A. constricta constricta* from Stations 182 and 201 on Peleliu differ slightly (table CXIV), but not significantly. In respect to height, "*t*" = 1.5554; for diameter, "*t*" = 1.1474; for H/D ratio, "*t*" = 1.4169; and for D/U ratio, "*t*" = 0.4803. On a two-sided test, with 15 df, the largest figures have a cumulative probability of between 10-20 per cent. A great contrast is seen when different subspecies are compared. *A. c. constricta* from Station 182 on Peleliu and *A. c. babelthuapi* from Station 15 on Babelthuap, with 11 df, are nearly identical in height ("*t*" = 0.2601); moderately distinctive in D/U ratio "*t*" = 1.8744, 2.5-5 per cent probability level with a one-sided test); and very different in respect to diameter ("*t*" = 5.7576) and H/D ratio ("*t*" = 4.5130) – a probability level of less than 0.05 per cent. *A. c. constricta* from Station 201 on Peleliu and *A. c. komakanensis* from Station 221 on Koror, with 8 df, are quite similar in diameter ("*t*" = 0.7844), but very different in height ("*t*" = 3.4515), H/D ratio ("*t*" = 3.9886) and D/U ratio ("*t*" = 6.6176) – less than 0.5 per cent probability level for a one-sided test. *A. c. babelthuapi* and *A. c. komakanensis*, with 4 df, are very different in diameter ("*t*" = 7.3874) and height ("*t*" = 3.8146), both with a probability level of less than 1 per cent, but quite similar in D/U ratio ("*t*" = 1.3665) and H/D ratio ("*t*" = 0.2189).

The scatter diagrams in Figures 201 and 202 provide simple means for separation of doubtful specimens. Plotting of the height and diameter will segregate *babelthuapi* and *komakanensis* from the nominate race (fig. 201). Separation of *angaurana* and *constricta constricta* is most clearly shown by plotting H/D and D/U ratios (fig. 202).

Aaadonta constricta constricta (Semper, 1874).
Figures 203a-c; 208d.

Endodonta constricta Semper, 1874, Reisen im Arch. der Philippinen, (2), **3,** p. 140 – Peleliu, Palau Islands.

Helix (*Endodonta*) *constricta* (Semper), Pfeiffer, 1876, Monog. helic. viv., **7,** p. 568; Tryon, 1887, Man. Conchol., (2), **3,** p. 67.

Endodonta (*Endodonta*) *constricta* Semper, Pilsbry, 1893, *op. cit.*, (2), **9,** p. 26.

Diagnosis. – Shell a little larger than average, diameter 3.81-4.27 mm. (mean 4.02 mm.), with 5⅛-6 moderately tightly coiled whorls. Apex and spire markedly and evenly elevated, whorls strongly rounded above protruding keel and prominent supraperipheral sulcus, H/D ratio 0.530-0.635 (mean 0.570). Umbilicus open, contained 4.91-6.63 times (mean 5.58) in the diameter. Apical whorls 1⅜, sculpture of 14-18 very fine, obscure spiral riblets with low radial swellings near end. Remaining whorls with few growth wrinkles and sculpture of fine radial riblets crossed by very fine, closely spaced spiral riblets with a few scattered secondary spiral cords. Sutures shallow, whorls strongly rounded below flattened shoulder, sides of spire flat. Aperture ovate with rostrate margin, strongly rounded above periphery. Parietal wall with 3 barriers, extending almost one-quarter whorl, the lower two reduced in height and closer together, rarely (one-fifth of time) with an accessory trace. Columellar barrier low, very deeply recessed. Palatal barriers 5, the upper 2 reduced in prominence, all extending about three-sixteenths of a whorl, only upper palatal supraperipheral. All major barriers regularly beaded above on posterior sections.

The smaller size, more strongly rounded whorls, and 3 parietal barriers effectively separate *A. constricta* from the larger *A. irregularis. A kinlochi* has a flat spire and a deeply recessed columellar barrier, while the much smaller *A. fuscozonata* and *A. pelewana* have a tiny umbilicus and are much more elevated. The nominate race from Peleliu is larger and more depressed than *A. c. babelthuapi* from Babelthuap and Ngemelis (diameter 3.44-3.54 mm., H/D ratio 0.625-0.682). *A. c. komakanensis* has the columellar barrier much more prominent and less recessed, a narrower umbilicus (D/U ratio 6.79-8.00), and is more elevated (H/D ratio 0.612-0.700).

Description (based on paratype). – Shell juvenile, with slightly less than 5 whorls. Apex and spire markedly and evenly elevated, last whorl not descending more rapidly, H/D ratio 0.575. Apical whorls slightly less than 1⅜, sculpture of about 19 fine spiral riblets. Postnuclear whorls with a lattice of coequal radials and spirals, former often obscured by growth wrinkles. Sutures shallow, whorls with flat shoulders, strongly rounded to supraperipheral sulcus. Periphery protruded into a cordlike keel, subperipheral sulcus weak, lower palatal wall somewhat flattened, sloping to strongly rounded umbilical margin. Color faint yellow-white, with strong, regularly spaced, reddish flammulations becoming narrow and zigzagged on base, flaring inside umbilicus. Latter small, almost U-shaped, slightly and regularly decoiling, contained 6.24 times in the diameter. Aperture elongate-ovate, with rostrate periphery, inclined about 15° from shell axis. Parietal barriers 3, with one accessory trace, extending posteriorly more than one-quarter whorl: upper high, thin, with sharp anterior descension, fine beads on posterior half; 2nd and 3rd parietals lower, looser together, with more gradual anterior descension, beading on posterior two-thirds. Accessory trace a low bladelike ridge located just below parietal-palatal margin. Columellar wall with single barrier, threadlike anteriorly, moderately elevated posteriorly, only extending partway across thick columellar callus. Palatal barriers 5, extending posteriorly three-sixteenths of a whorl, upper 2 reduced in size: lower palatal basal in position, high, twisted slightly upward in crossing basal callus, strongly beaded above; 2nd and 3rd palatals with progressively more gradual anterior descension, three very strong beads above on posterior two-thirds; 4th palatal subperipheral, greatly reduced in height, with three slender elongated beads; 5th palatal supraperipheral, a low ridge with three very faint elongated beads above. Height of paratype 2.01 mm., diameter 3.49 mm.

Lectotype. – Probably in Zoologisches Museum der Humboldt-Universität, Berlin.

Range. – Peleliu, Palau Islands.

Paratypes. – Peleliu, Palau Islands (FMNH 46245 ex Berlin Museum, Karl Semper).

Material. – Palau Islands (1 specimen, BPBM 106241): Peleliu, short distance from phosphate mine (Stations 201, 203) and 300-400 yd. north at 35-200 ft. elevation (52 specimens, BPBM 159938-43, BPBM 159989); Omurbrogol Mt. (Station 182), Asias village, one-half to three-fourths mile inland at 300-400 ft. elevation (27 specimens, BPBM 159423-7); 300 yd. north of NKK Club (Station 196) in phosphate testing ground at 50 ft. elevation (2 specimens, BPBM 159864); one-half to 1 mile north of Ngalkiok (Station

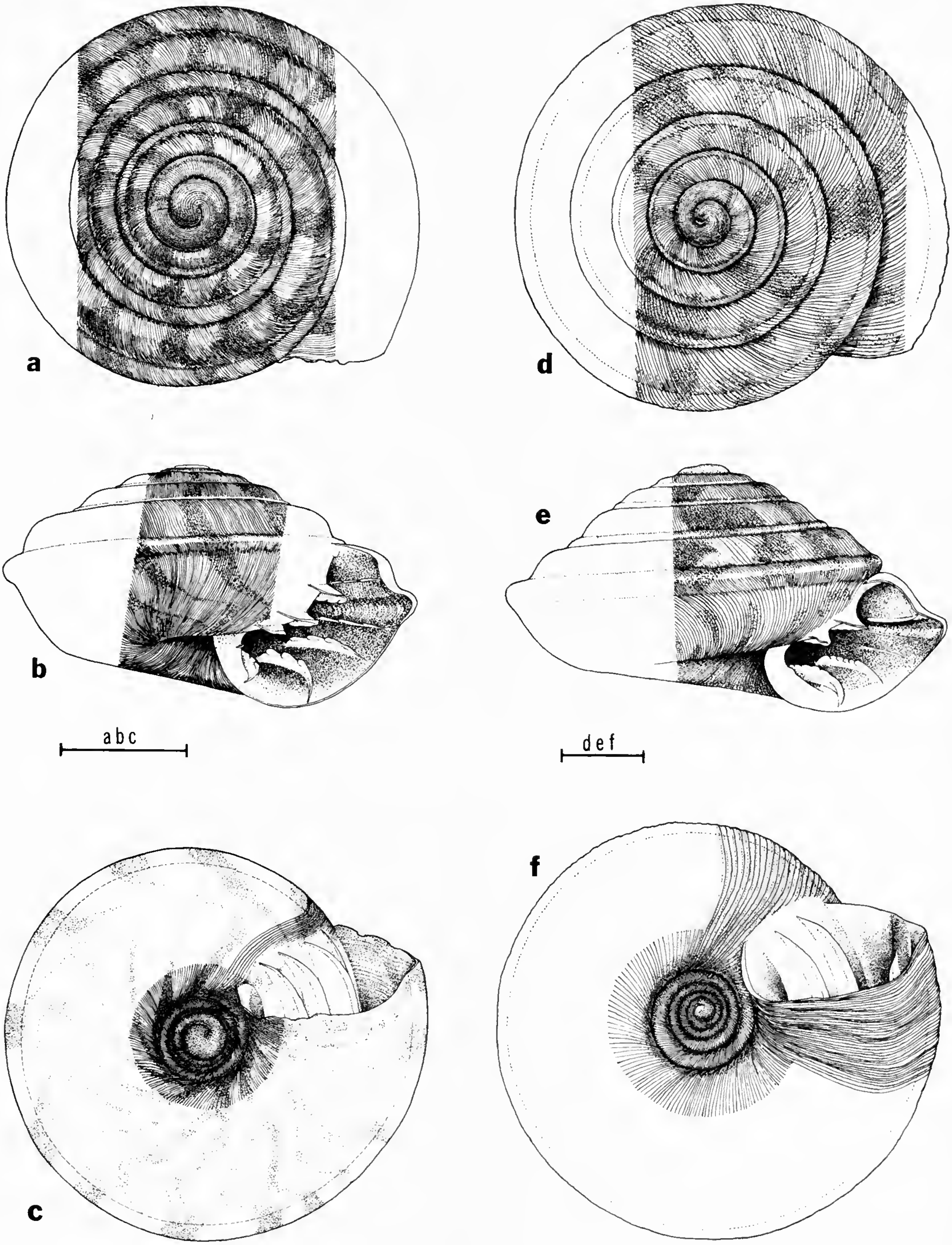

FIG. 203. **a-c**, *Aaadonta constricta constricta* (Semper). Peleliu. Palau Islands. Paratype. FMNH 46245 ex W. F. Webb. Zool. Mus. Berlin; **d-f**, *Aaadonta irregularis* (Semper). Station 201. Peleliu, Palau Islands. BPBM 159937. Scale lines equal 1 mm. (MM).

207) inland one-sixth to one-fifth mile at 5-10 ft. elevation (1 specimen, BPBM 160046).

Remarks. — Probably a lectotype can be selected from material in the Zoologisches Museum der Humboldt-Universität, Berlin. A subadult paratype (FMNH 46245) has been described, but not selected as lectotype. It is unusual only in having a small parietal trace just below the parietal-palatal margin. This lamellar trace was present in only about 20 per cent of the specimens.

Of the 82 specimens collected by the Micronesian Expedition, only 21 were adult.

Description of soft parts. — Foot and tail slender, elongated, not tapering posteriorly, bluntly rounded behind, truncated anteriorly with head projecting in front of foot. Sole smooth, undivided. Pedal grooves rather high on side of foot, suprapedal weaker than pedal, both uniting over tail, caudal horn absent, no middorsal groove visible. Slime network finely reticulated, more obvious on tail than head region. Ommatophores long, eyespot quite small and circular. Gonopore located directly below right ommatophore, slightly above and behind right rhinophore.

Body color light yellow-white in preservative, no darker markings.

Mantle collar elongated, heavily glandularized, with glandular extension marking areas of apertural barriers. Pneumostome a simple opening at parietal-palatal angle, no special development of mantle lobes. Anus opening just inside mantle collar at parietal-palatal angle, a slightly diagonal slit, no special groove through pneumostome visible.

Pallial region (fig. 199a) extending apically one-half whorl, flattened length from pneumostome to base of kidney about 4.15 mm. Lung roof clear, without granulation. Kidney (K) about 2.1 mm. long, thick base curved, indented below by abuttment of intestinal loop and spermatheca, posterior third reaching hindgut, tapering forward past heart to narrow blunt apex. Ureter (KD) a broad tube, passing apically along upper edge of kidney lobe, opening at point where kidney reaches hindgut. Heart (H) about one-half length of kidney, slightly angled in relation to hindgut, relatively large in proportion. Principal pulmonary vein (HV) paralleling hindgut, unbranched, fading out in area of glandular protrusions. Hindgut (HG) reaches palatal-parietal margin about one-eighth whorl above apex of pallial cavity, running forward without change in diameter to anus.

Ovotestis (G) as in *Endodonta fricki,* imbedded in digestive gland above apex of stomach, but not reaching to top of soft parts. Palmately clavate clumps strung along single collecting tubule. Hermaphroditic duct (GD) slender, highly convoluted at first, becoming expanded and straight along most of stomach length, making a right-angle turn before inserting into carrefour (X) (fig. 199c). Albumen gland (GG) poorly preserved, outline indistinct, lying above apex of pallial cavity next to intestinal loops and base of stomach. Carrefour (X) receiving ducts from talon (GT) and hermaphroditic duct (GD) at approximately right angles. Two channels lead from carrefour into prostate and uterus, but the available material did not allow accurate determination of the channel patterns inside carrefour. Figure 199c indicates the probable pattern through use of dotted lines. Duct of albumen gland opening into head of uterus, slightly below point where clear separation of uterine and prostatic channels can be observed. Carrefour itself a semi-translucent ovoid sac, narrowing abruptly to prostate-uterine heads. Channels obviously connect the talon and hermaphroditic duct to the area from which the prostatic and uterine channels depart, but the exact structure of the central area could not be determined. Prostate (DG) a narrow tube arising from carrefour, closely appressed to uterus. After first short section, two or three rows of alveolar sacs insert into tube, at first partly hiding uterus, then being partly hidden by uterus on lower section as they decrease in size. Uterus (UT) in two sections, upper a large tube, expanded after midsection to form a large bag that narrows just before changing to free oviduct.

Vas deferens (VD) slender, paralleling free oviduct to penioviducal angle, entering head of epiphallus through a pair of pilasters into a small chamber flanked by pilasters (fig. 199d). Epiphallus (E) little more than half length of penis, internally with two narrow pilasters, rugose apically, leading into penis without sharp differentiation of region. Penial retractor (PR) originating on diaphragm just below apex of pallial cavity, inserting on looped part of penial complex as a gradual fusion with the tissue and not as direct insertion of a muscle band. Penis (P) compact, about 1.4 mm. long, larger above and tapering anteriorly to junction with spermatheca just before entering atrium. Epiphallic pilasters enter, one expands and they merge (fig. 199d) forming a weak pocket, then continue towards gonopore, gradually tapering. Two secondary pilasters could be seen in a few specimens. Atrium (Y) a rather long tube with 2-3 narrow pilasters inside.

Free oviduct (UV) much thicker than vas deferens, internally with fine longitudinal pilasters, merging into atrium. Spermatheca (S) entering base of penis, slender shaft passing up free oviduct and prostate-uterus to the expanded head, which lies between anterior end of albumen gland and apical end of kidney above apex of pallial cavity and underneath anterior intestinal loop. Vagina (V) absent.

Free muscle system simple. Right ommatophoral retractor passing through penioviducal angle, uniting with right rhinophoral retractor about one-third of way to tail fan. Tentacular retractors unite separately with tail fan well in front of point where buccal retractors attach.

Buccal mass elongated, slender. Buccal retractors originating where tail fan attaches to shell, inserting on bottom posterior edge of buccal mass in a narrow band. Esophagus arising about midpoint of buccal mass, very slender, extending above apex of pallial cavity. Stomach taking less than one-quarter whorl to reach parietal-palatal margin, extending a total of 1¼ whorls. For most of length occupying outer wall as in *Endodonta fricki.* Intestinal looping as in *E. fricki*: after leaving stomach it follows inner wall margin; loops up across base of kidney and on top of spermathecal head; reflexes back for about 1.7 mm., angling downwards; then curving up to parietal-palatal margin and runs forward as hindgut, continuing anteriorly to anus.

Digestive glands typical. Salivary glands uniting over esophagus for posterior one-quarter.

Jaw not mounted successfully.

Radula partly fragmented during mounting. Central about 8μ wide and 9μ long. Laterals 5-6 in number, marginals more than 10 with split cusps.

(Based on BPBM 159938, four examples, whole specimen diameter 3.91 mm., with 5½ whorls.)

Aaadonta constricta babelthuapi, new subspecies. Figure 204c-d.

Diagnosis. — Shell small, diameter 3.44-3.54 mm. (mean 3.47 mm.), with 5⅛-5¼ tightly coiled whorls. Apex and spire strongly and evenly elevated, H/D ratio 0.625-0.682 (mean 0.647). Umbilicus narrow, U-shaped, regularly and slightly decoiling, contained 5.77-7.42 times (mean 6.50) in the diameter. Sculpture and color as in *A. c. constricta.* Whorls quite strongly rounded after flat shelf from suture, then dropping vertically to sharply defined supraperipheral sulcus. Keel, base of shell, and aperture as in nominate subspecies. Parietal and palatal barriers as in *A. c. constricta* with upper parietal trace present in type. Columellar barrier usually absent.

Although the height of the shell is the same as in *A. c. constricta,* the much smaller diameter results in a higher H/D ratio and smaller D/U ratio. *A. c.*

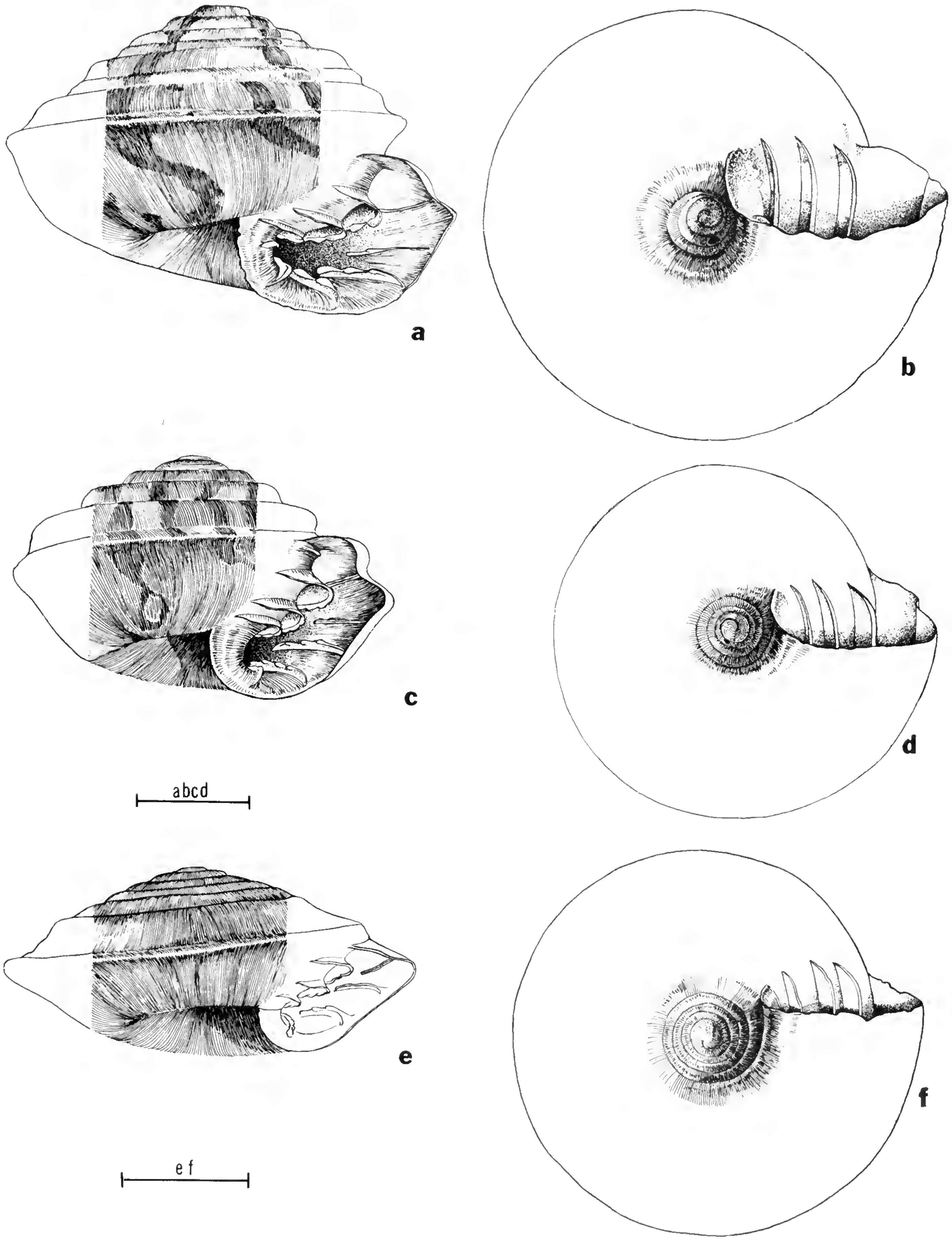

FIG. 204. **a-b**, *Aaadonta constricta komakanensis*, new subspecies. Station 221. Koror Island, Palau Islands. Holotype. BPBM 158862; **c-d**, *A. c. babelthuapi*, new subspecies. Station 15, Babelthuap Island, Palau Islands. Holotype. BPBM 160524; **e-f**, *A. angaurana*, new subspecies. Station 175, Angaur Island, Palau Islands. Holotype. BPBM 158310. Scale lines equal 1 mm. (SG).

babelthuapi also has lost the columellar barrier, which is weakly developed in *A. c. constricta* and strongly developed in *A. c. komakanensis.*

Description. — Shell small with 5⅛ tightly coiled whorls. Apex and spire strongly and evenly elevated, whorls acutely rounded above after flat shelf to suture, a protruded peripheral keel and a deep supraperipheral sulcus, H/D ratio 0.625. Apical whorls 1⅜, sculpture partially eroded, but traces of fine spiral riblets remaining. Lower whorls with irregular growth wrinkles somewhat masking the typical *Aaadonta* microsculpture. Sutures shallow, whorls flattened at shoulder, strongly rounded laterally, then dropping vertically to deep supraperipheral sulcus. Umbilicus open, U-shaped, slightly decoiling, a little constricted by umbilical lip, contained 5.77 times in the diameter. Aperture compressed ovate with birostrate upper margin, inclined about 15° from the shell axis. Parietal barriers 3, extending one-quarter whorl, regularly beaded above on posterior five-eighths, lower 2 crowded and reduced in height. Single parietal trace just below parietal-palatal margin. Columellar barrier absent. Palatal barriers 5, extending three-sixteenths of a whorl, regularly beaded above on posterior two-thirds, lower 3 reaching margin and equal in height, upper 2 recessed and reduced in height with very elongate, fine beading, 5th supraperipheral. Height of holotype 2.15 mm., diameter 3.44 mm.

Holotype. — Palau Islands: Babelthuap, Station 15, Adelulu Hill, Airai-Mura, 30 m. inland at 20-40 m. elevation. Collected by S. Ito on April 21, 1936. BPBM 160524.

Paratypes. — BPBM 160524, BPBM 160525.

Material. — Babelthuap: (Station 15) Adelulu Hill, Airai-Mura, 30 m. inland at 20-40 m. elevation (3 specimens, BPBM 160524, BPBM 160525). Ngemelis: Hillside (Station 210) at 2-35 ft. elevation (1 specimen, BPBM 159232).

Remarks. — A single shell from Ngemelis (height 2.25 mm., diameter 3.54 mm., H/D ratio 0.635, whorls 5¼, D/U ratio 6.30) agrees closely with the Babelthuap types in size and proportions and is included under this subspecific designation, despite having a rather prominent columellar barrier. When more material is available from Ngemelis, separation of these populations may be warranted.

Three of the four shells were adult, a much higher ratio than was found in most other *Aaadonta.*

Description of soft parts. — Two animals extracted from the shells were fragmented. Apical pallial organs and genitalia missing. Penial structures as in *A. c. constricta,* with exact pilaster pattern duplicated. No significant differences noted in anterior parts of animal from those of *A. constricta constricta.* Jaw very delicate, of separate plates connected by a thin membrane.

(Based on BPBM 160524.)

Aaadonta constricta komakanensis, new subspecies. Figure 204a-b.

Diagnosis. — Shell larger than average, diameter 3.97-4.27 mm. (mean 4.12 mm.), with 5½-5⅞ tightly coiled whorls. Apex and spire strongly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.612-0.700 (mean 0.660). Umbilicus narrow, U-shaped, not decoiling, contained 6.79-8.00 times (mean 7.47) in the diameter. Sculpture as in *A. c. constricta.* Suture shallow, whorls sloping to strongly rounded shoulder, angling into prominent supraperipheral sulcus. Periphery protruded into prominent keel, below which is a weak sulcus. Aperture ovate, broadly rounded below periphery. Parietal and palatal barriers as in *A. c. constricta,* except for greater size reduction of 3rd parietal. Columellar barrier prominent, crossing top of columellar callus.

The larger size, prominent columellar, and reduced 3rd parietal barrier separate *A. c. komakanensis* from *A. c. babelthuapi. A. c. constricta* differs in its much lower spire (mean H/D ratio 0.570) and wider umbilicus (mean D/U ratio 5.58).

Description. — Shell larger than average with 5⅞ tightly coiled whorls. Apex and spire strongly and evenly elevated, whorls moderately rounded above flat sutural shelf with protruded keel and prominent supraperipheral sulcus, last whorl descending more rapidly, H/D ratio 0.663. Apical whorls 1⅜, sculpture of about 16 fine spiral riblets with faint traces of radial undulations at end. Remaining whorls with sculpture of growth wrinkles and a microsculpture of fine radial riblets with finer spiral ribs and secondary sculpture of rather widely spaced spiral cords. Sutures shallow, whorls first flattened, then moderately rounded above peripheral sulcus, keel protruded, base of shell evenly rounded, not compressed, to strongly rounded umbilical margin. Umbilicus narrow, slightly constricted by coiling of last whorl and reflection of umbilical lip, U-shaped, contained 7.35 times in the diameter. Color light yellowish-white with irregular reddish, flammulations. Aperture with rostrate periphery, ovate, inclined about 15° from the shell axis. Parietal barriers 3, extending one-quarter whorl, posterior two-thirds regularly beaded above, 2nd and 3rd parietals crowded, with 3rd parietal greatly reduced in height. Columellar barrier parallel to plane of coiling, a low but prominent ridge, slightly recessed within aperture. Palatal barriers 5, extending three-sixteenths of a whorl, lower 3 nearly reaching margin and equal in height, upper 2 reduced in height, recessed, with much finer beading. Lower 3 palatals strongly beaded on posterior parts. Height of holotype 2.73 mm., diameter 4.11 mm.

Holotype. — Palau Islands: Koror, Station 221, southeast end of small peninsula near Komakan at 5-90 ft. elevation. Collected by Yoshio Kondo on May 11, 1936. BPBM 158862.

Range. — Koror, Palau Islands.

Paratypes. — BPBM 158862-9.

Material. — Koror: (Station 221) southeast end of small peninsula near Komakan at 5-90 ft. elevation (42 specimens, same as list of paratypes).

Remarks. — In slightly subadult shells, such as BPBM 158863, the descension of the body whorl is only slightly evident, and in metaneanic individuals is absent. The evenly rounded lower palatal wall contrasts with the normally compressed region in other *Aaadonta.* Although absent in the holotype, an upper parietal trace was present in nearly every specimen examined. The much greater reduction of the 3rd parietal seems to be correlated with the much greater development of the columellar, since in the other subspecies, where the columellar barrier is absent, or reduced, the 3rd parietal is proportionately nearer the 2nd in size.

Only four of the 42 specimens were adult.

Description of soft parts. — Inspection of several torn individuals revealed no differences in terminal structure from those observed in *A. c. constricta.* The preservation was not very good, so that pilaster patterns were indistinct. Jaw and radula not mounted.

(Based on BPBM 158862.)

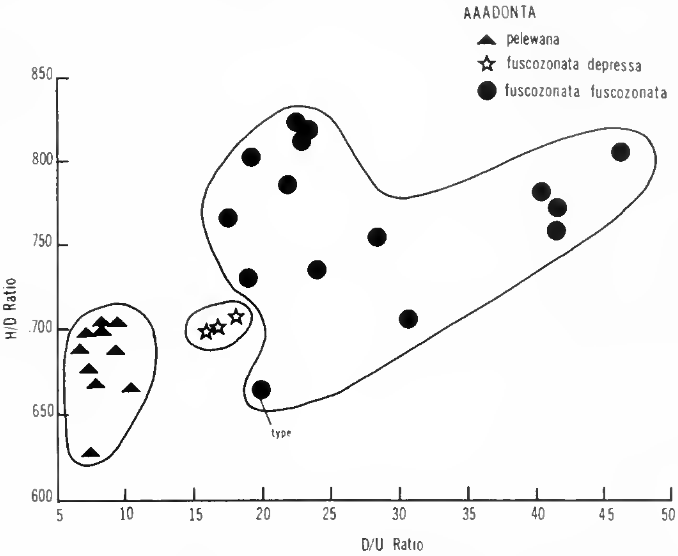

FIG. 205. Proportionate differences between *Aaadonta pelewana* and *A. fuscozonata*.

Aaadonta fuscozonata (Beddome, 1889)

This very small species is most likely to be confused with *A. pelewana*. The latter differs most obviously in having a more widely open umbilicus (D/U ratio 6.68-10.6) and an obtusely rounded periphery (fig. 205). In *fuscozonata* the umbilicus is minute (D/U ratio more than 15) and the periphery is distinctly rostrate. There are also differences in barriers. *A. fuscozonata* has the beading on the 1st parietal weaker and more widely spaced than on the 2nd and 3rd and there is a distinct, deeply recessed 2nd columellar barrier; *A. pelewana* usually has the parietal with equal-sized beading and there is no 2nd columellar.

I recognize two subspecies:

A. fuscozonata fuscozonata (Beddome, 1889) from Koror Island, which has 3 major palatal barriers extending nearly one-half whorl, the 2nd distinctly smaller, a higher spire (mean H/D ratio 0.767) and minute umbilicus (mean D/U ratio 27.7); and

A. fuscozonata depressa, new subspecies from Peleliu Island, which has 5 palatal barriers extending less than one-quarter whorl, the lower 3 coequal in size, a lower spire (mean H/D ratio 0.702) and a slightly more open umbilicus (mean D/U ratio 16.8).

If collection of additional material confirms these differences in palatal barriers as constant for all Peleliu shells, then *depressa* should be considered a distinct species. Since only three specimens were available, I preferred the conservative course of recognition at the subspecific level.

Aaadonta fuscozonata fuscozonata (Beddome, 1889). Figure 206a-c.

Helix (*Endodonta*) *fusco-zonata* Beddome, 1889, Proc. Zool. Soc. London, **1889**, p. 116, pl. 12, figs. 12,a-c – Koror, Palau Islands.

Patula (*Endodonta*) *fuscozonata* (Beddome), Pilsbry, 1892, Man. Conchol., (2), **8**, p. 83, pl. 30, figs. 39-42.

Endodonta (*Endodonta*) *fuscozonata* Beddome, Pilsbry, 1893, *op. cit.*, *(2)*, **9**, p. 26.

Diagnosis. – Shell very small, diameter 2.68-3.15 mm. (mean 2.93 mm.), with 5⅝-6½ tightly coiled whorls. Apex and spire very strongly elevated, slightly rounded above, H/D ratio 0.662-0.820 (mean 0.767). Umbilicus minutely perforate, contained 17.0-46.5 times (mean 27.7) in the diameter. Apical whorls 1⅜, sculpture of fine, close-set spiral riblets and weak radial swellings. Remaining whorls with irregular radial ribs and growth wrinkles, plus a microsculpture of a few, widely spaced radial and much finer spiral riblets. Sutures shallow, whorls gently rounded down to shallow supraperipheral sulcus and weakly protruded keel. Subperipheral sulcus equal in size, base of shell rounded to umbilical margin. Aperture ovate with slightly rostrate periphery and expanded basal lip. Parietal barriers 3, extending posteriorly beyond line of vision, lower reduced in prominence from 2nd and crowded more closely to it, all with small, widely spaced beading on posterior portion that is much more widely spaced on 1st barrier. Columellar barrier a very prominent, rounded ridge lying parallel to plane of coiling, then slanted downward across columellar callus, usually with a low broad upper accessory barrier. Major palatal barriers 3, extending beyond line of vision, with widely spaced beads above, 2nd palatal smaller than 1st and 3rd, occasionally with one or two upper accessory traces.

The much higher spire, barely perforate umbilicus, and 3 long palatals separate the nominate form of *A. fuscozonata* from the Peleliu Island subspecies of *A. f. depressa*, which has 5 short (less than one-quarter whorl) palatals, a more depressed spire, and a slightly more open umbilicus. *A. pelewana* has (usually) 4 palatals and a moderately open umbilicus. Other species of *Aaadonta* are much larger and less elevated with wider umbilici.

Description. – Shell small with 5⅝ tightly coiled whorls. Apex and spire very strongly and evenly elevated, a little rounded above, last whorl not descending more rapidly, H/D ratio 0.662. Apical whorls 1½, sculpture of very fine, crowded spiral riblets, partially eroded. Remaining whorls with low, irregular, close-set radial growth striae, slightly protractive, of varying strength and spacing. Microsculpture, where visible, of fine radial riblets crossed by much finer and more crowded spiral riblets. Sutures shallow, whorls almost evenly rounded above with prominent supra- and subperipheral sulci, a threadlike protruding keel and evenly rounded basal margin. Color light yellowish-white with broad, relatively regularly spaced, reddish flammulations becoming narrower, zigzag and fainter on base of shell. Umbilicus minute, not decoiling, contained 19.4 times in the diameter. Aperture elongately ovate with weakly beaked periphery, evenly rounded above and below, inclined about 10° from the shell axis. Parietal barriers 3, extending posteriorly beyond line of vision: upper thin, high, bladelike, sharply descending anteriorly with a few weak, elevated, regularly and widely spaced beads above; 2nd parietal slightly lower with more rounded, expanded and closely set beading; lower parietal a threadlike ridge with low, crowded beading above. Parietals 2 and 3 spaced closer together than 1 and 2, all beads minutely barbed. Columellar wall with moderately thick callus extending onto basal lip. Columellar barriers 2: upper a low, recessed, broad, threadlike ridge becoming higher posteriorly; second a prominent lamellar ridge extending across callus to lip edge and slanting slightly downward. Both columellars parallel to plane of coiling posteriorly. Palatal barriers 3, extending beyond line of vision: lower palatal basal in position, a high, slightly twisted lamella reaching lip edge with very sharp anterior descension, faintly beaded above posteriorly; 2nd palatal a low, threadlike ridge, more strongly beaded above, very slightly recessed from lip margin; 3rd palatal a moderately high, lamellate ridge with quite prominent swollen beads above, gradually descending anteriorly and reaching almost to lip edge. Height of holotype 1.89 mm., diameter 2.86 mm.

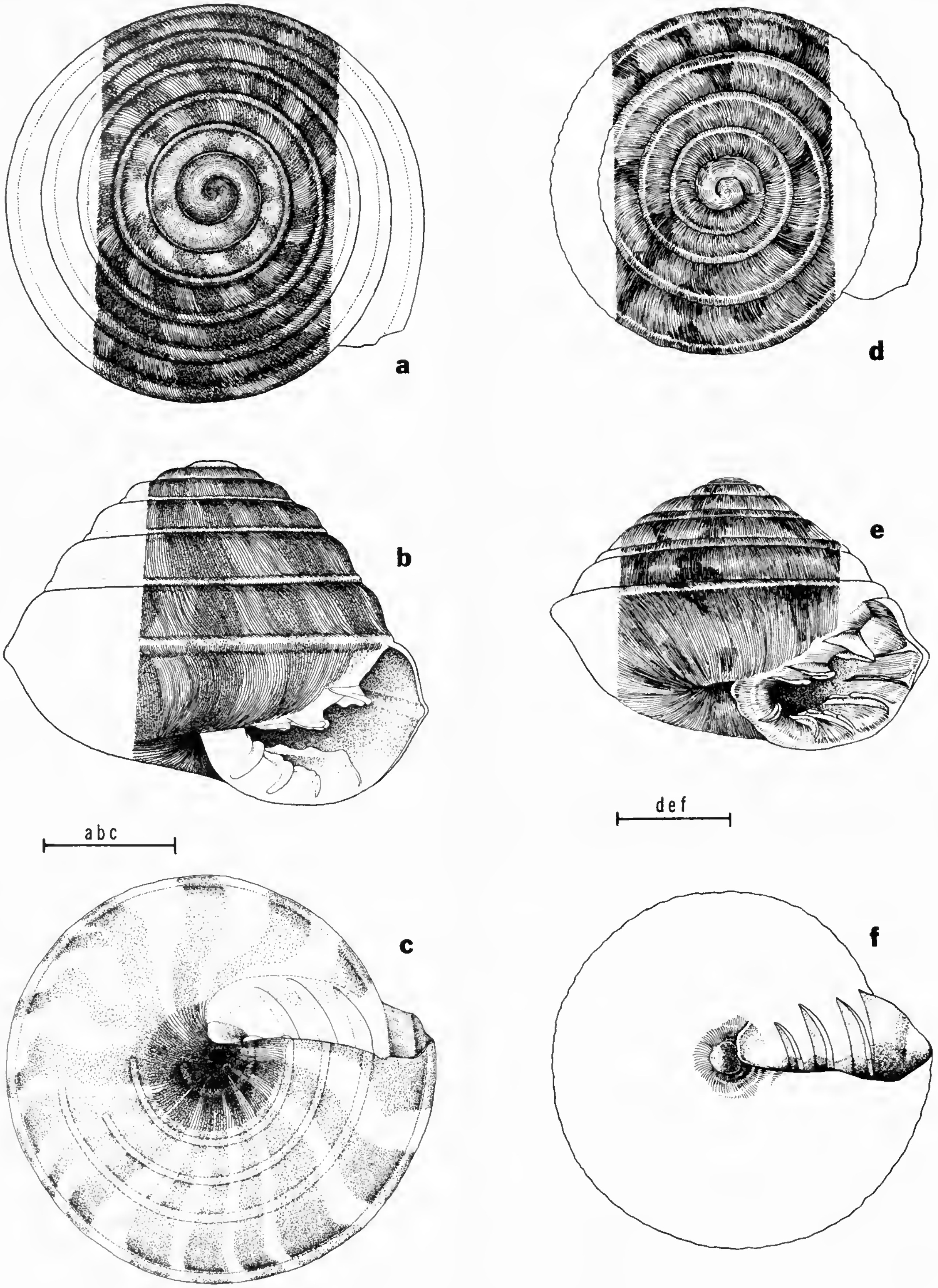

FIG. 206. **a-c**, *Aaadonta fuscozonata fuscozonata* (Beddome). Station 219, Koror Island, Palau Islands. BPBM 158778. **d-f**, *A. f. depressa*, new subspecies. Station 203, Peleliu, Palau Islands. Holotype. BPBM 159990. Scale lines equal 1 mm. (*a-c*, MM; *d-f*, SG).

Holotype. – Palau Islands: Koror. Collected by Hungerford. BMNH 91.3.17.1042.

Range. – Koror, Palau Islands.

Material. – Koror (1 specimen, BMNH 91.3.1.7.1042): Komakan (Station 222) at 100-200 ft. elevation (3 specimens, BPBM 154848-9); Komakan (Station 221) at 5-90 ft. elevation (12 specimens, BPBM 158870-3); Komakan (Station 219) at 75 ft. elevation (20 specimens, BPBM 158778-82).

Remarks. – The holotype is a very depressed, rather small specimen that has particularly strong development of the second columellar barrier. No specimens collected in recent years exactly match its characters. The next most depressed specimen had a H/D ratio of 0.706 and the mean for that set (table CXIV) was 0.774. Although the type of *fuscozonata* is within the shape range of *A. f. depressa,* the difference in palatal barriers is the significant factor separating the two subspecies.

As shown in Figure 206c, fresh specimens often reveal how far the palatal barriers extend posteriorly by the thick bases being visible through the shell in strong lighting. In *A. f. fuscozonata* they extend about one-half whorl, more than twice the distance the palatals extend in *A. f. depressa.*

Description of soft parts. – Foot about 2.3 mm. long, very slender, slightly tapering at tail, rounded behind, truncate anteriorly. Sole and pedal grooves typical, caudal horn and middorsal groove absent. Slime network very faint. Head slightly protruding in front of foot. Ommatophores long, eyespot small, circular. Gonopore a narrow groove below right ommatophore, behind and a little above right rhinophore.

Body color yellow-white in preservative, no darker markings.

Mantle collar (MC) thin, without obvious glandular extensions onto pallial roof. Pneumostome typical, no mantle lobes developed. Anus (A) in normal position.

Pallial region (fig. 199f) extending about 1⅛ whorls apically, flattened length about 4.9-5.3 mm. Lung roof clear, without granulations. Kidney (K) narrow, about 1.7 mm. long, base indented by spermathecal head and kidney loop, part abutting on hindgut. Ureter (KD) typical, opening near junction of kidney and hindgut after slight reflection apically. Heart (H) slightly less than half length of kidney, paralleling hindgut. Principal pulmonary vein (HV) simple, unbranched, could not be traced to mantle collar. Hindgut (HG) reaching parietal-palatal margin one-quarter whorl above apex of pallial cavity, diameter unchanged to anus.

Ovotestis (G) as in *A. constricta.* Hermaphroditic duct (GD) highly convoluted at first, slightly iridescent, last section straight before entering carrefour. Albumen gland (GG) typical, extending nearly to last intestinal loop, lying above pallial cavity apex. Head of talon (GT) enlarged, buried in albumen gland, shaft slender, rather long. Carrefour (X) less enlarged than in *A. constricta.* Prostate (DG) short, 2-3 rows of acini opening into slender duct. Weakly bound to uterus. Shaft of spermatheca bound to duct of prostate to just above acinar portion. Uterus (UT) less clearly differentiated into two sections than usual, very thin-walled.

Vas deferens (VD) typical, duct much larger than shaft of spermatheca (fig. 199e). Epiphallus (E) with same entry seen in *A. constricta,* two large pilasters continuing into penis. Penial retractor (PR) arising from diaphragm well below apex of pallial cavity, inserting on penis-epiphallus well below loop area. Penis (P) about 1.6-1.8 mm. long, with two pilasters, one splitting to form a pocket as in *A. kinlochi,* not tapering as much to atrium junction. Atrium (Y) long, weak pilasters inside.

Free oviduct (UV) not sharply differentiated from uterus, tapering gradually to atrium, very thin-walled. Spermatheca (S) as in *A. constricta,* inserting on base of penis. Vagina (V) absent.

Free muscle system typical.

Digestive system with stomach extending 1¼ whorls apically from pallial cavity apex. Otherwise typical.

(Based on BPBM 158778, four examples, whole specimen diameter 2.76 mm. with 6+ whorls.)

Aaadonta fuscozonata depressa, new subspecies.

Figure 206d-f.

Diagnosis. – Shell quite small, diameter 2.95-3.31 mm. (mean 3.15 mm.), with 5½-5⅝ tightly coiled whorls. Apex and spire quite strongly elevated, slightly rounded above, H/D ratio 0.698-0.707 (mean 0.702). Umbilicus minute, not decoiling, contained 16-17.8 times (mean 16.8) in the diameter. Sculpture, color and whorl contours as in *A. f. fuscozonata.* Parietal and columellar barriers also as in nominate race. Palatal barriers 5, extending three-sixteenths of a whorl, only upper supraperipheral: lower 3 coequal in height, reaching apertural margin, 3rd with more gradual anterior descension; upper 2 prominent and bladelike, reduced in height from lower 3. Beading equal on lower 2 palatals; reduced and more widely spaced on 3rd; greatly reduced on 4th; and apparently absent on 5th barrier.

The presence of 5 shorter palatal barriers and more depressed shape separate *A. f. depressa* from the nominate subspecies. *A. pelewana* differs in being distinctly smaller (mean diameter 2.75 mm.) and has a much more open umbilicus (mean D/U ratio 8.18) in addition to the altered palatal barriers.

Description. – Shell small with 5½ tightly coiled whorls. Apex and spire evenly elevated, whorls strongly rounded above prominent threadlike periphery with shallow supraperipheral sulcus, H/D ratio 0.700. Embryonic whorls 1⅜, sculpture partially eroded with traces of numerous, very fine spiral ribs remaining. Remaining whorls with irregular riblike growth wrinkles and a microsculpture of fine radial riblets and relatively more crowded spiral riblets. Sutures shallow, whorls moderately shouldered below, then sloping down to distinct supraperipheral sulcus. Umbilicus very narrowly open, not decoiling, partly covered by reflexion of columellar lip, contained 16.67 times in the diameter. Color light yellow-brown with relatively prominent, irregular, reddish flammulations, becoming wider and sinuated on base of shell. Aperture ovate with weakly rostrate periphery, inclined about 10° from the shell axis. Parietal barriers 3, extending beyond the line of vision, regularly beaded above after anterior sixteenth whorl, lower parietal markedly reduced in height. Beading on upper parietal finer and more widely spaced. Columellar barriers 2, upper deeply recessed and greatly reduced in prominence, lower a high lamella, slanting downward across columellar callus. Palatal barriers 5, extending three-sixteenths of a whorl, lower 3 equal in size and reaching lip margin, upper 2 reduced in prominence and slightly recessed. Lower 2 palatals with crowded, large beads; 3rd palatal with three widely spaced, finer beads; 4th palatal much lower with only traces of beading remaining; 5th palatal a bladelike ridge without trace of beading, located just above supraperipheral sulcus. Height of holotype 2.30 mm., diameter 3.29 mm.

Holotype. – Palau Islands: Peleliu, Station 203, 300-400 yd. north of phosphate mine at 35-200 ft. elevation. Collected by Yoshio Kondo on April 29, 1936. BPBM 159990.

Range. – Peleliu, Palau Islands.

Paratypes. – BPBM 159990, BPBM 159600.

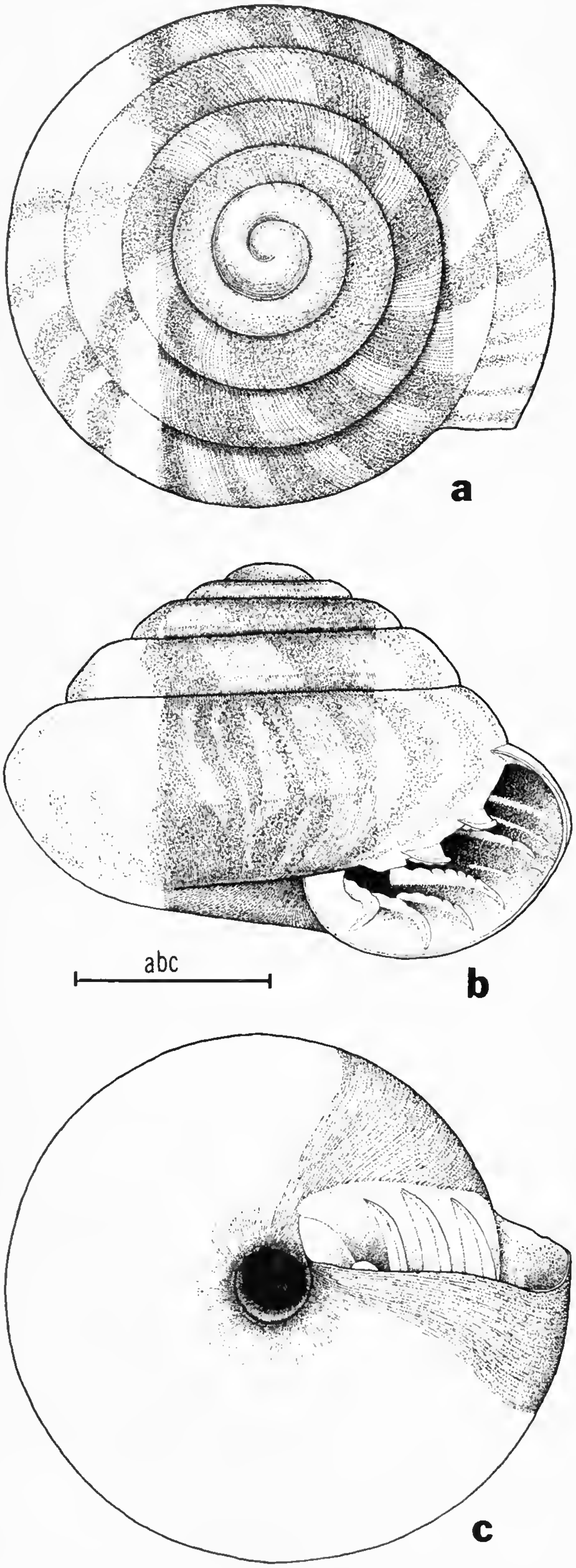

FIG. 207. **a-c**, *Aaadonta pelewana* new species. Palau Islands. Holotype. BM(NH) 91.3.17.443. Scale line equals 1 mm. (SG).

Material. — Peleliu: (Station 203) 300-400 yd. north of phosphate mine at 35-200 ft. elevation (2 specimens, BPBM 159990); Road to Asias (Station 187) at 80 ft. elevation (1 specimen, BPBM 159600).

Remarks. — All three specimens were adult. The differences from *A. f. fuscozonata* outlined in the diagnosis are large enough to indicate specific level differentiation, if collection of more material from Peleliu confirms that they are constant. Subspecific status is employed here in view of the limited material available.

Aaadonta pelewana, new species. Figure 207a-c.

Diagnosis. — Shell minute for genus, diameter 2.56-2.88 mm. (mean 2.75 mm.), with 5-5¾ tightly coiled whorls. Apex and spire quite strongly and evenly elevated, a little rounded on top, H/D ratio 0.628-0.704 (mean 0.682). Umbilicus very small, last whorl decoiling noticeably, contained 6.68-10.6 times (mean 8.18) in the diameter. Sculpture and color as in *A. f. fuscozonata.* Sutures impressed, whorls strongly rounded above, sloping down to very faint supraperipheral sulcus just above obtusely rounded periphery. Lower palatal wall evenly rounded to expanded basal-columellar margin. Parietal barriers 3, upper 2 coequal, 3rd distinctly reduced in size. All usually strongly beaded above, occasionally upper with more widely spaced beading. Columellar barrier high, thick, rounded above, slanting diagonally downward while crossing columellar-basal callus. Palatal barriers 3 (33 per cent) or 4 (67 per cent) plus one or two accessory traces, extending nearly one-quarter whorl: 1st and 3rd equal in size, with large bulbous beads above; 2nd (when present) lower and narrower with finer beading; upper slightly subperipheral, a low ridge with prominent beading. Usually a slightly supraperipheral accessory threadlike trace present, occasionally a weak thread present between 3rd and 4th palatals.

The obtusely rounded, not rostrate, periphery and minute size immediately separate *A. pelewana* from the other *Aaadonta. A. fuscozonata* is most similar, but has a slightly rostrate periphery (fig. 206b, e) and a much narrower umbilicus (D/U ratio 16-46.5).

Description. — Shell minute for genus, with a trifle more than 5¾ tightly coiled whorls. Apex and spire strongly elevated, a little rounded above, last whorl descending only a trifle more rapidly, H/D ratio 0.701. Apical whorls 1⅜, sculpture of about 18 fine spiral ribs with crowded, barely visible radial swellings. Postnuclear whorls with irregular growth wrinkles, plus a microsculpture of fine radial and much finer spiral riblets. A secondary microsculpture of fine spiral cords clearly visible on many parts of shell. Sutures well impressed, whorls flatly sloping down to extremely weak supraperipheral sulcus. Periphery obtusely rounded, not protruded, lower palatal wall evenly rounded, a little compressed laterally. Basal margin strongly rounded into umbilicus. Umbilicus narrow, U-shaped, last whorl decoiling a little more rapidly, only slightly covered by reflection of columellar lip, contained 7.91 times in the diameter. Aperture elongately-ovate, slightly compressed laterally below periphery, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly beyond line of vision, with large swollen beads, slightly more widely spaced on upper parietal, after smooth anterior portion: upper parietal very high and bladelike, with gradual anterior descension, beads clearly separated; 2nd equal in height, with sharper anterior descension, beading more closely spaced; 3rd situated closer to 2nd than 2nd is to 1st, about half the height, beading not separated by smooth area. Columellar barrier a high rounded ridge, posteriorly lying parallel to plane of coiling, anteriorly slanting diagonally downward across columellar callus, with blunted descension almost to lip edge. Palatals 4, extending one-quarter whorl, with two accessory traces: 1st palatal a thick high ridge with narrow, widely spaced beading, sharp anterior descension; 2nd palatal greatly reduced in height, beading similar but proportionately smaller; 3rd palatal equal in height to 1st, beading large and separated, with more gradual anterior descension; 4th palatal slightly subperipheral, lower than 3rd, beading prominent, with gradual anterior descension. A very fine accessory trace located between 3rd and 4th palatal; second trace slightly supraperipheral with faint trace of beading. An elongate bump located just above 4th palatal, a weaker bump just below. Basal and lower palatal lip with rather thick callus. Height of holotype 2.01 mm., diameter 2.86 mm.

Holotype. — Palau Islands. BMNH 91.3.17.443, ex Hungerford, Gibbons collections.

Range. — Unknown, but certainly on one of the Palau Islands.

Paratypes. — Palau Islands (BMNH 91.3.17.444, FMNH 147277).

Material. — Koror (5 specimens, SMF 165429 ex Moellendorff); Peleliu (2 specimens, Brussels ex Dautzenberg, Geret, Ancey, John H. Thomson).

Remarks. — Although no exact locality is known for this species, its minute size and very distinctive form merit nomenclatural recognition. The Natur-Museum Senckenberg and Brussels specimens were not directly utilized in drawing up the description and diagnosis, so they are not considered paratypes. Both island records are considered suspect, particularly in view of the many hands through which the specimens passed. I suspect Angaur or Babelthuap might be the correct locality.

The obtusely rounded, not rostrate, periphery and impressed sutures are unique among *Aaadonta.* In having the 2nd palatal barrier reduced (or absent) *A. pelewana* is more similar to *A. f. fuscozonata* than *A. f. depressa* where the 2nd palatal is equal in size to the 1st and 3rd. As in *depressa,* the palatals extend posteriorly less than one-quarter whorl.

Aaadonta irregularis (Semper, 1874). Figure 203d-f.

Endodonta irregularis Semper, 1874, Reisen im Arch. der Philippinen, (2), **3**, p. 141 — Peleliu, Palau Islands.

Helix (*Endodonta*) *irregularis* (Semper), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 568; Tryon, 1887, Man. Conchol., (2), **3**, p. 67.

Endodonta (*Endodonta*) *irregularis* Semper, Pilsbry, 1893, *op. cit.*, (2), **9**, p. 26.

Diagnosis. — Shell large, diameter 4.64-5.60 mm. (mean 5.10), with 5½-6⅛ rather loosely coiled whorls. Apex and spire markedly and evenly elevated, H/D ratio 0.541-0.666 (mean 0.589). Umbilicus V-shaped, open, regularly decoiling, contained 4.30-7.15 times (mean 5.57) in the diameter. Apical whorls 1⅜, sculpture of 18-22 very fine, crowded spiral riblets, with weak radial swellings on last portion. Remaining whorls with a combination of irregularly spaced growth wrinkles and a lattice of fine radial riblets with finer, more closely spaced spiral riblets. A secondary microsculpture of more widely spaced, finer spiral cords visible near periphery. Sutures shallow, whorls only slightly rounded with prominent sub- and supraperipheral sulci, keel rounded and markedly protruded. Sides of spire flat, slightly rounded above. Aperture ovate with rostrate periphery, inclined about 10° from shell axis. Parietal wall with 2 prominent barriers, extending posteriorly beyond line of vision, lower about two-thirds height of upper, one-third of time with lower accessory trace. Columellar wall with a single deeply recessed barrier, parallel to shell axis, high and rounded posteriorly, but greatly reduced anteriorly and not reaching across columellar callus. Palatal barriers 3, 1 supraperipheral, 2 subperipheral with two (67 per cent) or three (33 per cent) accessory traces located between upper two palatals. Major parietal and lower palatal barriers evenly beaded above, beading less prominent than in other *Aaadonta.*

The presence of only 2 major parietals and 2 subperipheral palatal barriers immediately separates *A. irregularis* from the smaller (diameter 3.44-4.27) *A. constricta* with its 3 major parietals and 5 palatals. *A. kinlochi* does not have the spire elevated, while the similarly shaped *A. angaurana* is much smaller (diameter 3.58-4.21 mm.), has 3 major subperipheral palatals and 3 parietals. The minute (diameter 2.56-3.31), very high spired (H/D ratio 0.628-0.820) *A. fuscozonata* and *A. pelewana* cannot be confused with *irregularis.*

Range. — Peleliu, Palau Islands.

Material. — Peleliu: short distance from phosphate mine (Stations 201, 203) and 300-400 yd. toward the north at 35-200 ft. elevation (4 specimens, BPBM 159937, BPBM 159987-8); Omurbrogol Mt. (Station 182) Asias village, one-half to three-quarters mile inland at 300-400 ft. elevation (2 specimens, BPBM 159428); (Station 188) nearly 2 miles from club after passing swamp at 75 ft. elevation (1 specimen, BPBM 159633).

Remarks. — No type specimens could be located. Since Semper's original description mentions six big barriers, a major diameter of 5.5 mm., elevated spire, and six whorls, no question of identification arises. Possibly potential lectotype specimens are preserved in the Zoologisches Museum der Humboldt-Universität, Berlin, but this collection was not seen. No selection of a lectotype has been attempted. A more detailed diagnosis is presented in the absence of a type description.

Six of the seven specimens collected by the Bishop Museum Micronesian Expedition were adult. In view of the high percentage of juveniles in most other species of *Aaadonta* (table CXII) this is quite surprising. If it were not for the different position of the major barriers and obviously flatter whorls, *irregularis* might be mistaken as a gerontic form of *constricta.* At three of the four stations where *irregularis* was collected (Station 182, 201, 203) *constricta* also occurred. The single exception, Station 188, had only a single specimen of *irregularis* taken. No other endodontid was found there.

In shape of the whorls and spire, *A. angaurana* is almost identical and probably is the closest relative.

Aaadonta angaurana, new species. Figure 204e-f.

Diagnosis. — Shell slightly larger than average, diameter 3.58-4.21 mm. (mean 3.92 mm.), with 5⅜-6⅛ normally coiled whorls. Apex and spire evenly elevated, rather low, rounded above, H/D ratio 0.471-0.565 (mean 0.511). Umbilicus widely open, U-shaped, slightly and regularly decoiling, contained 3.83-4.70 times (mean 4.35) in the diameter. Sculpture of apical and postnuclear whorls typical. Sutures shallow, whorls flat to slightly rounded down to prominent supraperipheral sulcus. Periphery strongly protruded into rostrate keel, with weak subperipheral sulcus. Aperture subrectangular, strongly compressed laterally below periphery, inclined about 15° from shell axis. Parietal barriers 3, lower 2 reduced in height. Columellar barrier a low bladelike ridge deeply recessed in aperture. Palatal barriers 4, upper supraperipheral and greatly reduced in height, lower 3 basal to subperipheral, 1st and 3rd distinctly lower than 2nd. Parietal and palatal barriers beaded posteriorly.

Most closely resembling *A. irregularis*, the possession of 3 major subperipheral palatals, 3 major parietals, and the smaller size at once separate *A. angaurana*. *A. constricta* is higher with a narrower umbilicus and much more strongly rounded whorls. *A. fuscozonata* and *A. pelewana* are much smaller and higher, while *A. kinlochi* is immediately separable by its flat spire and large size.

Description. – Shell smaller than average, with slightly less than 5¼ normally coiled whorls. Apex and spire markedly and evenly elevated, very slightly rounded above, last whorl descending more rapidly, H/D ratio 0.451. Apical whorls 1½, sculpture mainly eroded, traces of fine spiral ribbing remaining. Postnuclear whorls with irregular growth wrinkles and fine radial riblets with a lattice of finer and more crowded spiral riblets. Sutures shallow, whorls flatly sloping to broad and shallow supraperipheral sulcus. Periphery protruded into rostrate keel, a very weak subperipheral sulcus visible, lower palatal margin flattened to strongly shouldered umbilical margin. All color leached from shell except for a few faint, reddish markings on body whorl. Umbilicus wide, U-shaped, slightly and regularly decoiling, contained 3.98 times in the diameter. Aperture subquadrangular, with weakly rostrate periphery, flattened laterally above and below periphery, inclined about 10° from the shell axis. Parietal barriers 3, extending posteriorly more than one-quarter whorl: upper high, thin, bladelike, with sharp anterior descension, edge broken on anterior two-thirds, beaded posteriorly; 2nd slightly lower, more gradual anterior descension, broken off above anteriorly, beaded posteriorly; 3rd a little lower, anterior end broken off, strongly and closely beaded above. Columellar barrier a low, bladelike ridge parallel to plane of coiling, deeply recessed within aperture. Palatal barriers 4, extending posteriorly three-sixteenths of a whorl, upper supraperipheral and greatly reduced in size: lower basal in position, a high, bladelike lamellar ridge with gradual anterior descension, prominently beaded on posterior two-thirds, lying opposite lower parietal, distinctly lower than next 2 barriers; 2nd and 3rd palatals almost equal in height, lying opposite upper 2 parietals, strongly beaded above, 3rd lower and with more gradual anterior descension than 2nd; 4th palatal supraperipheral, a low V-shaped ridge only weakly beaded above and moderately deeply recessed. Height of holotype 1.65 mm., diameter 3.62 mm.

Holotype. – Palau Islands: Angaur, Station 175, north of shrine at edge of guano pit at 75-100 ft. elevation. Collected by Kiyoko and Yoshio Kondo on April 18, 1936. BPBM 158310.

Range. – Angaur Island, Palau Islands.

Paratypes. – BPBM 158310.

Material. – Angaur: (Station 175) north of shrine at edge of guano pit at 75-100 ft. elevation (128 specimens, BPBM 158310, BPBM 158311, BPBM 158264).

Remarks. – The type is a very depressed, slightly subadult specimen that was not included among the measured set (table CXIV). It was selected as holotype because of its excellent preservation. No living material was obtained and all the specimens were quite worn and heavily dirt encrusted. Only 14 examples were of adult size.

The form and general shape of *A. angaurana* is very similar to that of *A. irregularis*. The latter (table CXI) is distinctly larger (mean diameter 5.10 mm.), higher (mean H/D ratio 0.589), and has only 3 major palatal barriers. The size and general appearance of *A. angaurana* are quite similar to those of *A. c. constricta*, although the differences in whorl contour and presence of 5 palatal barriers in the latter should be sufficient for identification. Plotting of the H/D ratio against the D/U ratio (fig. 202) provides complete separation of available material. Size and proportion differences between *A. c. constricta* from Station 182 and *A. angaurana* (table CXIV) are insignificant in respect to diameter ("*t*" = 0.7609 with 23 df), but very significant for height ("*t*" = 4.0817), H/D ratio ("*t*" = 4.4346) and D/U ratio ("*t*" = 7.4420) – the last three all being well within the 5 per cent probability level.

Aaadonta kinlochi, new species. Figures 200; 208 a-c.

Diagnosis. – Shell large, diameter 4.27-5.03 mm. (mean 4.68 mm.), with 4⅝-5¼ rather loosely coiled whorls. Apex and spire flat, not protruding, last whorl not or only slightly descending, H/D ratio 0.342-0.413 (mean 0.374). Umbilicus V-shaped, widely open, regularly decoiling, contained 3.07-4.44 times (mean 3.81) in the diameter. Apical whorls 1⅜, sculpture of approximately 18 fine spiral ribs and finer, more crowded radial swellings. Postnuclear whorls with close-set, irregularly protractively sinuated radial riblets, often with periostracal lamellar extensions, growth striae, and vague, much finer spirals. Sutures very shallow, whorls flat to broad and shallow supraperipheral sulcus. Periphery with rostrate, prominent keel, below which is a deep subperipheral sulcus. Lower palatal wall slightly flattened to strongly rounded umbilical margin. Aperture elongate-ovate, with very strongly protruding periphery, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly beyond line of vision, finely and regularly beaded after short anterior portion. Upper slightly higher than 2nd parietal, 3rd usually markedly reduced in height. Columellar barrier rarely visible in adults, more frequently in young, a low V-shaped ridge deeply recessed in aperture, often visible only by extreme tilting of aperture, not beaded above. Palatal barriers 3-4, lower 3 subperipheral, upper (when present) supraperipheral. Lower 3 palatals extend posteriorly one-quarter whorl, finely beaded above for most of length, lower 2 reaching margin, 3rd slightly recessed. Upper palatal varying from low, beaded ridge less than half height of lower palatals, to a series of separated tubercles mounted directly on body wall without an elevated ridge.

The large size, flat spire and non-elevated apex, wide umbilicus and having the subperipheral sulcus stronger than the supraperipheral immediately separate *A. kinlochi* from the other *Aaadonta*. All other species have quite elevated spires and their umbilici are much narrower.

Description. – Shell large with 5 rather loosely coiled whorls. Apex and spire flat, last whorl barely descending below rostrately keeled periphery of penultimate whorl, H/D ratio 0.369. Keel with weak supra- and prominent subperipheral sulci. Apical whorls 1⅜, sculpture of crowded, very fine spiral riblets, partially eroded, with weaker radial swellings. Remaining whorls with very irregular, protractively sinuated radial riblets, occasionally with periostracal lamellar extensions. Sutures very shallow, whorls flattened above

TABLE CXIV. - LOCAL VARIATION IN AAADONTA

Name	Number of Specimens	Height	Diameter	H/D Ratio	Whorls	D/U Ratio
pelewana						
Brussells	2	1.95±0.017 (1.94-1.97)	2.83±0.033 (2.80-2.86)	0.690±0.0141 (0.676-0.704)	5 1/2 (5 1/2)	8.31±1.089 (7.22-9.40)
SMF 165429	5	1.79±0.049 (1.62-1.90)	2.67±0.050 (2.57-2.81)	0.669±0.0121 (0.628-0.697)	5 1/4+ (5-5 3/8)	7.94±0.689 (6.68-10.62)
BM(NH) 91.3.17.443-5	3	1.98±0.031 (1.92-2.02)	2.84±0.024 (2.80-2.88)	0.697±0.0054 (0.686-0.703)	5 3/4 (5 5/8-5 3/4)	8.50±0.456 (7.91-9.39)
fuscozonata fuscozonata						
BPBM 154848, BPBM 154849, BPBM 158870, BPBM 158778	14	2.27±0.043 (2.09-2.52)	2.94±0.041 (2.68-3.15)	0.774±0.0094 (0.706-0.820)	6+ (5 1/2-6 1/2)	28.34±2.68 (17.0-46.5)
fuscozonata depressa						
BPBM 159990, BPBM 159600	3	2.21±0.067 (2.09-2.32)	3.15±0.106 (2.95-3.31)	0.702±0.0027 (0.698-0.707)	5 1/2+ (5 1/2-5 5/8)	16.82±0.525 (16.0-17.8)
constricta constricta						
BPBM 159938	11	2.34±0.061 (2.02-2.72)	4.05±0.051 (3.81-4.27)	0.578±0.0105 (0.530-0.635)	5 1/2 (5 1/8-6)	5.54±0.148 (5.08-6.35)
BPBM 159423, BPBM 159427	10	2.23±0.041 (2.09-2.48)	3.97±0.034 (3.81-4.17)	0.559±0.0079 (0.531-0.598)	5 3/8+ (5 1/4-5 3/4)	5.65±0.177 (4.91-6.63)
constricta babelthuapi						
BPBM 160524	2	2.25±0.099 (2.15-2.35)	3.44	0.653±0.0283 (0.625-0.682)	5 1/8 (5 1/8)	6.59±0.827 (5.77-7.42)
BPBM 159232	1	2.25	3.54	0.635	5 1/4	6.30
constricta komakanensis						
BPBM 158862	4	2.72±0.072 (2.52-2.85)	4.12±0.061 (3.97-4.27)	0.660±0.0180 (0.612-0.700)	5 5/8+ (5 1/2-5 7/8)	7.47±0.265 (6.79-8.00)
angaurana						
BPBM 158310	14	2.01±0.035 (1.82-2.18)	3.92±0.047 (3.58-4.21)	0.511±0.0075 (0.471-0.565)	5 3/4+ (5 3/8-6 1/8)	4.35±0.078 (3.83-4.70)
irregularis						
BPBM 159937, BPBM 159428, BPBM 159633, BPBM 159987	6	3.01±0.133 (2.58-3.31)	5.10±0.151 (4.64-5.60)	0.589±0.0175 (0.541-0.666)	5 7/8- (5 1/2-6 1/8)	5.57±0.410 (4.30-7.15)
kinlochi						
BPBM 158265, BPBM 158267, BPBM 158268	29	1.75±0.020 (1.59-1.95)	4.68±0.044 (4.27-5.03)	0.374±0.0033 (0.342-0.413)	5 1/8 (4 5/8-5 1/2)	3.81±0.059 (3.07-4.44)

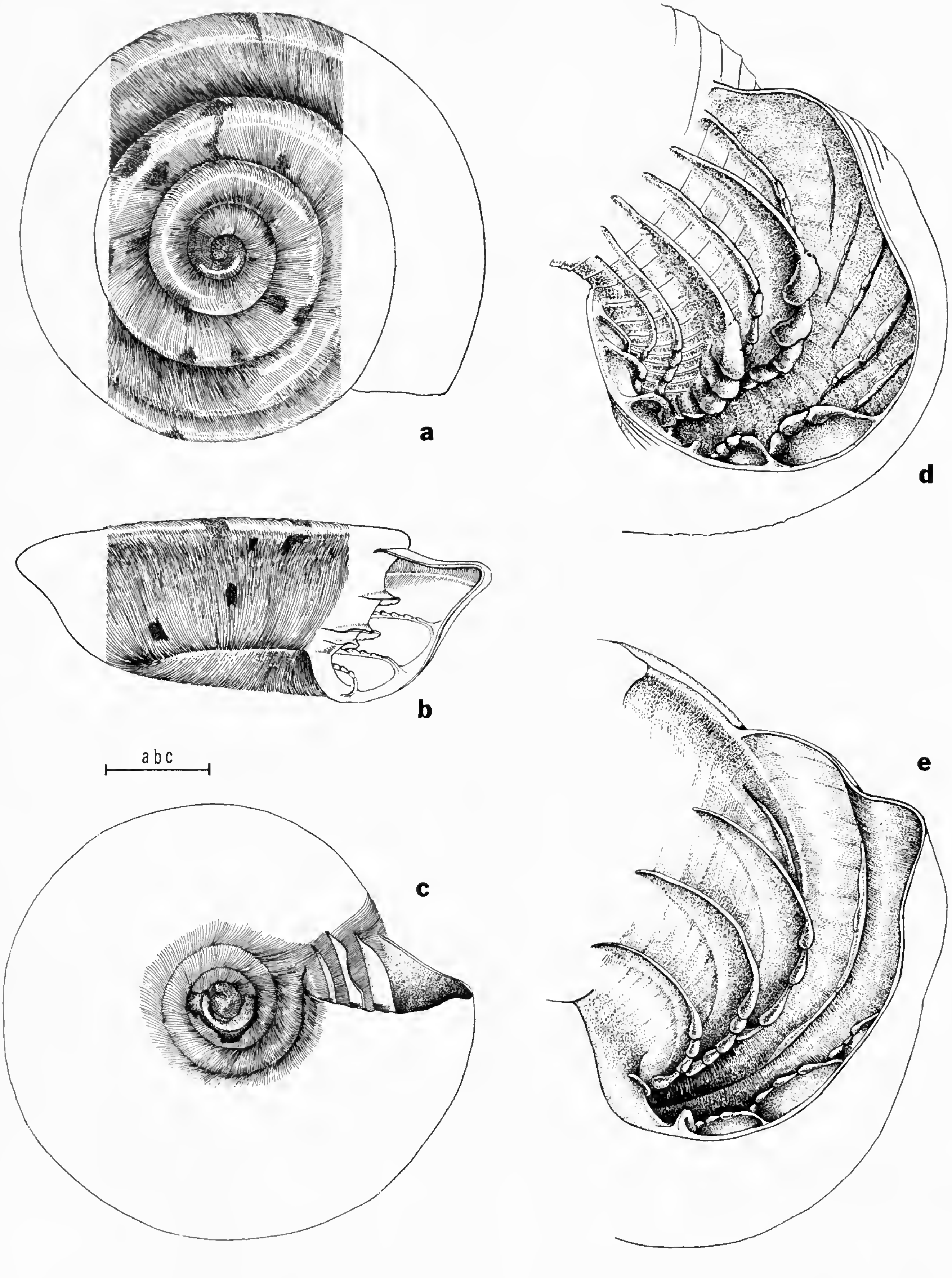

FIG. 208. **a-c**, *Aaadonta kinlochi,* new species. Station 175, Angaur Island, Palau Islands. Holotype. BPBM 158267; **d**, aperture of *Aaadonta constricta constricta* (Semper). Paratype. FMNH 46245; **e**, aperture of *Thaumatodon hystricelloides* (Mousson). Paratype. Zurich. Scale line equals 1 mm., *d-e,* greatly enlarged. (SG).

with shallow supraperipheral sulcus and acutely protruded rostrate keel, only slightly compressed laterally. Color yellow-white, with a few irregular, reddish markings above, prominent near periphery, fading out to suture and on lower palatal wall, quite prominent in umbilicus. Apex reddish in tone, without discrete markings. Umbilicus broadly open, V-shaped, regularly decoiling, contained 3.84 times in the diameter. Aperture subquadrangular with rostrate periphery, upper palatal margin parallel to plane of coiling, lower palatal wall slightly flattened, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly beyond line of vision, regularly and finely beaded after anterior fourth; upper very high, 2nd slightly, and 3rd markedly reduced in height and also in size of beading. Columellar barrier not visible except by extreme tilting of aperture, a very deeply recessed, weak ridge without beading. Palatal barriers 3, all subperipheral, about equal in height, lower 2 reaching apertural margin, 3rd slightly recessed, all prominently and finely beaded above. Above periphery, a row of small tubercles represents remnants of a 4th palatal barrier (not visible in standard drawings of shell). Height of holotype 1.68 mm., diameter 4.54 mm.

Holotype. — Palau Islands: Angaur, Station 175, area north of shrine, near edge of guano pit at 75-100 ft. elevation. Collected by Kiyoko and Yoshio Kondo on April 18, 1936. BPBM 158267.

Range. — Angaur, Palau Islands.

Paratypes. — BPBM 158265-8, BPBM 158312-3.

Material. — All from type locality (173 specimens, same as list of paratypes).

Remarks. — The flattened or at most barely protruding spire is an immediate criterion for identification. Most examples had the spire flat, but rarely it was a trifle elevated. More variation was seen in the apertural barriers. The great majority of larger individuals had the columellar barrier a deeply recessed trace, often visible only by severe tilting of the aperture. In many younger individuals, however, the barrier reached nearly to the lip edge and was visible from all angles. Other young shells had the barrier recessed as deeply as in the type. The presence or absence of the supraperipheral palatal trace barrier showed no age-correlated pattern of variation. Even when present it was rather weak and time did not permit cleaning of enough apertures to work out its pattern of occurrence. About 45 apertures were checked with all stages of development being observed.

Only 29 of the 173 specimens were adult, and only 12 examples were collected alive.

Great pleasure is taken in dedicating this beautiful species to the late George G. Kinloch, whose early interest in his nephew's shell collection diverted me on the road to malacology instead of entomology.

Description of soft parts. — Foot and tail as in *A. constricta,* extended length less than diameter of shell. Sole and pedal grooves typical, no caudal horn or middorsal groove. Slime network weakly reticulated. Head protruded beyond edge of foot, ommatophores long, eyespot small, circular. Gonopore in normal position.

Body color yellow-white, no darker markings.

Mantle collar (MC) swollen in drowning, edges at parietal-palatal margin masking pneumostome, glandular extensions onto pallial roof extensive on lower part of palatal and parietal walls. Anus (A) without clear external groove through mantle collar.

Pallial region (fig. 200a) extending nearly two-thirds of a whorl apically, length about 5.8 mm. Lung roof clear, without granulations. Kidney (K) about 1.7 mm. long, base lying above intestinal loop, head of spermatheca indenting lower side, part of kidney abutting on hindgut. Ureter (KD) a wide tube opening (KX) where kidney reaches hindgut margin. Heart (H) slightly more than half length of kidney, nearly paralleling hindgut. Principal pulmonary vein (HV) simple, unbranched, paralleling hindgut, fading out short of mantle collar. Hindgut (HG) typical.

Ovotestis (G) (fig. 200b) typical of subfamily, individual alveoli appearing iridescent. Hermaphroditic duct (G) long, more convoluted than in *A. constricta,* narrowing abruptly and running straight before entering carrefour (X). Latter smaller and more elongated. Albumen gland (GG) of loosely connected alveoli, opening into head of uterus. Talon (GT) very elongated, slender, lying imbedded in surface of albumen gland. Prostate (DG) short, a slender tube into which three rows of large acinar alveoli empty, lying next to uterus but not attached in any way. Uterus (UT) a thin-walled tube, slender above, broadly expanded for basal three-eighths, sharply constricted just before entering free oviduct (UV).

Vas deferens (VD) slender, passing down to penioviducal angle, then up alongside penis to enter head of epiphallus. Vas not bound to other organs, but lying free. Epiphallus (E) sharply delineated from vas deferens, one-half length of penis, internally with two longitudinal pilasters that continue into penis. Penial retractor (PR) arising from diaphragm just below apex of pallial cavity, inserting onto apex of epiphallic-penial loop and fusing with tissue. Penis (P) about 1.7 mm. long, tapering from upper section to distal end. Epiphallic pilasters continuing into penis, one splitting to form a weak pocket, the larger arm continuing into atrium (not shown in fig. 200c), shorter arm ending. Second pilaster extending to atrium. Atrium (Y) long, with 2-3 pilasters.

Free oviduct (UV) and spermatheca (S) as in *A. constricta.* Vagina (V) absent.

Free muscle system as in *A. constricta.* Digestive system differing from *A. constricta* only in having stomach extend over a slightly longer area.

Jaw fragmented on mounting, separate plates four or five times as long as wide, not fused.

Radula with 6 laterals, marginal sections folded under in mount. Central tooth about 6-7μ wide, 7μ long.

(Based on BPBM 158265, BPBM 158266, five examples, whole specimen diameter 4.90 mm. with 5¼ whorls.)

ZOOGEOGRAPHY

Throughout much of the Pacific Islands region, the Endodontidae and the Charopidae have overlapping distributions. Both families were common or at least represented in Palau, the Lau Archipelago of Fiji, Ellice Islands, Tonga, Western Samoa, American Samoa, Cook Islands, and the Society Islands quite early in this century. The Endodontidae extended further into Polynesia and speciated widely in the Tuamotu, Austral, Marquesas, Gambier, and Hawaiian Islands. Both families are known as fossils from the Marshall Islands. The Charopidae are common in the Mariana, Caroline, Palau, Fiji, Tonga, Ellice, Western Samoa, American Samoa, Cook and Society Islands, plus many extra-limital Pacific areas, including Juan Fernandez, Kermadec, Lord Howe, Norfolk, New Caledonia, New Hebrides, and the Austrozelandic region. Detailed zoogeographic analysis is deferred until Part II of this monograph, since questions of species diversity, island area and species abundance, possible replacement phenomena, and relative abundance species require discussing both families.

Thus the present discussion is limited to a review of the general distributional patterns found in the Endodontidae, and a few comments on the Rapa Island radiation. Earlier (pp. 107-108) evidence was presented for the Endodontidae being a more generalized group than the Charopidae. It was suggested that the Charopidae could be derived from the endodontid structural patterns, but not the reverse. The fact that some genera of extant Charopidae show relict Gondwanaland distributions (Solem, *unpublished*), whereas the Endodontidae are strictly Pacific Island inhabitants, leads to difficulties in zoogeographic interpretation according to today's conventional wisdom.

It is virtually universally accepted now that the Polynesian Islands have been populated by overseas dispersal in quite recent times. The brilliant synthesis of Zimmerman (1948) has been amply bolstered by subsequent studies. Yet the highly endemic and antique nature of the Pacific Island land snail fauna, first pointed out by Pilsbry (1900b), and subsequently commented on by Pilsbry (1916, 1921), Cooke (1926), Germain (1932, 1934), and Solem (1959a, 1969c) cannot be dismissed. The recent demonstration (Solem and Yochelson, in press) that one of the earliest known fossil land snails, the Pennsylvanian *Anthracopupa,* cannot be separated on more than generic level from the present day Tornatellinidae, also basically restricted to the Pacific Islands, serves to reinforce the phyletic age of these taxa. There is ample evidence of sea-floor subsidence in Micronesia, and the former high-island status of Bikini, Eniwetok (Leopold, 1969), and Midway (Ladd et al., 1967, 1970) atolls has been well established by work of the past decade. The exciting data from plate tectonics are creating a revolution in the zoogeographic interpretations of continental areas, but to date has shed little light on the problems of Pacific Island organisms.

Prior to the Tertiary, there undoubtedly were many more islands in the Pacific Basin than there are today. Gaps between islands would have been less, hence the chances for successful overseas dispersal greatly increased over those that now exist. While probably few, if any, of the present islands date from earlier than the Eocene, the existence of many scattered islands in the Pacific Basin must be accepted. Hence I stand by my earlier conclusion (Solem, 1959a, p. 326) that "...the present land snail fauna of the Pacific Islands originated in at least the early Mesozoic and has been able to survive by being passively dispersed at *very* infrequent intervals from island to island."

The proposed great age of the Pacific Island land snail fauna thus stands in great contrast to the very recent vintage proposed for the other components of the fauna and flora, yet it is consistent with available fossil and biogeographic evidence.

The fossil land snails from Bikini and Eniwetok (pp. 116-118) all can be assigned to modern species groups, although ranging in age to mid-Miocene. In a biogeographic sense, they demonstrate the presence of both Endodontidae and Charopidae in the Marshall Islands during the Miocene to Pliocene. Both groups subsequently became extinct as the high islands sunk and became atolls. These fossils demonstrate that little shift occurred in basic distributions, other than range restrictions because of extinctions, since the Miocene. The fossils yield no data concerning actual rates of evolution, since they are referable to extant species groups. The two endodontid fossils, *Cookeconcha subpacificus* (fig. 92) and *Minidonta inexpectans* (fig. 62d), both belong to the most generalized extant groups (figs. 57, 58), while the two charopids belong to highly specialized genera. *Cookeconcha* is limited to the Hawaiian Islands, while *Minidonta* has a fringing distribution around the

Cook-Society-Tuamotu-Austral-Marquesas center of diversification (pp. 128-129). The most generalized species of *Minidonta* are found on scattered islands (Henderson, Mangareva, Raivavae, the Manua group of American Samoa) and fossil on Bikini Atoll. Specialized species lived until recently on Mangareva (*simulata* group), Raivavae and Rurutu (*anatonuana* group), Raivavae (*micraconica* group), and Aitutaki (*rotellina*). The 2,700 mile range, Henderson to Samoa, does not include the Pliocene or Pleistocene Bikini species, which effectively doubles the known distributional range.

Primary derivatives from *Minidonta* (figs. 57, 58) include *Mautodontha* (Cook, Society, Tuamotu), *Anceyodonta* (Mangareva), and *Australdonta* (Austral Islands exclusive of Rapa). *Mautodontha* probably represents the stem group for *Taipidon* (Marquesas) and *Opanara* (Rapa) of the genera extra-limital to its basic distribution, plus local derivatives such as *Kleokyphus* and *Pseudolibera* in the Tuamotus, and *Nesodiscus* and *Libera* in different parts of the Society and Cook Islands. *Gambiodonta* and *Rikitea* are local Mangarevan developments, while the Marquesan *Planudonta* evolved locally from *Taipidon*. On Rapa, there was an extensive radiation (see below). In Hawaii, *Cookeconcha* represents the group from which both *Endodonta* and *Nesophila* are descended.

The vast majority of the endodontid genera thus show a quite coherent and simple distributional pattern clustered around the two generalized taxa, *Minidonta* and *Cookeconcha*. The latter led to the Hawaiian radiation; the former produced the Polynesian diversity, with the Rapan and Marquesan genera representing the greatest degree of anatomical change from the generalized *Minidonta*. Since *Cookeconcha* is known as a Miocene fossil and *Minidonta* as a Pliocene or Pleistocene taxon, the conventional interpretation would be to view these as relatively recent radiations, probably occurring no earlier than the Miocene and much more probably in the Pliocene or Pleistocene. Arguing against this are three major facts: 1) the peculiar distribution shown by the most advanced endodontids; 2) the total absence of endodontids from other areas of the world; and 3) the very generalized, "protosigmurethran" anatomy of the Endodontidae.

Thaumatodon, *Aaadonta*, *Zyzzyxdonta*, and *Priceconcha* are an anatomically uniform group of genera that are sharply distinguished from the remaining endodontids (pp. 110-112). *Aaadonta*, which is specialized in shell sculpture, is restricted to the Palau Group; *Zyzzyxdonta* and *Priceconcha* are specialized taxa from Lau Archipelago; while *Thaumatodon* ranges from Lau and Ellice Islands to Rarotonga, with a relatively simple intrageneric distributional pattern (pp. 446-448; fig. 190). The most generalized species are *T. decemplicata* (Mousson) from Vaitupu and Nukufetau in the Ellice Islands, plus *T. multilamellata* (Garrett) from Rarotonga, Cook Islands. *T. hystricelloides* (Mousson) from Upolu, Western Samoa, and two Tongan species, *T. euaensis* from Eua and *T. vavauensis* from Vavau, show a coherent pattern of greater specialization. Four species from the Lau Archipelago, *T. corrugata, T. subdaedalea* (Mousson), *T. laddi,* and *T. spirrhymatum,* show yet a third level of specialization. These occurrences are most easily interpreted as representing a radiating pattern outward from a focus on the Lau Archipelago, with the Ellice and Cook species representing one wave, the very similar Tongan and Samoan snails a second, and the most specialized Lau taxa forming a third group from which the local genera, *Priceconcha* and *Zyzzyxdonta,* were derived. The Palau Island *Aaadonta* shows a different pattern of conchological specialization (loss of major radial sculpture, keel development) than any of the species groups in *Thaumatodon,* but is unquestionably very closely related, despite its retention of low penial pilasters.

Thus this complex of genera has a distributional pattern suggesting dispersal from the "New Guinea core" with subsequent extinction in the core region. Despite their obvious specializations, they are endodontids, although with a distinct structural gap from the other genera. In comparison with the Charopidae, the "*Thaumatodon* complex" species have penetrated a shorter distance into both Micronesia (charopids are common on the Caroline and Mariana Islands) and Polynesia (charopids reach the Society Islands). Whereas the bulk of endodontid genera suggest *in situ* radiation, the *Thaumatodon-Aaadonta* complex suggests colonization after diversification.

As emphasized repeatedly, no endodontids are reported from other parts of the world, and the anatomy of the Endodontidae is the most generalized of the sigmurethran lineage. The Charopidae are dominant in Australia, New Zealand, New Caledonia, South Africa (Solem, 1970c), southern South America, and a few islands such as Lord Howe and St. Helena, but are only weakly represented in New Guinea (Solem, 1959b, 1970a) and Indonesia (Solem, 1964). They seem to have been replaced by the more advanced limacoids and helicoids in most continental areas. As mentioned above, some charopid genera show relict Gondwanaland distributions, yet the Charopidae have colonized more of the Pacific Islands than the advanced endodontids of the *Thaumatodon-Aaadonta* lineage.

The endodontids thus present a distributional anomaly, in that their most generalized complex shows a simple and coherent Polynesian radiation pattern, yet their most advanced group shows a less successful Pacific Island colonization pattern than does the Charopidae, a family with Gondwanaland relict distributions that itself has been effectively replaced on continental areas. The Charopidae could be derived from the Endodontidae, but not the reverse. Explanation of this pattern must be speculative, at least until the relationships within the Charopidae are sorted out, but one hypothesis can be offered as a thought-provoking suggestion. Based on recent work on plate tectonics in the Australian region, summarized by Raven and Axelrod (1972), I suggest that the Charopidae came north with the Australian plate, gaining entrance to the Polynesian region when the Pacific and Australian plates collided and underwent fragmentation about the Eocene. New Guinea is a highly complex mass of tectonic fragments. It is conceivable that the advanced endodontids were present on the pre-Australian plate-New Guinea collision area, were able to start their colonization movement as an early byproduct of the initial collision, only to be subsequently replaced by Asian taxa and bypassed by the more vagile charopids. This assumes that 1) the generalized endodontids have been stable on the Pacific Islands since the Mesozoic; 2) advanced endodontids (*Aaadonta-Thaumatodon*) date from early Eocene to pre-Eocene; 3) charopids are a late Eocene to post-Eocene wave of immigrants into the Pacific; and 4) endodontids and most charopids have been replaced in the Indonesia-New Guinea axis by advanced continental land snails of Asian origin probably in Oligocene or more recent times.

The above summarizes the basic outline of distribution, with more detailed discussions postponed until data from the Charopidae can be incorporated to provide discussions of abundance and local diversity. It is appropriate, however, to review here the distribution patterns of the quite extraordinary Rapa Island radiation. This comprises one-eighth of the total species, one-fifth of the genera, and 22 per cent of the total specimens reviewed in Part I. Because anatomical and detailed locality data were available, far more can be said about the patterns on Rapa than for other islands of the Pacific.

Sometime between May 13 and May 17, 1828, Hugh Cuming, or one of his assistants (see St. John, 1940 for Cuming's itinerary), collected *Ruatara oparica oparica* on Mt. Tanga, Rapa. It is surprising, in view of the many tornatellinids and other species dating from this trip, that only one Rapan endodontid was taken by his party. Almost 100 years later, in July, 1921, Mrs. A. M. Stokes collected 10 specimens of *Ruatara oparica normalis* near Morongoto.

All of the remaining 4,078 endodontids studied during this project were assembled by members of the Mangarevan Expedition from the Bernice P. Bishop Museum during the month of July, 1934. Brief discussions of the mollusks collected on Rapa have been published by Cooke *in* Gregory (1936, pp. 45-47) and Kondo and Clench (1952, pp. 81-21). From published data and the field notebooks in the Bishop Museum, it is obvious that more intensive collecting was done on Rapa in July, 1934 than ever has been done on any other Polynesian Island.

Rapa Island is the remnant of a large volcanic crater, open at one side to the sea, with a rim of steep mountains, ranging from 600-2,000 ft. elevation. There is some valley formation (Chubb, 1927, pp. 293, 295), but much of the terrain is nearly vertical (Cooke and Kondo, 1960, p. 23, top). While Fosberg and St. John reached the top of its highest mountain, Mt. Perahu, most collecting was done at lower elevation. Quoting Cooke *in* Gregory (1936, p. 45) "A very large part of the island has been burned over by the natives." Earlier on the same page, he indicated that "The peaks, where not too precipitous, and the heads of the valleys and gullies are well covered with endemic forests." Even in 1934, much of the native forest had been denuded, and Clarke (1971, p. 9) reported that forest cover had shrunk subsequently. As outlined above (p. 101), it is quite possible that the endodontid radiation is now extinct.

The 4,105 specimens of Rapan endodontids belong to five genera and 17 species. Thirteen of the species are monotypic, one has two races; and three species have three geographically isolated morphs. Soft anatomy was illustrated for 22 of the 24 taxa and parts noted for the other two. These species form a monophyletic unit, separated from extra-limital taxa primarily by modifications in the penial region. From any single extralimital genus the Rapan taxa show different average patterns of conchological criteria, but the basic difference is anatomical. The typical penial pilaster pattern in the Endodontidae is for two equal-sized pilasters that unite apically and normally are at most slightly higher than wide. In the Rapan taxa, unless secondarily modified, the pilasters are much higher than wide and form lamellar stimulatory organs. *Rhysoconcha* is secondarily modified to the low pattern, and in *Ruatara* there is fusion of the two pilasters into one, probably as an elaboration of the pilaster change seen in *Opanara perahuensis* (fig. 97i). Generally the Rapan species have a fleshy extension to the penis head, a character shared with *Australdonta* and the Marquesan genera, but this apparently has been secondarily reduced in several Rapan species. Changes in talon length, shape of the hermaphroditic duct, and relative lengths of the prostate-uterus are minor.

Opanara is the most generalized genus found on Rapa, and represents an approximation of the base stock from which *Rhysoconcha, Ruatara, Orangia,* and *Kondoconcha* were derived. *Rhysoconcha* is the result of secondary size reduction (pp. 255-256), and the changes shown by the *Rhysoconcha* species are sufficiently large that it is impossible to equate current species groups of *Opanara* with the possible ancestral form leading to *Rhysoconcha.* To the limited extent that it has an exceptionally high mean whorl count and lacks a fleshy extension to the penis head, *O. depasoapicata,* one of the smaller *Opanara,* suggests how the reduction trend might have started.

It is not considered to be an intermediate or ancestral form.

Ruatara is characterized by umbilical closure through contraction, coiling of the hermaphroditic duct, presence of only a single pilaster in the penis which lacks a fleshy extension to the head, has a distinct vaginal region and an elevated spire. *Opanara perahuensis* has the umbilical form and elevated spire of *Ruatara*, while the penial pilaster pattern is intermediate between the condition found in typical *Opanara* and the modified *Ruatara* pattern. The apical genitalia of *O. perahuensis* are unknown, but the remaining features of the terminal genitalia, shell sculpture, and apertural barriers are of the *Opanara* pattern. While *O. perahuensis* indicates how the distinctive features of *Ruatara* can be derived from the *Opanara* structures, it is not an intermediate species. There are, however, more similarities between *Ruatara* and *Opanara* than between any other pair of Rapan genera.

Orangia shows more conchological than anatomical changes, the latter consisting mainly of talon elongation and unequal size of the penial pilasters. The species of *Orangia* show rather gross differences in penial size and pilaster formation (fig. 121), but otherwise it is anatomically conservative. Conchological differences of greatest importance are the reduction to 2 parietals, closure of the umbilicus by lip reflexion (fig. 118), tendency toward development of a keeled periphery, weak supraperipheral sulcus, and development of secondary spiral sculpture. The form of umbilical closure is quite different from that seen in *Ruatara*, which is simple umbilical contraction. *Opanara*, *Ruatara*, and *Rhysoconcha* all show no tendency toward formation of a keel, secondary sculpture, or a supraperipheral sulcus. *Kondoconcha* is similar to *Orangia* in having only 2 parietals, developing a tendency toward peripheral angulation, and in its large size. The open umbilicus, striking reduction of sculpture, unique development of lateral accessory lamellae on the parietals, very high whorl count (mean 6⅜ –) and many accessory palatal traces offer a marked contrast to *Orangia*. Separate derivations of *Orangia* and *Kondoconcha* from the *Opanara* base stock are certain. Their similarities are correlatives of large size, while their differences are not size dependent.

Geographical patterns of distribution on Rapa are consistent with the idea of *Opanara* being generalized and close to the basic structural pattern of the colonizing stock, while the other genera are more specialized and structurally modified. Distribution patterns of *Opanara* are shown in Figures 99, 100, and 101. The closely related *O. altiapica* and *O. caliculata* plus *O. megomphala* show a relict pattern of geographically isolated populations restricted to small areas. *O. areaensis* has a moderately wide distribution in lowland areas, with two pockets of subspeciation, one (*densa*) contiguous to the main area, the other (*microtorma*) isolated by geographical distance (fig. 101). All the remaining species are restricted, so far as is known, to the upper reaches of Mt. Perahu (fig. 99). The gross differences in penial size and alteration in penial pilasters seen in the Mt. Perahu species (figs. 96b, d, f, h; 97b, i) are far greater than the differences seen between the geographically isolated taxa. Since the Mt. Perahu species live at the same stations, emphasis of isolating mechanisms is required to lessen the possibility of accidental interspecific matings and thus preserve specific isolation.

Of the derivative genera, *Orangia* has the greatest morphologic gap from *Opanara* and shows the greatest degree of internal differentiation. The most specialized species, *Orangia sporadica* and *O. maituatensis*, are widely distributed or geographically isolated, respectively, in lowland areas, while the least specialized form, *O. cookei*, is fragmented into isolated subspecies and reaches higher elevations (fig. 117). *Kondoconcha* is known only from the restricted area between Morongoto and Mt. Tevaitahu at about 750 ft. elevation and thus is not referable to any particular geographic pattern. *Rhysoconcha* (fig. 109) is widely distributed at lower and middle elevations, but apparently does not reach the upper elevations. *Ruatara* is, at the same time, the most widely distributed and least clearly internally differentiated genus. It is quite common at low and middle elevations, but also reaches 1,850 ft. on Mt. Perahu and 1,000 ft. on Mt. Mangaoa. A subspecies with greatly reduced palatal barriers has developed in one lowland area (*reductidenta*), while a form with normal barriers, crowded ribbing, and reduced size lives at intermediate elevations on Mt. Tanga (*oparica*). Besides the nomenclaturally recognized subspecies, there is a dichotomy in regard to number of parietal barriers between the northern and southern parts of Rapa (pp. 268-269).

There is a clear pattern on Rapa of generalized species being confined to or mainly present at higher elevation, while derivative taxa are prevalent at lower elevations, showing subspeciation tendencies when penetrating to upper elevations. This pattern does suggest that species replacement has occurred and that competitive exclusion may exist. Analysis of station records and discussion of relative abundance will be given in Part II.

The most striking morphological change on Rapa concerns the frequency of umbilical closure. Of the 185 endodontid taxa, seven of the eight with closed umbilici, (the other is the Cook Island *Mautodontha punctiperforata*), and all three taxa with barely perforate umbilici are found on Rapa. This closure has been effected at least two different times, since the pattern in *Ruatara* is closure by simple contraction, while in *Orangia* the closure is effected by reflection of the columellar lip over a narrowed umbilicus (fig. 118). On Mangareva, there is frequent narrowing of the umbilicus until the last whorl decoils rapidly (figs. 83b; 87f) or the umbilicus remains very narrow (figs. 81b; 90b, c, f). In all other areas, with rare exceptions, the umbilicus is widely open or modified to form a brood chamber.

Rapa is by far the most southern of the Polynesian Islands from which endodontids are known and is washed by a cold current. Almost certainly the warm equatorial countercurrent never extends this far south. The climate is temperate, with mean temperatures of 76°F in summer and 58°F in winter. Although rainfall statistics are limited (Clarke, 1971, p. 11), the position of the island is such that a relatively evenly spaced and extensive rainfall pattern is indicated. The growing of coffee at low elevations (500 ft.) similarly implies wet conditions. Under these circumstances, the need for an umbilical brood chamber is lessened and the inconvenience of arthropod egg laying in the umbilicus could combine to provide selective pressure for umbilical closure.

The second major change on Rapa concerns a pattern of variation within species. In several species, *Opanara areaensis, Opanara megomphala, Ruatara oparica,* and *Orangia cookei,* there have been subspecies developed characterized by reduced diameter, reduced whorl count, increased number of major radial ribs, and greatly increased crowding of the radial ribs. Two pairs of species, *Opanara altiapica* and *O. caliculata,* then *Rhysoconcha variumbilicata* and *R. atanuiensis,* have similar variations, but in a different pattern. In these pairs, the largest morph has the increased rib count, much more crowded ribbing, and possibly a lower whorl count, although the evidence for the latter is fragmentary as yet.

SUMMARY

The 154 non-Hawaiian species of Endodontidae are reviewed in detail and the 31 Hawaiian taxa are surveyed to a lesser extent. A total of 102 species level taxa and 19 genera are described as new (see "List of Taxa," pp. 122-124).

Patterns of conchological and anatomical variation within the family are reviewed and correlated patterns of variation outlined. Shell sculpture, for example, is shown to become greatly reduced in prominence once a shell size of 4.75 mm. is attained, but variation in the characteristic apertural barriers is more phyletically correlated than size influenced. Progressive anatomical trends within the Endodontidae include two experiments in forming an epiphallic zone, one by adding glandular tissue between the penis apex and penial retractor muscle, the other by forming an epiphallic section to the penis. Marquesan genera show a unique additive pustulose zone in the penis.

Sympatric congeners are demonstrated to differ in terminal genital structures, suggesting character displacement has occurred to aid species isolation.

The species are shown to follow a repetitive pattern of specializations in different areas, termed the *Minidonta, Mautodontha, Nesodiscus,* and brood-chamber levels (figs. 57, 58). Each level shows distinctive conchological features, but arrived at in different ways in each geographic area.

Major emphasis is given to determining direction of character change and to place the endodontids within a broader context of land-snail phylogeny. New interpretations of land-snail phylogeny are outlined, and a revised family classification of the endodontoids proposed.

The monograph ends with a brief review of overall zoogeography of the endodontids and a review of local distribution and variation patterns on Rapa Island.

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APPENDIX

Explanation of anatomical abbreviations used on illustrations.

A - anus
B - buccal mass
BE - esophagus
BGN - buccal ganglion
BR - buccal retractor
CR - columellar retractor
DG - prostate
DP - vas opening into penis or epiphallus
E - epiphallus
EP - pore from epiphallus into penis
F - foot
FS - foot grooves
G - ovotestis
GD - hermaphroditic duct
GG - albumen gland and ducts
GT - talon
H - heart
HG - hindgut or rectum
HV - principal pulmonary vein
I - intestine
IZ - stomach
K - kidney
KD - ureter
KX - ureteric pore
LP - pneumostome
MC - mantle collar
MD - mantle retractor muscle
MG - mantle glands
OG - salivary glands
OGD - salivary gland ducts
P - penis
PP - penial stimulator, papilla or pilaster
PR - penial retractor muscle
S - spermathecal shaft and its sac
TE - ommatophores
TV - rhinophoral tentacle
UT - uterus
UT_1- section of uterus
UT_2- section of uterus
UT_3- section of uterus
UT_4- section of uterus
UV - free or post-uterine oviduct
V - vagina
VD - vas deferens
X - carrefour
Y - genital atrium
Z - digestive gland or liver

INDICES

Two indices are presented, a geographic and a systematic. The geographic lists every reference to that unit in the monograph, without differentiating between description, discussion, and biogeographic content. The systematic index discriminates between mention in a table, distribution figure, or text (Roman type); illustration of shell, anatomy, or in a graph or diagram (*italics*); and the principal systematic discussion (**bold face**). In the systematic index, to save space, cross-referencing is limited to the principal systematic discussion for species reviewed in this monograph.

Systematic Index

Geographic Index