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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

BIVALVE MOLLUSKS OF THE WESTERN BEAUFORT SEA

By F.R. BERNARD



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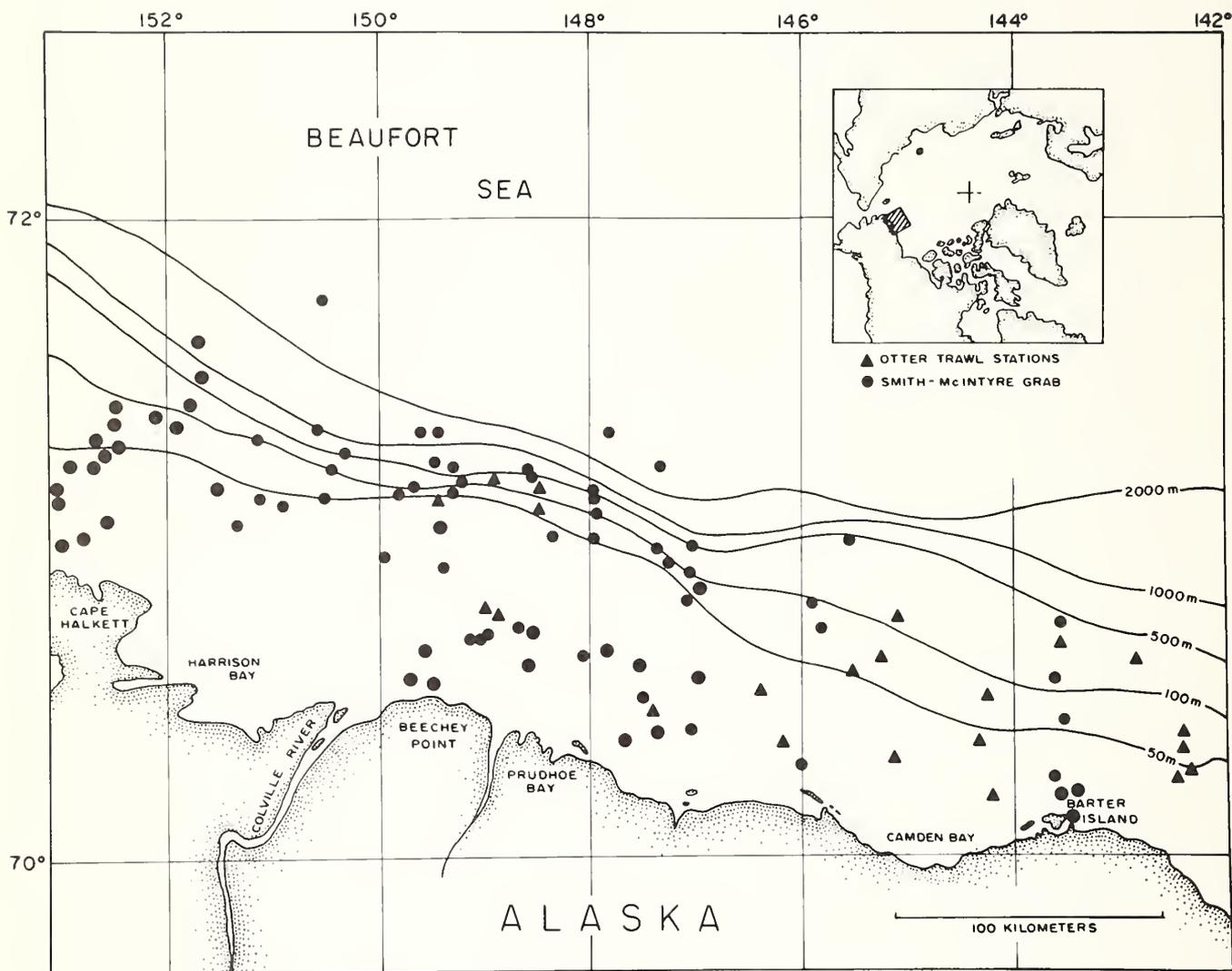
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BIVALVE MOLLUSKS OF THE WESTERN BEAUFORT SEA^{1,2}

By F.R. Bernard³

ABSTRACT: This report is a systematic review and identification guide to 58 species of bivalve mollusks collected between 0–2560 m in the western part of the Beaufort Sea. Oceanographically the region is an integral portion of the Arctic Ocean, but faunally it consists of contributions from both the Atlantic and Pacific oceans. Six species are stenobathyal endemics with no close boreal relatives, their presence showing that at least a fraction of the deep-water benthic fauna survived the past several periods of glaciation. During these periods the shelf was emergent and ice-scoured and its fauna obliterated. As conditions ameliorated, adaptable species migrated from adjacent boreal seas, notably the Beringia refugium and also the Atlantic sector to colonize the newly submerged shelf. 24 species are of Atlantic and 20 of Pacific origin, a pattern probably largely dictated by the oligohaline region of the Mackenzie River estuary which is an effective barrier to many species. The fauna is not depauperated and is numerically comparable to temperate regions with similar limited habitat niches.

One new genus, *Boreacola* in the family Montacutidae, with the new species *B. vadosa* is described. A new species, *Axinulus careyi* in the family Thyasiridae is also proposed.

The many thousand specimens were collected by Oregon State University and supplemented with material collected by Western Washington State College and the United States Geological Survey.

INTRODUCTION

The marine biota of the Arctic Ocean is of particular significance as it provides a partial key to the complex evaluation of the northern boreal faunas. Mollusks, especially the Bivalvia, are important as they are abundantly represented in Tertiary and Quaternary deposits and may be used to follow periods of interchange and colonization between the Pacific and Atlantic oceans. The continental shelf of Arctic Alaska and Canada is a critical region for the interpretation of northern faunal distribution, as it is near the Bering Strait and is one of the two possible dispersal routes from adjacent regions.

The bivalve mollusks that are the subject of this report were largely collected by A. G. Carey, Jr., of the School of Oceanography, Oregon State University, supported by National Science Foundation grant GA-36679 and by Exxon, U.S.A., with a grant to the Smithsonian Institution, during the summers of 1971, 1972, and 1976. The series of bottom stations occupied by Smith-McIntyre Grab and Otter Trawl samples comprise the most comprehensive coverage to date of the Beaufort Sea from 10–2560 m (Frontispiece). A preliminary report on the general ecology of the benthos has already appeared (Carey et al., 1974). This material was supplemented by 16 quantitative and qualitative stations taken in 49–1289 m by United States Geological Survey with R/V Glacier in 1976, collected by A. Grant and R.

Arnold, the bivalves submitted to me by the kindness of L. Marincovich, Jr. Additional material, particularly from shallow water, was examined at Western Washington State College.

The Beaufort Sea is an integral part of the Arctic Ocean, extending over 30° of longitude between Point Barrow, Alaska, and the westernmost islands of the Canadian Arctic Archipelago (Frontispiece). It encompasses the continental shelf of North America which extends on average 150 km northwards, and drops rapidly into the Laurentian or Canadian Basin. The Beaufort Sea is strongly influenced by the outflow of the Mackenzie River, the major drainage north from the American continent

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which results in an extensive superficial estuarine zone. This inflow of cold fresh water, coupled with the net eastwards current, make Point Barrow a boundary between the relatively warm saline Chukchi Sea, and the much colder, more brackish Beaufort Sea extending east to Banks Island where the salinity and temperature increase (Tully 1952). The oligohaline estuarine waters of the Mackenzie overlie the high salinity Arctic waters, but the high turbidity of the widespread river plume influences primary productivity, and the continuous settlement of sediments influences the character of the continental shelf bottom. A low annual primary production is indicated for the entire region (English 1961, Grainger 1975).

Many thousands of bivalves, representing 58 species were present in the survey area, and include virtually the entire known fauna of the region. This report describes the species, discusses the taxonomy, and presents illustrations. Outside the untranslated Soviet literature, no comprehensive reference to the regional fauna is available, so this effort is directed primarily as an identification guide for biologists monitoring the benthic ecology of the region. Quantitative aspects of the benthic ecology and its statistical treatment, will be published by others.

ACKNOWLEDGMENTS

The collection was made available through the auspices of the Natural History Museum of Los Angeles County, and I am indebted to J.H. McLean, curator of Malacology, for his kind assistance. The major part of the review was undertaken at the National Museum of Canada and I am grateful to the curator A.H. Clarke for permitting me access to the American Arctic and boreal collections. The extensive collections of the British Museum (Natural History), particularly material from the early Arctic explorations, and British Crag series of fossils, were examined. The MacGinitie and Dall specimens in the United States National Museum of Natural History were also consulted, as well as the relevant collections in the Redpath Museum, McGill University. At various times critical comparisons were made with the Arctic materials of the Universitets Zoologiske Museum, Copenhagen; the Zoologica Museum, Oslo; the Naturhistoriska Riksmuseet, Stockholm; the Museum d'Histoire Naturelle, Paris; and the Royal Scottish Museum, Edinburgh. I am very grateful to the curators and staff of these and other institutions for their assistance and advice during my visits and for various suggestions acknowledged in the text. I am indebted to A.H. Clarke, now of the U.S. National Museum of Natural History, for his kind criticism of the manuscript, to D.M. Hopkins, U.S. Geological Survey, for many helpful suggestions, and to R. Baxter of the Alaska Department of Fish and Game, for his comments and loan of material.

PREVIOUS RESEARCH

Knowledge of the existence of an ocean occupying the north polar region may be dated from Nansen's voyage of the *Fram* (1793-96), but some molluscan descriptions appeared earlier, for example Fabricius (1786) discussed and named a number of Arctic Greenland species. Despite this early biological interest, the difficulties of polar exploration, coupled with the high degree of morphological plasticity and the complex biogeography of a fauna subjected to numerous, sometimes catastrophic, environmental changes, result in the Arctic being one of the least under-

stood biological regions. The fauna of the Eurasian Arctic is relatively well known (Zenkevitch 1963), and the bivalves of east Greenland have been thoroughly reviewed by Ockelmann (1958). The American Arctic is less known, particularly the Beaufort Sea area. The earliest published report is by Dall (1919), dealing with materials collected by the Canadian Arctic Expedition (1913-18). The western boundary of the Beaufort Sea was covered by the intensive studies of G. MacGinitie (1955) and the mollusks were reported by N. MacGinitie (1959), but the only published works dealing with the Beaufort Sea region proper are a brief report by Hulsemann (1962), listing 12 bivalve species from 15 shallow water (4-23 m) stations taken by the United States Coast and Geodetic Survey in 1953. The Canada Department of the Environment has supported studies in the Canadian portion of the Beaufort Sea, and after this paper was drafted, Wacasey (1975) published a preliminary report listing marine invertebrates, chiefly from the Mackenzie Bay area. The bivalve fauna appears sparser, but includes many of the species identified here, indicating a degree of homogeneity in the bivalve fauna. After completion of the present paper, I received a copy of a palaeobathymetric discussion and list of mollusks collected east of Herschel Island (Wagner 1977). I have not examined the specimens but have added them to the *Records* section and included additional species in the discussion.

BIOGEOGRAPHY

There is little doubt concerning the great age of the Arctic Ocean Basin (Eardly 1948), which was certainly established in the Cretaceous (Herron et al. 1974), but the contemporary fauna does not appear ancient, or even well-established. Substantial Mesozoic sedimentary features indicate a close affinity with the Pacific, but no evidence supports the assumption that the contemporary fauna is a Mesozoic relict. The origin of this fauna is subject of continuing debate, the majority of workers subscribing to a diverse boreal origin, but extreme schools exist. The one represented by Gur'yanova (1939), who considered it almost entirely derived from the Atlantic Pleistocene, the other by Gorbunov (1946b), who thought the present Arctic fauna to be exclusively of Pacific origin.

The Bering Strait opened and closed repeatedly in the late Miocene, Pliocene and Pleistocene; Hopkins (1973) reviewed and interpreted the sequence of fluctuating sea levels of the Bering Sea. These changes in climatic and geographic features were accompanied by periods of migration and local extinction of benthic invertebrates. Substantial faunal exchange between the Pacific-Arctic and Atlantic is evident after the Upper Pliocene, though the Arctic route was probably open long before this. This led Strauch (1970) to present convincing evidence to resurrect the hypothesis of the Thule Land Bridge. This body of land, now represented by the North Atlantic islands, separated the Atlantic Ocean and the Norwegian Sea, permitting only indirect and ephemeral channels until its submergence at the end of the Pliocene. The presence of this barrier allowed Pacific migrants to colonize only the American Atlantic and Greenland shelves.

At the peak periods of glaciation, it is doubtful that any open waters remained and the entire boreal continental shelf was ice-scoured. The scale and nature of these climatic changes probably resulted in the extermination of entire groups, and the rapidity of the change precluded local genetic adaptation. While it is probable that abyssal groups remained, it is almost certain that during these severest glacial episodes the Arctic continental shelf was a

tabula rasa, to which, as conditions ameliorated, migrated adaptable species from adjacent boreal seas, notably from an endemic Arctic fauna bordering the Beringia refugium (Hultén 1937) on the Alaskan or East Siberian Sector. According to Hopkins (pers. comm.) the initial opening of the Bering Strait is associated with the Beringian faunas in Northern Alaska and the European Red Crag, and by the subsequent appearance of numbers of Pacific migrants in the Pliocene and Pleistocene sediments of Iceland (Einarsson & Hopkins 1967). Evidence in Alaska shows this event to be older than 2.2 m.y., and the Iceland correlation between 3.0 and 3.5 m.y. ago.

Faunal interchange through the Arctic Ocean must be correlated with periods of benign climate in the Arctic, followed by more severe regimes. The important migrations of Pacific species to Iceland occurred at least 0.5 m.y. and perhaps > 1.0 m.y. prior to the widespread Pleistocene glaciation of Iceland (Einarsson, Hopkins & Doell 1967). Though a permanent ice-cover has persisted on the Arctic Ocean for the past 70,000 y. (Herman 1970), it is evident that during the last glaciation the Arctic continental shelf area was free of glacial ice, and may have supported much reduced fauna. It is during the Middle Pleistocene glaciation (Illinoian) that the Arctic Ocean was icebound (Herman 1970) and the shelf and much of the deepwater fauna eradicated. Accepting this interpretation makes it likely that the contemporary Beaufort Sea fauna invaded the shelf after the retreat of the ice, during the last interglaciation, less than 100,000 y. ago. Further evidence is provided by the occurrence over a large area of the submerged shelf of frozen sediments and permafrost (Hunter et al. 1976). Some 20 to 40,000 y. ago the sea level lowered approximately 100 m below its present level during a period when the climate was sufficiently severe to form permafrost which was inundated 5 to 20,000 y. ago (Lewellen 1974).

If the present Arctic fauna is a young colonizing biocenosis with a very small endemic fauna as suggested by Clarke (1963), and with contributions from both the Atlantic and Pacific, it remains to discuss the relative importance of the contributing regions. The Atlantic species *Astarte alaskensis* Dall and *Hiatella arctica* (Linné) first appear in the Pacific in the Pliocene of the Gulf of Alaska (MacNeil 1965). The majority of transarctic migrants became extinct in the high Arctic, giving rise to isolated boreal populations, although a number did remain. Soot-Ryen (1932) listed 12 such species, but three did not become established in the Atlantic, and doubtfully even entered the Arctic (i.e. *Saxidomus giganteus* [Deshayes]; *Protothaca staminea* [Conrad]; and *Zirfaea gabbi* [Tryon]).

The appearance of the molluscan lists in the recent publications by Wacasey (1975) and Wagner (1977), covering that region of the Beaufort Sea extending approximately 128° to 140°W, are complementary to the present paper which covers 142° to 153°W. A synopsis of these collections and the species included by MacGinitie (1959) from Point Barrow (157°W), is given in Table 1.

TABLE 1.

Synopsis of bivalvia recorded in major collections from the Beaufort Sea area.

Species	MacGinitie 1959	Bernard	Wacasey 1975	Wagner 1977
<i>Arctinula greenlandica</i>		X	X	X
<i>Astarte borealis</i>	X	X	X	X
<i>A. crenata</i>		X	X	X
<i>A. esquimalti</i>		X		

<i>A. montagui</i> et form.	X		X	X
<i>Axinopsida orbiculata</i>	X		X	X
<i>Axinulus careyi</i>			X	
<i>Bathyarca frielei</i>				X
<i>B. glacialis</i>			X	X
<i>B. varidentata</i>			X	
<i>Boreacola vadosa</i>			X	
<i>Cerastoderma echinatum</i>				X
<i>C. elegantulum</i>				X
<i>Chlamys pseudislandica</i>	X		X	
<i>Clinocardium ciliatum</i>	X		X	X
<i>Crenella decussata</i>			X	
<i>Cuspidaria glacialis</i>			X	
<i>C. subtorta</i>			X	
<i>Cyclocardia crassidens</i>	X			
<i>C. crebricostata</i>	X		X	
<i>Cyrtodaria kurriana</i>			X	X
<i>Dacrydium vitreum</i>	X		X	
<i>Diplodonta aleutica</i>	X			
<i>Hiatella arctica</i>	X		X	X
<i>Limatula hyperborea</i>			X	X
<i>Liocyma fluctuosa</i>	X		X	X
<i>L. viridis</i>	X		X	
<i>Lyonsia arenosa</i>	X		X	X
<i>L. norwegica</i>				X
<i>L. schinkewitsci</i>				X
<i>Lyonsiella uschakovi</i>		X		
<i>Lyonsiella sp.</i>				X
<i>Macoma balthica</i>			X	X
<i>M. calcarea</i>	X		X	X
<i>M. loveni</i>			X	X
<i>M. moesta</i>	X		X	X
<i>M. obliqua</i>	X			
<i>M. torelli</i>			X	X
<i>Malletia abyssopolaris</i>		X		
<i>Modiolus modiolus</i>				X
<i>Montacuta dawsoni</i>		X		
<i>M. maltzani</i>			X	
<i>Musculus corrugatus</i>	X		X	X
<i>M. discors</i>	X		X	X
<i>M. niger</i>	X		X	X
<i>Mya arenaria</i>				X
<i>M. pseudoarenaria</i>	X		X	X
<i>M. truncata</i>	X		X	X
<i>Mysella planata</i>	X		X	X
<i>M. tumida</i>	X		X	
<i>Mytilus edulis</i>	X		X	
<i>Nucula bellotii</i>	X		X	X
<i>N. zophos</i>			X	
<i>Nuculana minuta</i>	X		X	X
<i>N. pernula</i>			X	X
<i>N. radiata</i>	X		X	
<i>Pandora glacialis</i>	X		X	X
<i>Panomya ampla</i>	X			
<i>P. arctica</i>	X			
<i>Periploma abyssorum</i>			X	
<i>P. aleutica</i>			X	
<i>Portlandia arctica</i>	X		X	X
<i>P. fraterna</i>			X	X
<i>P. frigida</i>			X	X
<i>P. intermedia</i>			X	X
<i>P. lenticula</i>			X	X
<i>P. tamara</i>			X	
<i>Pseudopythina compressa</i>	X			
<i>Serripes groenlandicus</i>	X		X	X
<i>Tellina lutea</i>	X			
<i>Tellina sp.</i>				X
<i>Thracia adamsi</i>	X			
<i>Thracia devexa</i>	X		X	X
<i>T. myopsis</i>	X		X	
<i>Thyasira equalis</i>			X	
<i>T. gouldii</i>	X		X	X
<i>Yoldia hyperborea</i>	X		X	X
<i>Y. myalis</i>	X		X	
<i>Y. scissurata</i>	X		X	

This table may serve as a check-list of the bivalve fauna of the Beaufort Sea. Until further collections are taken, particularly between Barter and Herschel Islands, distributional conclusions must be considered unreliable. From casual examination of Table 1 it is apparent that Point Barrow supports a fauna demonstrating close affinity with the Bering Sea, while the more eastern part of the Beaufort Sea has a stronger Atlantic connection, but the region west of Herschel Island has a more diverse bivalve fauna than that region influenced by the Mackenzie River. The record by Wagner (1977) of two species of *Cerastoderma* Poli 1795, typically a low Arctic and Atlantic genus is of particular interest and supports the notion that the oligohaline Mackenzie estuary is a potent barrier to westward penetration of shallow shelf fauna of Atlantic origin.

Of the 58 species in the OSU collection (Table 2), six are stenobathyal endemics with no close boreal relatives, and probably limited to the Laurentian Basin. Twenty-four are of Atlantic and 20 of Pacific origin. Seven are of unknown origin. This distribution is contrary to current concepts that Pacific elements are dominant (Durham & MacNeil 1967), supposedly due, in part, to the prevailing eastward currents of the American Arctic (MacNeil 1965), or the dispersive potential of the more diverse Pacific fauna (Ekman 1935). The eastward flowing currents have a dominant influence upon colonization patterns, especially for those species with planktonic larvae (rare in Arctic bivalves), but Huggett et al., (1975) emphasized the variability of the Beaufort Sea currents, featuring localized directional changes during ice-free periods, though the average trend is northeastern. There is no direct evidence to suggest that in the Pliocene and Pleistocene the dominant flow was easterly. Indeed, that most stable Arctic feature, the northward flow through the Bering Strait (Arsen'ev 1964), was reversed during the Kotzebuan Transgression (Mid-Pleistocene) with Arctic waters passing through the Bering Sea (Hopkins et al. 1972). This situation was certainly accompanied by a western flow along the shores of the Beaufort Sea, facilitating transmigration of Atlantic species.

The narrow and shallow Strait opening to the Bering Sea, compared to the wide Arctic-Atlantic connection, restricted colonization by Pacific species. The situation further favors Atlantic migrants by the massive influx deep into the Arctic of a northward extension of the Gulf Stream over the Faroe Island-Greenland Ridge. Brooding forms are relatively independent of prevailing currents, and in fact do colonize against them, though range extension is slow. An alternative path for Atlantic forms to the Beaufort Sea is via the Eurasian coasts, but it is likely that the Siberian Sea is an effective barrier to all except the most euryhaline forms, due to the presence of extensive oligohaline zones. The larval type will greatly influence the distributional ability of organisms. Planktotrophs are characterized by large dispersions from the established region when favourable conditions coincide with larval production. The majority of Arctic marine bivalves undergo lecithotrophic development (Thorson 1946, 1959), where metamorphosis is attained solely on nutrient matter in the egg. Mileikosky (1974) refined Thorson's scheme of classification and expanded it to include duration of pelagic life. If Arctic mollusks are separated into developmental groups, no overlying patterns are evident: some lecithotrophs have a limited distribution, while planktotrophs include some most successful colonizers. Chia (1974) advanced the view that, rather than the direct effect of limited availability of pelagic food for the larvae, the change is one of the metabolic partitioning of the resources of

TABLE 2.
Synopsis of bivalves collected in the Western Beaufort Sea, with their distributions and postulated areas of origin.

	Endemic	Arctic	Panarctic	Atlantic	Bering Sea	Pacific	Origin
<i>Arctinula greenlandica</i>			X	X			Atlantic
<i>Astarte borealis</i>			X	X	X	X	Atlantic
<i>Astarte crenata</i>			X	X			Atlantic
<i>Astarte esquamalti</i>		X			X	X	Pacific
<i>Astarte montaguui</i>			X	X	X	X	Atlantic
<i>Axinopsida orbiculata</i>			X	X			Pacific
<i>Axinulus careyi</i>	X						
<i>Batharca glacialis</i>			X	X			Atlantic
<i>Batharca varidentata</i>			X	X			Atlantic
<i>Boreacola vadosa</i>	X	X					
<i>Chlamys pseudislandica</i>		X			X		Pacific
<i>Clinocardium ciliatum</i>			X	X	X	X	Pacific
<i>Crenella decussata</i>			X	X	X	X	Pacific
<i>Cuspidaria glacialis</i>			X	X	X		Atlantic
<i>Cuspidaria subtorata</i>			X?	X			Atlantic
<i>Cyclocardia crebricostata</i>		X			X	X	Atlantic?
<i>Cyrtodaria kurrjana</i>			X	X			
<i>Dacrydium vitreum</i>			X	X			Atlantic
<i>Hiatella arctica</i>			X	X	X	X	Pacific
<i>Limatula hyperborea</i>			X	X			Atlantic
<i>Liocyma fluctuosa</i>			X	X	X	X	Pacific
<i>Liocyma viridis</i>		X			X		Pacific
<i>Lyonsia arenosa</i>			X	X	X		Pacific
<i>Lyonsiella uschakovi</i>	X						
<i>Macoma balthica</i>		X		X	X	X	Pacific
<i>Macoma calcarea</i>			X	X	X	X	Pacific
<i>Macoma loveni</i>			X	X	X		?
<i>Macoma moesta</i>			X	X	X	X	Pacific
<i>Malletia abyssopolaris</i>	X						
<i>Montacuta dawsoni</i>			X	X			Atlantic
<i>Musculus corrugatus</i>			X		X		Pacific
<i>Musculus discors</i>			X	X	X	X	Pacific
<i>Musculus niger</i>			X	X	X	X	Pacific
<i>Mya pseudoarenaria</i>		X		X			Atlantic
<i>Mya truncata</i>			X	X	X	X	Atlantic
<i>Mysella planata</i>		X			X		Pacific
<i>Mysella tumida</i>		X			X	X	Pacific
<i>Nucula bellotii</i>			X	X	X	X	Atlantic
<i>Nucula zophos</i>	X						
<i>Nuculana minuta</i>			X	X			Atlantic
<i>Nuculana pernula</i>			X	X	X	X	Atlantic
<i>Nuculana radiata</i>		X			X	X	?
<i>Pandora glacialis</i>			X	X	X	X	Atlantic
<i>Periploma aleutica</i>		X			X	X	Pacific
<i>Portlandia arctica</i>			X	X			Atlantic
<i>Portlandia fraternata</i>			X	X			Atlantic
<i>Portlandia frigida</i>			X	X			Atlantic
<i>Portlandia intermedia</i>			X	X			Atlantic
<i>Portlandia lenticula</i>			X	X	X		?
<i>Portlandia tamara</i>	X						
<i>Serripes groenlandicus</i>			X	X	X	X	Pacific
<i>Thracia devexa</i>		X		X			?
<i>Thracia myopsis</i>			X?	X	X		?
<i>Thyasira equalis</i>			X?	X			Atlantic
<i>Thyasira gouldii</i>			X	X	X	X	Atlantic
<i>Yoldia hyperborea</i>			X	X	X		Pacific
<i>Yoldia myalis</i>			X	X	X	X	Atlantic
<i>Yoldia scissurata</i>		X			X	X	Pacific

the adult. Under conditions of little available food for gamete production the reproductive strategy is shifted to greater efficiency in terms of per unit cost. The gamete index (vol. gametes/vol. animal) is higher in planktotrophic than lecitho-

trophic organisms. However, my observations show that caloric reserves of lecithotrophic eggs are substantially higher per organism unit. In my opinion the determining factors are food availability for the larvae and ambient temperature which may be too low to maintain feeding activity, particularly in a discontinuous pelagic environment.

FAUNAL DIVERSITY

The Arctic has been considered to support only a depauperated fauna and a number of arguments have been advanced to account for this. These include difficulties of physiological adaptation to hypothermy, the low level of primary productivity, limited habitat variety, and the result of recent colonization. The OSU materials provide clear evidence that the Beaufort Sea bivalve fauna is richer than previously assumed, especially if the lack of an intertidal habit is considered. It is worthy of note that the total species present are numerically similar to the bivalves in other high boreal and subarctic seas (White Sea 38; Kara Sea 63; Laptev Sea 50; Eastern Siberian 54; Chukchi Sea 48 species, *vide* Filatova 1962). Limited habitat niches are certainly determining factors, as is the fact that the intertidal zone and shallow nearshore bottom is subject to ice-scour. However, by no means is the entire shallow habitat destroyed by the annual movement of ice. According to Brooks (1974), there is less ice-scour inside the 18 m contour than in deeper water.

The shallow habitat survey (0.5–5 m) by Western Washington State College collected many young and immature bivalves, but a number were in at least their 3rd year. It must be concluded that only part of the bottom is ice-scoured and limited regions may remain undisturbed for several years at a time. The presence of these young individuals, several hundred meters from deeper reproductive populations, nearly all producing lecithotrophic larvae or benthic young, suggests that transportation even of brooded young may be active. Sigurdsson et al. (1976) showed that dispersal of recently settled bivalves in a number of families may occur by current drifting using a byssal thread, analogous to the gossamer flight of young spiders.

The majority of specimens are smaller than those present in the Chukchi or Bering Sea, a fact that may be partially explained by the low primary production, low temperature, and ice cover during much of the year. The entire Arctic bivalve fauna demonstrates persistent morphological characters summarized by Nicol (1967). These include thin shells, lack of bright coloration and the absence of spines. Recently Vermeij & Veil (1978) have noted a higher proportion of bivalves with persistent posterior shell gapes and suggested this was attributable to higher predation in warmer waters. My view is that tightly closing shells are frequently found in stable, nearly static substrates that demand little movement from the infauna. Arctic forms are adapted to unstable substrates, subjected to current transportation, ice-scour,

and high rates of deposition from adjacent rivers. In these conditions the ability to burrow rapidly and move freely may be important attributes. The lack of stable substrates is further demonstrated by the complete absence of cemented and pleurothetic (lying on the bottom on one valve) forms in Arctic waters (Nicol 1964). It is unlikely to be a direct result of low temperatures, as cemented genera such as *Hinnites* DeFrance 1821 and *Crassostrea* Sacco 1897 are found in boreal waters.

FORMAT

Families are arranged according to the system used in Moore (1969). Inasmuch as a full classification is readily available in that work, supra-families are omitted here.

The generic accounts include remarks on the distribution and biology of the group as well as a morphological description. I have included original drawings of the type species of each of the genera, showing the interior of the right valve.

For each species the important systematic references are listed in chronological order. The *Description* paragraph is not the original description, but an expanded comparative statement which can be easily used to find the diagnostic features. The *Records* section lists the fossil and living records in chronological order, but no indication is given whether the record is under a synonymous name. Not all literature records were verified, but only those included where supported by contemporary distributions. Some difficulty was experienced citing Soviet Union palaeontological records, as they place the Pliocene/Pleistocene boundary at 1 m.y. b.p., rather than the accepted international 1.8 m.y. so I have altered Soviet citations to conform to the international stratigraphic usage.

ABBREVIATIONS

CAS	California Academy of Sciences
LACM	Natural History Museum of Los Angeles County
NMC	National Museum of Canada
OSU	Oregon State University
USGS	United States Geological Survey
USNM	United States National Museum of Natural History

SYSTEMATIC ACCOUNT

The key to the families is designed for Arctic and northern boreal species only, but attention must be drawn to the great variability in shape and frequent erosion of shell features, which may limit the usefulness of any key. A further difficulty is the evanescent character of hinge dentition in some representatives of the Hiattellidae and Cardiidae. In all cases, key identifications should be cross-checked with the text.

ARTIFICIAL KEY TO THE FAMILIES

1.	Hinge edentulous (ridges and tubercles may be present)	2
	Hinge with developed dentition	13
2.(1)	Shell with posterior calcareous siphonal tube	Cuspidariidae
	Shell without posterior siphonal tube	3
3.(2)	Beaks terminal	Mytilidae
	Beaks not terminal	4
4.(3)	Hinge with projecting chondrophore	5
	Hinge without projecting chondrophore	6

5.(4)	Chondrophore in left valve only	Myidae
	Chondrophore in both valves	Periplomatidae
6.(4)	Single adductor muscle scar	7
	Two adductor muscle scars	8
7.(6)	Valve with unsymmetrical ears, byssal notch present	Pectinidae
	Valve with small symmetrical ears, no byssal notch	Limidae
8.(6)	Valve with posterior radial ridge or flexure	Thyasiridae
	Valve without radial ridge or flexure	9
9.(8)	Ligament supported by lithodesma	10
	Ligament not supported by lithodesma	12
10.(9)	Shell inflated, oval to quadrate	Verticordiidae
	Shell elongated	11
11.(10)	One valve flat, other convex	Pandoridae
	Both valves convex	Lyonsiidae
12.(9)	Surface granular, sometimes with concentric lines	Thraciidae
	Surface smooth, sculpture radial	Cardiidae
13.(1)	Dentition taxodont	14
	Dentition not taxodont	17
14.(13)	Ligament mostly external	15
	Ligament mostly internal	16
15.(14)	Shell inflated, lateral teeth oblique	Arcidae
	Shell compressed, posterior teeth largest	Mallettiidae
16.(14)	Shell rotund, no pallial sinus	Nuculidae
	Shell elongated, with pallial sinus	Nuculanidae
17.(13)	Hinge with developed cardinal teeth	18
	Hinge with no true cardinal teeth	Montacutidae
18.(17)	Hinge with two cardinal teeth in each valve	19
	Hinge with more than two cardinal teeth in one or both valves	21
19.(18)	Shell compressed, sculpture absent	Tellinidae
	Shell inflated, radial sculpture present	20
20.(19)	Posterior cardinal teeth elongated	Carditidae
	Posterior cardinal tooth peg-like	Cardiidae
21.(18)	Three cardinal teeth in each valve	Veneridae
	Three cardinal teeth in LV, two in RV	Astartidae

Family NUCULIDAE Gray 1824

Genus *Nucula* Lamarck 1799

Figure 1

Type species (monotypy): *Arca nucleus* Linné 1758. Recent. North Atlantic.

DESCRIPTION: Shell ovate to trigonal, surface unornamented or with concentric and radial striae. Beaks opisthogyrate, lunule and escutcheon obscure to prominent. Interior nacreous, margins plain or crenulate. Hinge with central oblique resilifer separating taxodont dentition into two series. Ligament internal. No pallial sinus.

RANGE: Jurassic to Recent. Recent distribution cosmopolitan, generally in cold or deep waters and well represented in boreal and Arctic regions. Shallow infaunal in fine-grained sediments, usually with high organic content.

DEVELOPMENT: Ova large, development lecithotrophic with reduced or no planktonic stage (Thorson 1946). Drew (1901) showed development in *N. delphinodonta* Mighels & Adams to be direct in an attached gelatinous egg capsule.

REMARKS: The group is structurally modified for deposit feeding, but at least some species are facultative filter-feeders (Casper 1940). Two subgenera are present in the study area.

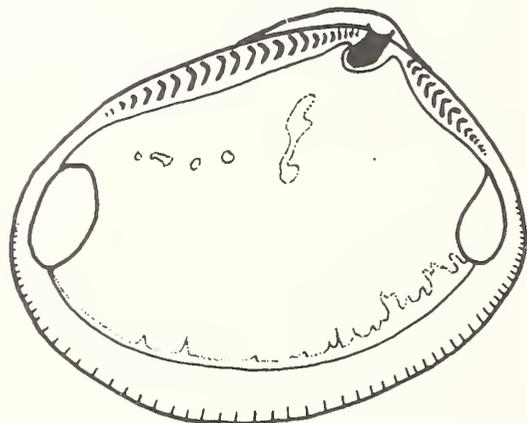


FIGURE 1. Interior of right valve of *Nucula nucleus* (Linné).

KEY TO SUBGENERA OF *NUCULA*

- Margins crenated, sculpture including radial striae
 *Nucula* s. str.
- Margins smooth, surface smooth *Leionucula*

Subgenus *Nucula* s. str.

Nucula (Nucula) zophos Clarke 1960

Figure 2

Nucula zophos Clarke 1960:5, pl.1, f.15-18; Clarke 1963:99; Paul & Menzies 1973:127.

DESCRIPTION: Shell length to 18 mm. Surface sculptured with numerous fine concentric ridges and intersecting radial lines giving a reticulated appearance. Periostracum thin and dehiscent. Interior brilliantly nacreous, with some of the radial lines carrying through. Shell margins strongly crenulated. Hinge line well developed with deep anteriorly directed chondrophore dividing dentition into two series, the anterior series having twice as many teeth as the posterior set.

COMPARISONS: The large size and curious reticulate sculpture is unlike any other boreal or Arctic representative of the genus. It is similar to the Panamic *N. iphigenia* Dall 1896 which is larger and with a proportionally thicker and coarsely sculptured shell.

COLLECTION: Five single valves from 2377 m at 71°19.3'N, 147°47.1'W.

DISTRIBUTION: The type locality is 84°28'N, 148°28'W in approximately 1700 m, so the present record is an extension of over 1200 km south. This species is widely distributed in the archibenthal regions of the Laurentian Basin.

Subgenus *Leionucula* Quenstedt 1930.

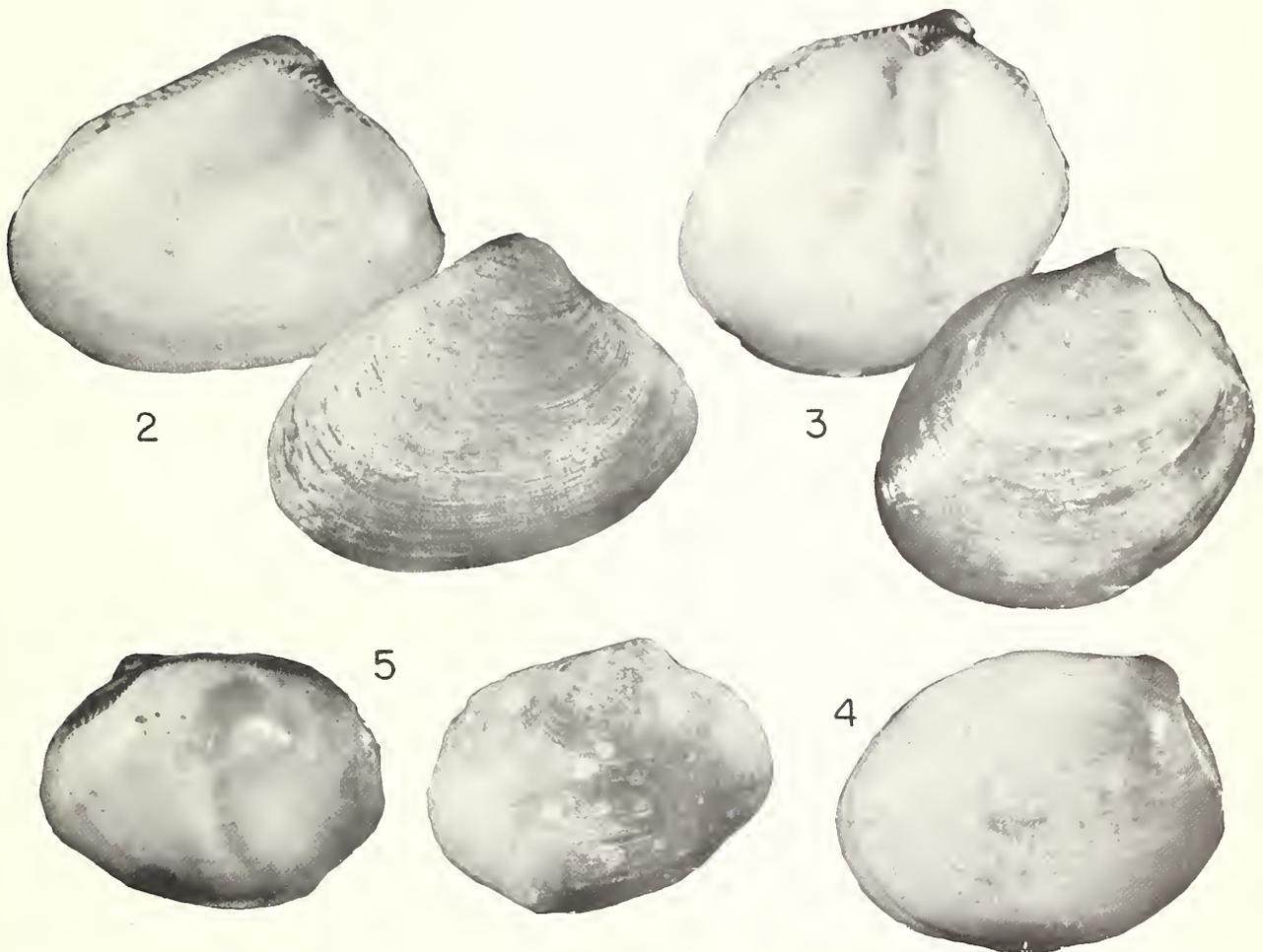
Type species (original designation): *Nucula albensis* Orbigny 1844. Cretaceous. Europe.

Nucula (Leionucula) bellottii A. Adams 1856

Figures 3, 4

Nucula bellottii A. Adams 1856:51.

Nucula (Emucula) bellottii A. Adams, Schenck 1939:30, pl.6, f.10, 11, 13, 16-20.



FIGURES 2-5. 2, *Nucula (Nucula) zophos* Clarke, length 12.9 mm; 3, *Nucula (Leionucula) bellottii* A. Adams, length 15.3 mm; 4, *N. (L.) bellottii*, elongated form, length 10.4 mm; 5, *Malletia abyssopolaris* Clarke, length 11.6 mm.

- Arca tenuis auctt* [not Montagu 1808:56, pl. 29, f.1.]
Nucula tenuis (Montagu), Oldroyd 1925:13, pl.5, f. 12; Filatova 1948:415, pl.105, f.1; Scarlato 1955:186, pl.49, f.1.
Nucula tenuis typica G. Sars 1878:34.
Nucula inflata Hancock 1846:333, pl.5, f.13, 14, [not Sowerby 1827, not Wissmann & Munster 1841]; Harley in Sowerby 1860:162, pl.229, f. 115, 116.
Nucula tenuis inflata (Hancock), Jeffreys 1863:151.
Nucula expansa Reeve in Belcher 1855:397, pl.33, f.2, [not Wissmann & Munster 1841]; Jeffreys 1863:152.
Nucula tenuis expansa (Reeve in Belcher), G. Sars 1878:33.

DESCRIPTION: Shell length to 20 mm, inflated, surface smooth, sometimes with incremental lirae and growth checkmarks. Periostracum yellow to dark-brown, brilliantly varnished. Shell tightly closing, margins smooth. Interior of shell nacreous. Hinge with large oblique resilifer and taxodont dentition in two series, the anterior teeth approximately twice as numerous. Pallial line entire, difficult to see.

COMPARISONS: This is a variable species, with two extreme varieties, a compressed form close to the type but with a light colored periostracum ("*N. expansa*"), and a larger, thin-shelled inflated form with a generally darker periostracum ("*N. inflata*"). Numerous transitional forms occur and there is no satisfactory way to separate them. The unsculptured exterior with brilliant periostracum and smooth shell margins distinguish *N. bellotii* from *N. zophos* Clarke.

COLLECTION: This species occurred at 132 stations for a total of 420 specimens and numerous dead valves. Living specimens were found from 10–2560 m, but were most abundant in less than 200 m.

RECORDS: *Pleistocene*—Wood 1851:84 (Britain); Wagner 1959:6 (British Columbia); Merklin et al. 1962:22, pl.1, f.1 (Chukotsk Peninsula); Petrov 1966:182, pl.10, f.1–8 (Chukotsk Peninsula); Petrov 1967:154 (Chukotsk Peninsula); Troitskiy, 1974:265 (Siberia). *Recent*—Møller 1842:17 (Greenland); M. Sars 1859:56 (European Arctic); Crosse 1877:118 (Bering and Chukchi Seas); E.A. Smith 1877:141 (European Arctic); D'Urban 1880:253 (Barents Sea); Leche 1883:449 (Novaya Zemlya); Krause 1885:21 (Bering Sea); Stuxberg 1886:149 (Novaya Zemlya); Jensen 1905:299 (Greenland); Dall. 1921:9 (Bering and Arctic Seas); Soot-Ryen 1939:8 (Franz Josef Land); Madsen 1949:11 (Iceland); Kuroda & Habe 1952:26 (Northern Japan); Filatova 1957b:51 (Eurasian Arctic); Ockelmann 1958:13 (Greenland); MacGinitie 1959:149, pl.18, f.4 (Point Barrow, Alaska); Ellis 1960:38 (Baffin Island and Greenland); Hulsemann 1962:70 (Beaufort Sea); McLaughlin 1963:24 (Bering Sea); Sparks & Pereyra 1966:834 (Chukchi Sea); Ishikawa 1969:49, pl.3, f.5 (Sea of Japan); Bernard 1970:86 (British Columbia); Clarke 1974:8 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal in shallow water but occasional specimens may be found down to 2400 m.

REMARKS: Schenck (1939) first proposed that the neglected name *N. bellotii* Adams should be applied to Arctic *Nucula* then included in *N. tenuis* (Montagu). It is possible that careful study will show that the two species intergrade, but I consider *N. bellotii* to be a closely related cold water species. *N. quirica* Dall, 1916, from Cook Inlet, Alaska has also been considered a synonym, but until its relationship with Californian material is elucidated I prefer to treat it as a separate taxon probably falling into the synonymy of Pacific *N. tenuis* and related to *N. balboana* Hertlein & Grant 1972, from the Pliocene of southern California.

Family MALLETIIDAE H. & A. Adams 1858 Genus *Malletia* Des Moulins 1832

Figure 6

Type species (monotypy): *Malletia chilensis* Des Moulins 1832. Recent. Southeast Pacific.

DESCRIPTION: Shell elongate, thin. Surface unornamented, but fine concentric striae and growth checkmarks may be present. Periostracum yellow to brown, brilliantly polished. Lunule and escutcheon absent or indistinct. Interior porcelaneous, shell margins smooth. Hinge with taxodont teeth in two series, the posterior teeth longer and more numerous. Ligament predominantly external. Pallial sinus small to extensive.

RANGE: Ordovician to Recent. Recent distribution cosmopolitan in archibenthal and abyssal seas. Malletiids are shallow burrowers in fine sediments.

DEVELOPMENT: No published description is available: a specimen of *M. flora* Dall, 1916, from deep water off the Queen Charlotte Islands, contained large ova, indicating lecithotrophic development.

REMARKS: The anatomy of the soft parts of this family is poorly known, but appears to be closely related to the Nuculanidae. Malletiids are probably detritivores and facultative filter feeders. Arctic representatives fall into two groups, those with and without the pallial sinus; although there appear to be intermediate forms, it is possible that anatomical work will result in separation at the subgeneric level.

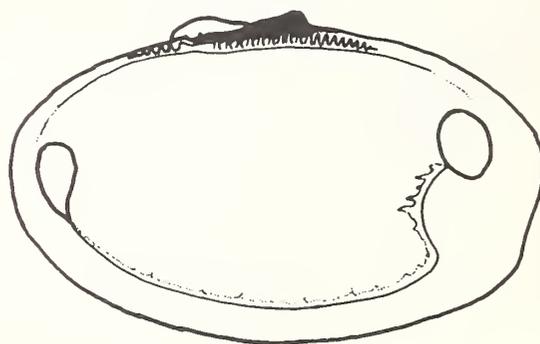


FIGURE 6. Interior of right valve of *Malletia chilensis* (Des Moulins).

Malletia abyssopolaris Clarke 1960

Figure 5

Malletia abyssopolaris Clarke 1960:7, pl.1, f.19–22; Paul & Menzies 1973:128.

DESCRIPTION: Shell outline commonly ovate, but may vary between subcircular to rhomboidal, length to 15 mm. Surface unornamented except for a few concentric lirae. Some specimens may have very fine radial lines which may carry through to the interior. Periostracum thin and dehiscent. Interior porcelaneous,

shell margins smooth. Hinge plate concave in front and convex posteriorly. Taxodont teeth short, V-shaped. Pallial line feebly impressed, no pallial sinus.

COMPARISONS: The species is easily distinguished by the dual curvature of the hinge line and the absence of a resilifer. Clarke (1960) compared his material to *M. abyssorum* Verrill & Bush 1898, from bathyal northwestern Atlantic, and *M. dunkeri* Smith 1855, from Japan, but these are both minute shells with a different surface pattern. The equivalent species from the Angara Basin is *M. kolthoffi* (Hägg 1904), thought by Soot-Ryen (1966) to be identical to *M. cuneata* Jeffreys 1876.

COLLECTION: Four single valves from 2560 m at 71°19.6'N, 147°48.2'W.

DISTRIBUTION: The type locality is 84°28'N, 148°28'W in 1690–1709 m. This new record extends the range some 1300 km south. The species is probably distributed throughout the Laurentian Basin in bathyal and archibenthal environments.

RANGE: Triassic to Recent. Recent distribution cosmopolitan, most numerous in boreal and temperate regions. The genus has an extended bathymetric range, from the shallow subtidal zone to hadal depths, and colonizes a wide range of sediments ranging from coarse sand and gravel to the finest silts. Nuculanids are generally medium depth infauna, depending upon the palp appendages to collect detritus, though at least some food may be obtained by filter feeding.

DEVELOPMENT: Ova large, development lecithotrophic with an abbreviated planktonic stage (Thorson 1946).

REMARKS: The anatomy of this group is well-known and conforms to the typical protobranchiate pattern with large palp appendages, a complete exhalant siphon and unfused inhalant siphon. The siphonal structures permit deeper burial in unconsolidated sediments, and they may be extended over the surface and used to sweep in epibenthic detritus.

Family NUCULANIDAE H. and A. Adams 1858
KEY TO THE GENERA OF NUCULANIDAE

- 1. Shell tightly closing 2
- Shell with posterior gape *Yoldia*
- 2.(1) Shell elongated, with concentric sculpture
..... *Nuculana*
- Shell with rostrum, surface unornamented
..... *Portlandia*

Subgenus *Nuculana* s. str.

Nuculana (Nuculana) minuta (Fabricius 1776)

Figures 8, 9

Arca minuta Fabricius 1776:414; Montagu 1803:140 (of "Gmelin"); Dillwyn 1817:245 (of "Müller").
Leda minuta (Fabricius) G. Sars 1878:36, pl.5, f.2a, 6; Oldroyd 1925:15, pl.5, f.5, pl.19, f.2, a; Filatova 1948:417, pl.105, f.6 (of "Müller"); Filatova and Barsonova 1964:34 (of "Müller"); Petrov 1966:184, pl.10, f.11 (of "Müller").
Nuculana minuta (Fabricius), MacGinitie 1959:150, pl.18, f.3.

Genus *Nuculana* Link 1807

Figure 7

Type species (original designation): *Arca pernula* Müller 1771. Recent. North Atlantic.

DESCRIPTION: Shell elongate, usually rostrate. Surface smooth or with concentric sculpture. Periostracum polished, adherent. Lunule obscure, escutcheon well developed. Interior porcelaneous, shell margins smooth. Hinge with wide posteriorly directed resilifer. Ligament partly external. Taxodont dentition in two series, posterior teeth approximately twice as numerous as anterior series. Pallial line impressed, pallial sinus small.

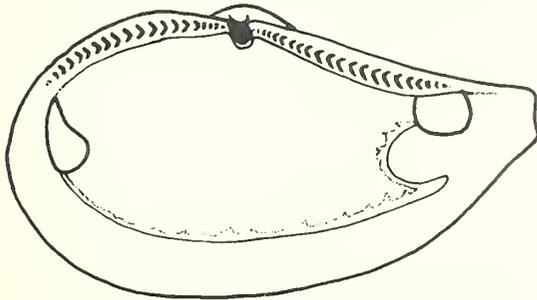


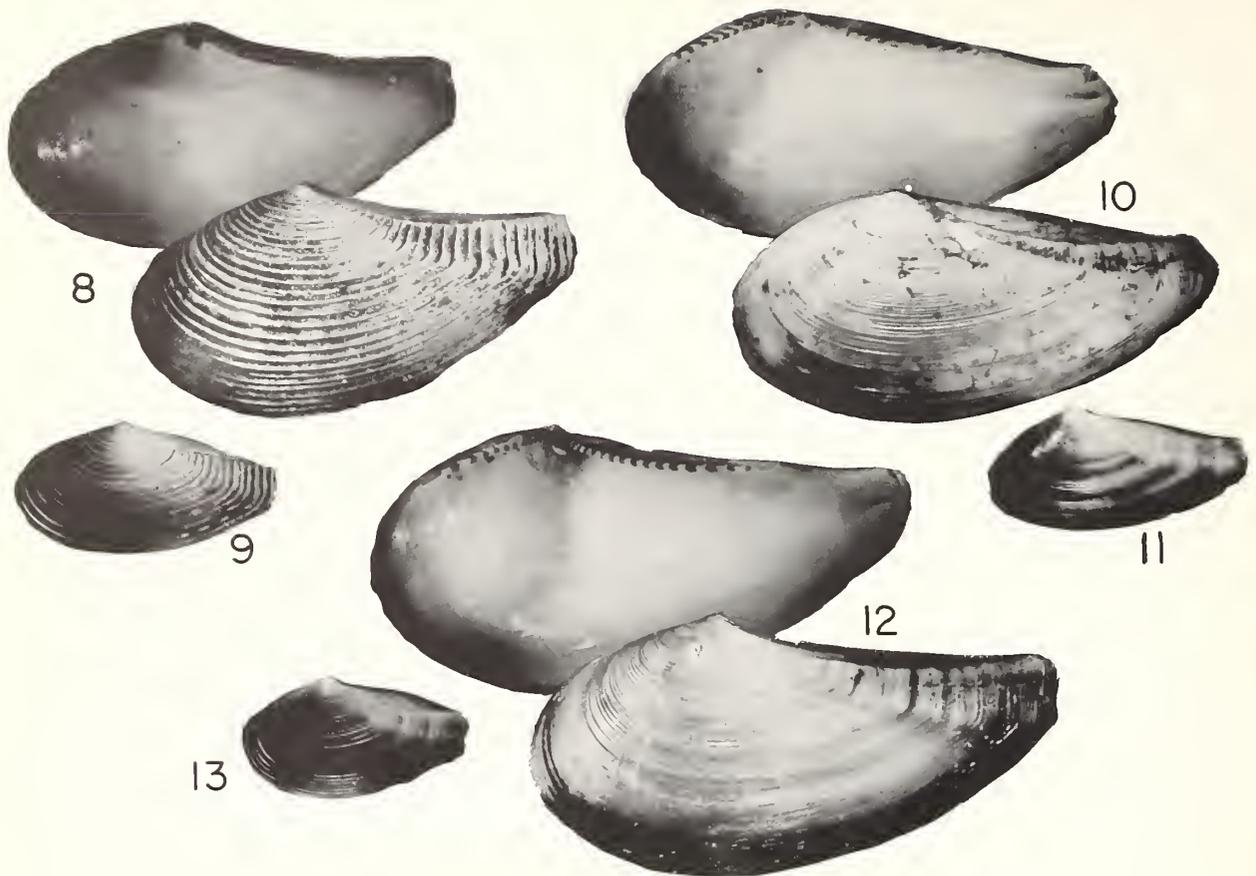
FIGURE 7. Interior of right valve of *Nuculana pernula* (Müller).

DESCRIPTION: Shell elongate, inflated, with short obliquely truncated rostrum. Length to 20 mm. Surface ornamented with coarse concentric ribs. Periostracum light yellow to dark brown, strongly adherent. Escutcheon very prominent, bounded by a raised line. Interior polished, not nacreous. Hinge line nearly straight, resilifer narrow and posteriorly directed. Taxodont dentition in two series, more teeth in the posterior set. Pallial line not deeply impressed, pallial sinus well developed.

COMPARISON: This species may be confused with *N. pernula* (Müller), but it reaches only half the size and the rostrum is shorter. The radial sculpture is not as pronounced, and in *N. pernula* there is a tendency for the dorsal rostral margin to be concave and the rostrum to be ornamented with several radial lines, whereas in *N. minuta* the rostrum is straight and the radial ornamentation is absent.

COLLECTION: The species occurred at 24 stations for a total of 79 specimens and some single valves. Living representatives were found in 23–270 m.

RECORDS: *Pleistocene*—Richards 1962:52, pl.1, f.16 (Labrador, Quebec); *Recent*—Gould 1841:101 (Massachusetts); Jeffreys 1869:173, pl.29, f.6 (Britain); Gould 1870:164, f.470 (Massachusetts); Leche 1883:448 "Beck MS" (Novaya Zemlya); Krause 1885:22 (of "Müller") (Bering Sea); Whiteaves 1887:119 (British Columbia); Dautzenberg and Fischer 1910:16 (Novaya Zemlya); Massey 1930:238 (North Atlantic); Johnson 1934:16 (Labrador to Nova Scotia); Gorbunov 1946: 46 (of "Müller") (Eurasian Arctic); Madsen 1949:14 (of "Müller") (Iceland); Filatova 1957b: 51 (of "Müller") (Eurasian Arctic); Ockelmann 1958:19,



FIGURES 8-13. 8. *Nuculana (Nuculana) minuta* (Fabricius), length 12.2 mm; 9. *N. (N.) minuta*, juvenile, length 7.7 mm; 10. *Nuculana (Nuculana) pernula* (Müller), length 19.9 mm; 11. *N. (N.) pernula*, juvenile, length 7.6 mm; 12. *Nuculana (Nuculana) radiata* (Krause), length 24.3 mm; 13. *N. (N.) radiata*, juvenile, length 6.1 mm.

pl.1, f.10 (Greenland); Ellis 1960:38 (Baffin Island and Greenland); Clarke 1962:53 (Canadian Arctic); Sparks and Pereyra 1966:834 (Chukchi Sea); Petersen 1968:5 (of "Müller") (Faroe Islands); Clarke 1974:8 (Baffin Bay); Wacasey 1974:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and north Atlantic. The species is represented in the Bering, and possibly the Okhotsk Sea. Records from Vancouver Island and California should be assigned to *N. pernula* (Müller).

Nuculana (Nuculana) pernula (Müller 1779)

Figures 10, 11

Arca pernula Müller 1779:55.

Leda pernula (Müller), G. Sars 1878:35, pl.5, f.1a-d; Oldroyd 1925:19, pl.19, f.7; Filatova 1948:417, pl.105, f.4-5; Petrov 1966:185, pl.10, f.12-15.

Nuculana pernula (Müller), Morch 1869:229.

Leda pernula costigera Leche 1883:447, pl.33, f.23-25 (ex Beck MS *Nuculana costigera*).

Leda pernula lamellosa Leche 1883:448, pl.33, f.26.

Leda rostrata Schumacher 1817:173, pl.19, f.4a-b [not Wood 1825]; Forbes 1846:420.

Nucula obsoleta Brown 1827:72, pl.25, f.17.

Nucula oblonga Brown 1845:84, pl.33, f.17

Leda pernuloides Dunker 1882:238.

DESCRIPTION: Shell elongate, inflated, with a long rostrum which tends to a concave curve on its upper surface, total length of shell to 38 mm. Surface with fine concentric lines, especially on dorsal part of disc. Periostracum light brown to black, polished and adherent. Valve with small anterior gape. Interior polished, porcelaneous, shell margins smooth. Pallial line slightly impressed, pallial sinus small.

COMPARISONS: This species appears less polymorphic than many Arctic bivalves. It may only be confused with *N. minuta* (Fabricius), but the latter is much smaller with a proportionately shorter rostrum and more pronounced sculpture.

COLLECTION: The species occurred at 57 stations for a total of 432 individuals in 23-455 m, but most abundant in less than 200 m.

RECORDS: *Miocene*—Yokohama 1925:9, pl.2, f.7-9 *lapsus* "penula" (Northern Japan). *Pliocene*—Petrov 1966:185, pl.10, f.12-15 (Chukotsk Peninsula). *Pleistocene*—Wood 1851: 93, pl.10, f.13a, b (Britain); Meek 1923:414 (Alaska); Richards 1962:51 (Labrador to Maine). *Recent*—Loven 1846:34 (Norway); M. Sars 1850:173 (Norway); Jeffreys 1877a:232 (Britain); Leche 1878:27 (Novaya Zemlya); D'Urban 1880:253 (Barents Sea); Leche 1883:446 (Novaya Zemlya); Stuxberg 1886:149 (Novaya Zemlya); Hägg 1904:8 (Greenland); Dautzenberg and Fischer 1910:16 (Novaya Zemlya); Massy 1930:242 (North Atlantic); Mesjatev 1931:46 (Barents Sea); Soot-Ryen 1939:8 (Franz Josef Land); Gorbunov 1946a:15 (Siberian Arctic); Madsen 1949:15 (Iceland); Kuroda and Habe 1952:26 (Northern Japan); Filatova 1957b:51 (Eurasian Arctic);

Ockelmann 1958:15, pl.1, f.9 (Greenland); Ellis 1960:38 (Baffin Island and Greenland); Merklin et al. 1962:23, pl.1, f.2 (Chukotsk Peninsula); Kuznetsov 1963:66 (Kamchatka); Filatova & Barsanova 1964:54 (Western Bering Sea); Soot-Ryen 1966:4 (Northeastern Atlantic); Petersen 1968:5 (Faroe Islands); Skalkin and Tabunkov 1969:1147 (Sakhalin Islands); Bernard 1970:86 (British Columbia); Kuroda et al. 1971:319, pl.66, f.13 (Japan); Clarke 1974:8 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal, throughout the North Atlantic, Bering Sea, Sea of Okhotsk, and in the North Pacific as far south as the Queen Charlotte Islands and northern Japan in 20–1400 m.

REMARKS: As this species is widely distributed throughout the Canadian Arctic Archipelago, the North Atlantic and Pacific oceans, its occurrence in the Beaufort Sea is not surprising. Arctic representatives are frequently referred to the subspecies *N. p. costigera* Leche, distinguished by an upturned rostrum. This character varies continuously however, and it cannot be given taxonomic status. Juvenile specimens, particularly from shallow water, frequently display a light color with concentric darker bands.

Nuculana (Nuculana) radiata (Krause 1885)

Figures 12, 13

Leda pernula radiata Krause 1885:23, pl.3, f.2a–c.

Leda radiata (Krause), Oldroyd 1925:25; Filatova 1948:418, pl.105, f.7.

Nuculana radiata (Krause), Kuroda and Habe 1952:62.

DESCRIPTION: Shell inflated, rostrum short. Length to 30 mm, generally smaller. Surface with prominent concentric ribs, crossed by fine radial ridges on periostracum: more pronounced in posterior region. Periostracum smooth and polished, light green to almost black, strongly adherent. Interior polished, margins smooth. Hinge line not well developed, resilifer small, elongated. Taxodont dentition in two series, teeth not numerous. Pallial line feebly impressed, pallial sinus small.

COMPARISONS: This species, with radial periostracal threads crossing the concentric ribs, is unlike any other Arctic nuculanid. The hinge resembles *N. minuta* (Fabricius), but the teeth are proportionally fewer.

COLLECTION: The species was represented at nine stations for a total of 280 specimens in 27–55 m.

RECORDS: *Pleistocene*—Petrov 1966: 186 (Chukotsk Peninsula). *Recent*—Soot-Ryen 1932:6, pl.1, f.7–8 (Pacific Arctic, Bering and Okhotsk seas); Gorbunov 1946a:46 (Siberia); Filatova 1957b:52 (Siberia), MacGinitie 1959:151, pl.18, f.2 (Point Barrow, Alaska); McLaughlin 1963:24 (Bering Sea); Sparks and Pereyra 1966:834 (Chukchi Sea).

DISTRIBUTION: Panarctic along the North American coast probably as far east as Union Strait and along the Siberian coasts of the Soviet Union. The species is distributed throughout the Bering Sea and extends to Northern Japan. It has not been collected south of the Aleutian Archipelago. All Beaufort Sea collections are in shallow water, usually less than 40 m.

REMARKS: Although proposed as a variety of *N. pernula*

(Müller) it is more closely related to *N. minuta* (Fabricius) but is sufficiently and consistently distinct to warrant full separation. It probably arose in the eastern Bering Sea and only recently colonized the Chukchi Sea and adjacent Arctic.

Genus *Portlandia* Mörch 1857

Figure 14

Type species (subsequent designation ICZN 1966): *Nucula arctica* Gray 1824. Recent. North Atlantic.

DESCRIPTION: Shell solid, ovate to elliptical, with a small rostrum. Surface smooth, or with irregular incremental lirae. Periostracum thick, light brown to black, adherent. Interior porcelaneous, margins smooth. Hinge line well developed, resilifer large, taxodont dentition in two series, approximately equal in number, but anterior teeth slightly smaller. Pallial line impressed, pallial sinus small, in some cases absent.

RANGE: Miocene to Recent. Recent distribution cosmopolitan, usually in deep water, but also in shallow boreal and Arctic environments. The genus is a member of the shallow infauna of fine-grained sediments.

DEVELOPMENT: The ova are large, development is probably lecithotrophic with no planktonic phase (Bernard MS).

REMARKS: Anatomically the genus is closely related to nuculanids, and is characterized by short, often incomplete siphons, and large palp appendages. Members of the genus are probably entirely deposit feeders, actively plowing through the superficial sediments. Filatova (1951) has discussed the geographical distribution of the genus.

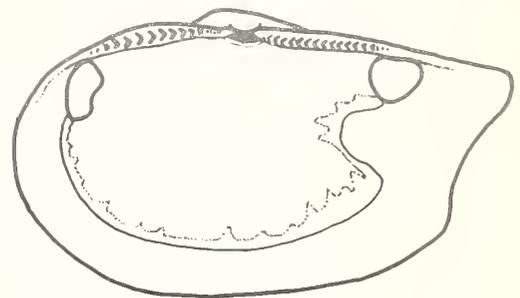


FIGURE 14. Interior of right valve of *Portlandia arctica* (Gray).

KEY TO THE SUBGENERA OF PORTLANDIA

1. Pallial sinus small or absent *Yoldiella*
Pallial sinus developed 2
- 2.(1) Resilifer large, subtriangular *Portlandia* s. str.
Resilifer small, rectangular *Ledella*

Subgenus *Portlandia* s. str.
Portlandia (Portlandia) arctica (Gray 1824)

Figures 15, 16, 17

Nucula arctica Gray 1824:241.

Leda arctica (Gray), Dall 1874: 250 (of "Broderip"); Oldroyd 1925:26, pl.19, f.6, a.

Yoldia arctica (Gray), Mossewitsch 1928:1, pl.1; MacGinitie 1959:151, pl.18, f.8.

Portlandia arctica (Gray), G. Sars 1878:37, pl.4, f.7a-b; Filatova and Zenkevich 1957:67; Petrov 1966:190.

Nucula siliqua Reeve in Belcher 1855:396, pl.33, f.4; Crosse 1877:119.

Yoldia arctica siliqua (Reeve in Belcher), Petrov 1966:191, pl.11, f.1-7.

Leda (Portlandia) collinsoni Dall 1919:19A, pl.2, f.3, 4.

DESCRIPTION: Shell oval to elongate, total length to 30 mm, but usually half this. Posterior produced, set off by a radial sulcus to form a small pointed rostrum. Surface unsculptured, sometimes with feeble incremental lines and concentric wrinkles. Periostracum thick, color variable, ranging from light yellow-green to black but generally rich maroon. Interior of shell porcelainous, margins smooth. Hinge line substantial, with large spoon-shaped resilifer, taxodont dentition in two series, with approximately the same number of teeth, the anterior series smaller. Pallial line clearly impressed, pallial sinus deeply indented.

COMPARISONS: This species may be confused with *P.*

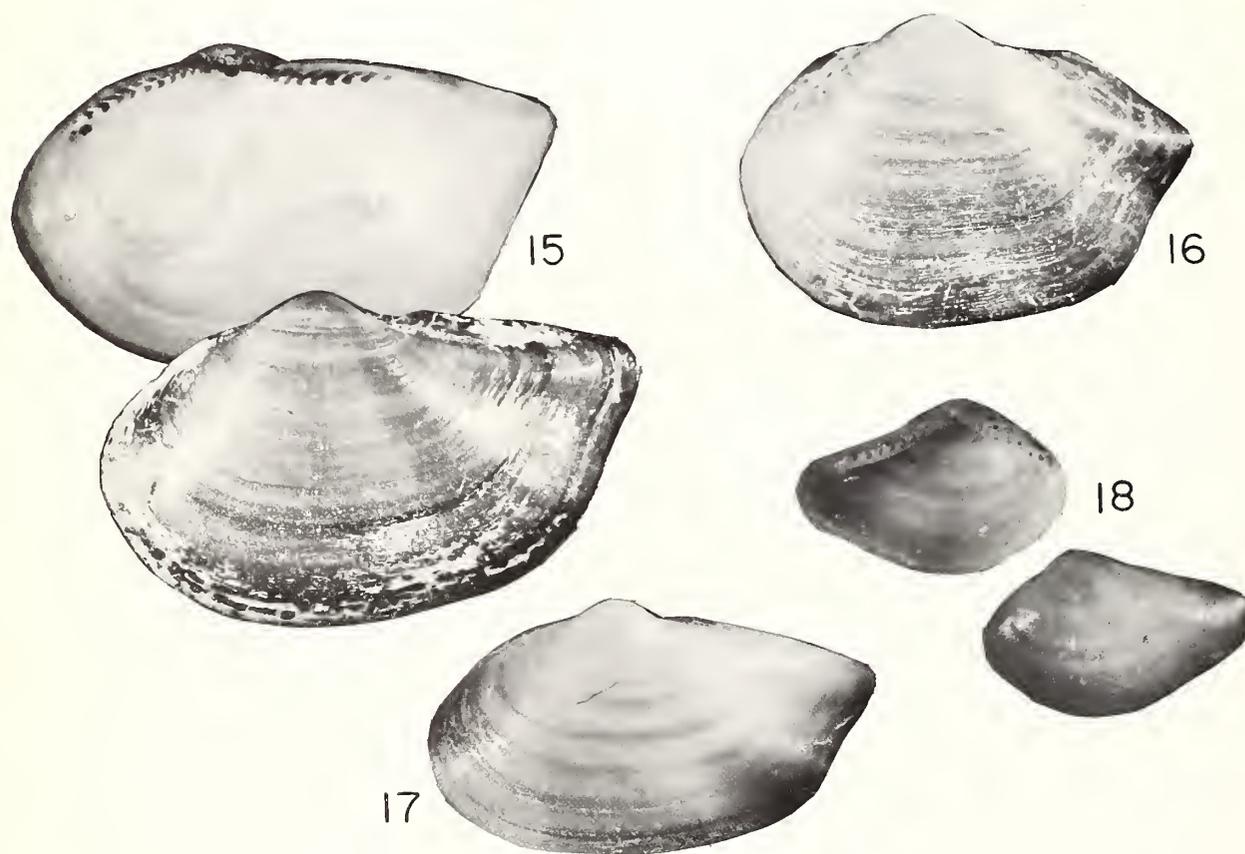
intermedia (M. Sars), but the latter is a thinner-shelled, more inflated species and the posterior region is not set off by a radial sulcus, the resilifer is smaller and the pallial sinus only slightly indented.

COLLECTION: The species is abundantly represented in the collection, occurring at 85 stations for a total of 2944 specimens and numerous single valves. Living representatives were found between 10-2560 m, but were most abundant in shallow water.

RECORDS: *Pleistocene*—Jeffreys 1877:489 (Greenland and Spitzbergen); Lamplugh 1886:280 (British Columbia); Dall 1924:32A (Arctic Canada); Merklin et al. 1962:25 pl.1, f.4-8 (Chukotsk Peninsula); Richards 1962:52, pl.1, f.18-20, 27, 28 (Newfoundland to Vermont); Petrov 1967:190 (Bering Strait). *Recent*—Møller 1842:18 (Greenland); Crosse 1877:119 (Arctic); Leche 1878:27 (Novaya Zemlya); Leche 1883:444, pl.33, f.18, 19 (European Arctic); Stuxberg 1886:147 (Novaya Zemlya); Posselt 1898:68 (Greenland); Hagg 1904:14 (Greenland and Jan Mayen); Odhner 1915:60 (Spitzbergen); Mesjatev 1931:30 (Barents Sea); Soot-Ryen 1932:8 (Arctic); Gorbunov 1946a:42 (Siberia); Filatova 1951:119, f.1-3 (Eurasian Arctic); Filatova 1957b: 52 (Eurasian Arctic); Soot-Ryen 1958:8 (Greenland); Ockelmann 1958:23 (Greenland); Ellis 1960:38 (Baffin Island and Greenland); Hulsemann 1962:70 (Beaufort Sea); Wacasey 1975: 27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: This is the most characteristic high Arctic species, panarctic in distribution and also found in the northernmost Atlantic and south into Hudson Bay.

REMARKS: This is a variable species, with the elevated form



FIGURES 15-18. 15, *Portlandia (Portlandia) arctica* (Gray), length 17.9 mm; 16, *P. (P.) arctica*, abbreviated form, length 11.1 mm; 17, *P. (P.) arctica*, elongated form, length 11.2 mm; 18, *Portlandia (Ledella) tamara* (Gorbunov), length 2.7 mm.

referred to *P. collinsoni* (Dall), but as the proportions present a continuous spectrum, no systematic importance to the latter can be accorded. Dall (1919) stated his new species displayed a vermiculately wrinkled periostracum but type material lodged in the National Museum of Canada falls within the expected variability. Similarly, the Siberian *P. aestuariorum* Mossewitsch 1928 is probably also a morph. Remarks on feeding are given by Bubnova (1971, 1972) and the species is almost exclusively a detritus feeder. It is a member of the shallow-water fauna, so it is surprising that the OSU collection contained juvenile specimens from deepwater stations. The proportions of these representatives are slightly different from typical shallow *P. arctica*, but there is insufficient reason to separate them. I am grateful to R. Baxter for the loan of specimens collected in deep water from Prince William Sound, Alaska. They bear a close resemblance to *P. arctica*, but the profile of the rostrum and sculpture of the periostracum are different. It is my tentative opinion that the Gulf of Alaska representatives should be separated at the species level and will require a new name.

Subgenus *Ledella* Verrill and Bush 1897

Type species (subsequent designation Verrill and Bush 1897): *Leda mesanensis* Seguenza 1877. Miocene. Europe.

Portlandia (Ledella) tamara (Gorbunov 1946)

Figure 18

Ledella tamara Gorbunov 1946b: 320, pl.3, f.4.

DESCRIPTION: Shell ovate, inflated, total length to 5 mm. Posterior with short rounded rostrum. Surface unornamented, except for sporadic feeble incremental striae. Periostracum thin, polished, strongly adherent. Shell interior porcelaneous, margins smooth. Hinge line straight in posterior region and convex anteriorly. Resilifer small, folded below beaks. Taxodont dentition in two series, approximately equal in number, but posterior teeth larger. Pallial line not impressed, pallial sinus not evident.

COMPARISON: This subgenus, with its *Portlandia*-like exterior and *Yoldiella*-like dentition, is separated from the latter by an internal ligament and is unmistakable. This is the sole Arctic representative of the taxon and its relationship to other members of group has not been elucidated.

COLLECTION: One right valve from 71°45.0'N, 150°35.0'W in 2130 m.

DISTRIBUTION: *Recent*—Wagner 1962:10 (Canadian Arctic Archipelago); Clarke 1963:100, pl.2, f.10, 11 (Laurentian Basin). The type locality is the New Siberian Islands (75°22'N, 135°00'E) in 3700–3800 m. Clarke (1963) reported numerous dead shells north of Point Barrow in 530–2278 m. Wagner's (1962) record from Eastern Arctic Canada, suggests that this species is widely distributed in the deeper waters of the Laurentian Basin.

REMARKS: *Ledella* was proposed by Verrill & Bush (1897) as a substitute name for the preoccupied *Junonia* Seguenza 1877, and placed as a subgenus of *Nuculana* by Moore (1960). It appears closer to *Yoldiella* on conchological grounds, but the internal ligament and shell shape suggest it should be accorded subgeneric status within *Portlandia*.

Subgenus *Yoldiella* Verrill and Bush 1897

Type species (original designation): *Yoldia lucida* Lovén 1846. *Recent*. North Atlantic.

Portlandia (Yoldiella) fraterna (Verrill & Bush 1897)

Figure 19

Yoldiella fraterna Verrill and Bush 1898:867, pl.80, f.5, pl.82, f.8.
Portlandia fraterna (Verrill and Bush), Odhner 1915:68, pl.1, f.26–29.
Portlandia frigida nana Jensen 1905:320 (*vide* Ockelmann, 1958), [not
Yoldia nana M. Sars 1865.]

DESCRIPTION: Shell elliptical to elongate, total length to 5 mm but usually less than 3 mm. Surface smooth, rarely with fine incremental striae. Periostracum brilliantly varnished, light yellow to grey-brown in color, dehiscent. Interior polished, porcelaneous, margins smooth. Hinge line rather delicate, straight, with central small deep resilifer. Ligament mostly internal, with small protrusion just below the beaks. Teeth nearly equal in size. Pallial line obscure, pallial sinus feebly impressed.

COMPARISONS: This species may be confused with *P. frigida* (Torell) which is larger and the posterior end is set off from the disc by a radial flexure. *P. fraterna* has a thinner and more compressed shell.

COLLECTION: This species occurred at two stations, represented by three specimens and one valve, in 585–991 m.

RECORDS: *Pleistocene*—Merklin et al. 1962:27, pl.1, f.18 (Chukotsk Peninsula); Petrov 1967a:184 (Chukotsk Peninsula). *Recent*—Mesjatsjev 1931:45 (Barents Sea); Filatova 1957b:52 (Eurasian Arctic); Filatova and Zenkevich 1957:65 (Kara Sea); Petrov 1967:184 (Chukotsk Peninsula); Ockelmann 1958:37, pl.1, f.15 (Greenland); Wacasey 1975:24 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and throughout the northern part of the Atlantic, into Hudson Bay and in deep water along the American eastern seaboard as far south as Georgia. The species has not been collected in the eastern Bering Sea and does not occur in the Pacific.

REMARKS: It is with some trepidation that I identify the OSU material with this species, there are small differences in the shell proportions, but within the range of polymorphism so characteristic of Arctic bivalves; however, there is too little material to make an extensive comparison. It is possible that *P. minuscula* Verrill & Bush 1898 is conspecific. The authors, in the original description, remark on the deep pallial sinus that is not visible in most specimens due to being weakly impressed. I am unable to detect a trace of a sinus in the material I have examined and consider this species to belong to the group of *Yoldiella* which lacks a pallial sinus.

Portlandia (Yoldiella) frigida (Torell 1859)

Figures 20, 21

Yoldia frigida Torell 1859:148, pl.1, f.3
Leda frigida (Torell), Jeffreys 1877a:232.
Portlandia frigida (Torell), G. Sars 1878:39, pl.4, f.11a, b.
Portlandia (Yoldiella) frigida (Torell), Filatova 1948:420, pl.106, f.6

DESCRIPTION: Shell ovate, inflation variable, but usually rather compressed. Total length to 8 mm, usually less than 4 mm. Posterior region sharply angulated, set off by a radial flexure. Surface unsculptured, sometimes with slight concentric lirae. Periostracum highly polished, color straw yellow to light brown, frequently with concentric bands of darker coloration. Interior porcelaneous, margins smooth. Hinge line with taxodont dentition in two nearly straight series of approximately equal numbers of teeth. Resilifer small, ligament partly external. Pallial

line slightly impressed, pallial sinus vestigial or absent.

COMPARISONS: This species is the most ovate of the subgenus, externally appearing very much like a small *P. arctica* (Gray), but is easily separated by the lack of a pallial sinus, the small resilifer and the external ligament. *P. fraterna* (Verrill & Bush) is a thinner shelled and more delicate species, and the hinge line is more nearly straight.

COLLECTION: This species is abundantly represented in the collection, occurring at 117 stations for a total of 1434 specimens and numerous single valves, in 27–2560 m.

RECORDS: *Recent*—Leche 1878:25, pl.1, f.62-d (Novaya Zemlya); Friele 1878:222 (North Atlantic); Friele and Grieg 1901:15 (Barents Sea); Jensen 1905:320 (Greenland); Odhner 1915:66, pl.1, f.20–32 (European Arctic); Mesjatsev 1931:44 (Barents Sea); Soot-Ryen 1939:9 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:18 (Iceland); Filatova 1957b:52 (Eurasian Arctic); Ockelmann 1958:34, pl.1, f.14 (Greenland); Wagner 1962:10 (Arctic Canada); Clarke 1963:100, pl.2, f.6–8 (Laurentian Basin); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and throughout the high latitudes of the Atlantic. Ockelmann (1958) has concluded that this species

has a more limited distribution in the Atlantic than that suggested by the literature. I concur that the illustration given by Verrill and Bush (1898, pl.79, f.4) is not this species and is unlikely that it occurs as far south as New England. It is not present in the Bering Sea or Pacific.

REMARKS: I am grateful to K.W. Ockelmann who identified this species for me.

Portlandia (Yoldiella) intermedia (M. Sars 1865)
Figure 22

Yoldia intermedia [M. Sars 1859:57, *nom. nud.*] M. Sars 1865:38, f.92–96; Oldroyd 1925:35, pl.1, f.1, 10.

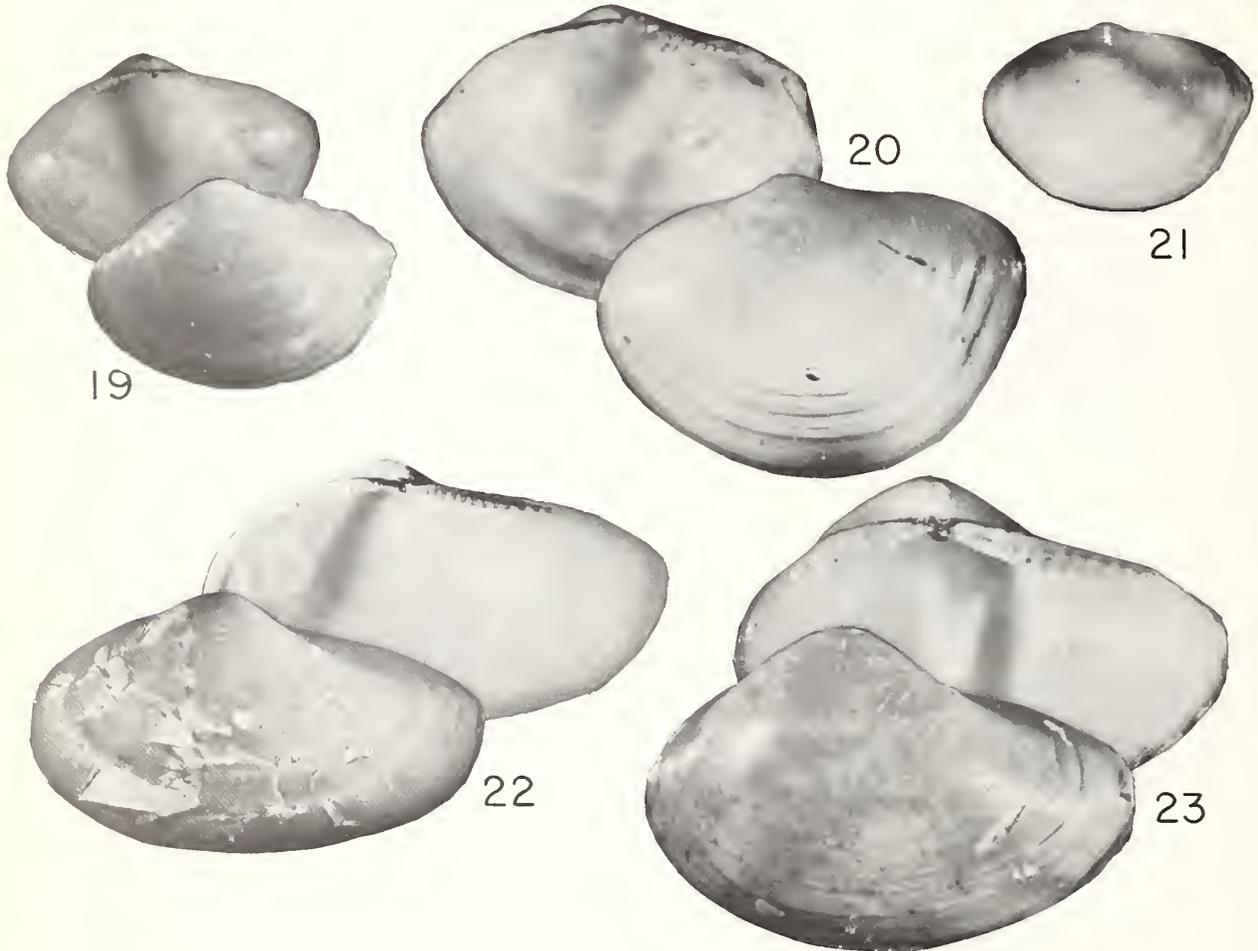
Portlandia intermedia (Sars), Jensen 1905:319.

Portlandia (Yoldiella) intermedia (Sars), Filatova 1948:420, pl.106, f.3 (of "Møller").

Yoldiella intermedia (Sars), Petrov 1966:193, pl.11, f.11–14.

Yoldiella intermedia major Leche 1878:24, pl.1, f.5.

DESCRIPTION: Shell elongate, inflated, total length to 15 mm. Anterior margin rounded, posterior sharply angulate.



FIGURES 19–23. 19, *Portlandia (Yoldiella) fraterna* (Verrill and Bush), length 3.9 mm; 20, *Portlandia (Yoldiella) frigida* (Torell), length 4.6 mm; 21, *P. (Y.) frigida*, elongated form, length 4.5 mm; 22, *Portlandia (Yoldiella) intermedia* (Sars), length 12.3 mm; 23, *Portlandia (Yoldiella) lenticula* (Møller), length 5.6 mm.

Umbones prominent. Surface smooth, sometimes with weak incremental striae. Periostracum brilliantly varnished, often with an iridescent sheen, color a light straw yellow to a grey brownish. Interior porcelaneous, polished, margins smooth. Hinge line weak, taxodont dentition in two series, the posterior row straight, and the anterior series in curve parallel to shell margin. Resilifer small, deeply set in a vertical position below beaks. Ligament mostly internal, but small part protruding. Pallial line almost invisible, pallial sinus vestigial.

COMPARISONS: This large *Yoldiella* is easily distinguishable from others by the inflated and elongate shell and the small deeply set resilifer. The extensive peeling of the periostracum from dried shells to reveal the chalky shell surface is also characteristic.

COLLECTION: This species did not occur frequently in the collection, being present at four stations only for a total of 52 specimens and a few dead valves, in 270–455 m.

RECORDS: *Recent*—Dall 1874:250 (of "Carpenter") (Bering Sea); Friele 1878:222 (Greenland); Leche 1878:24 (Novaya Zemlya); D'Urban 1880:253 (Barents Sea); Leche 1883:446 (Novaya Zemlya); Hägg 1904:11 (Greenland); Jensen 1905:319 (Greenland); Dautzenberg & Fischer 1910:17 (Novaya Zemlya); Odhner 1915:60 (Spitzbergen); Massy 1930:244 (North Atlantic); Mesjatsjev 1931:35 (Barents Sea); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:17 (Iceland); Filatova 1957b:52 (Eurasian Arctic); Ockelmann 1958:27, pl.1, f.12 (Greenland); Ellis 1960:38 (Baffin Island and Greenland); Clarke 1960:8, pl.1, f.6–8 (Laurentian Basin); Clarke 1963:100 (Laurentian Basin); Petrov 1967:184 (Bering Sea); Clarke 1974:9 (Baffin Bay); Wacasey 1974:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and widely distributed in the North Atlantic on the European side. This species has not been recorded in Hudson Bay or along the United States Atlantic seaboard. It extends into the northeastern part of the Bering Sea and has been collected several times in Norton Sound.

REMARKS: Ockelmann (1958) pointed out that, unlike other members of the genus, *P. intermedia* is rather uniform in its external morphology. It is possible that this species is a variety of *P. lucida* (Loven, 1846). It may be identical to *P. kolthoffi* Hägg 1904 from Jan Mayen, but that species is more compressed posteriorly and is ornamented with pronounced radial lirae.

Portlandia (Yoldiella) lenticula (Møller 1842)

Figure 23

Nucula lenticula Møller 1842:17.

Yoldia lenticula (Møller), Stuxberg 1886:148.

Portlandia lenticula (Møller), G. Sars 1878:39, p.4, f.10a, b.

Yoldiella lenticula (Møller), Petrov 1966:194, pl.11, f.15–20.

Yoldiella lenticula ambliata Verrill & Bush 1898:866, pl.80, f.9, pl.81, f.4.

Yoldia abyssicola Torell 1859:149, pl.1, f.4a–b.

Portlandia (Yoldiella) persei Mesjatsjev 1931:44; Filatova, 1957b: 52.

DESCRIPTION: Shell elliptical to elongate, inflated, total length to 10 mm but usually smaller. Surface smooth, with fine concentric striae and growth checkmarks. Periostracum polished, straw yellow to dark brown in color. Interior porcelaneous, margins smooth. Hinge line narrow with two series of long taxodont teeth separated by a deeply set resilifer. Ligament mostly internal. Pallial line not discernible; pallial sinus absent.

COMPARISONS: This species may be confused with *P. intermedia* (M. Sars), but the posterior part is shorter, the shell less inflated, and the resilifer shallower.

COLLECTION: This species was abundantly represented at 56

stations for a total of 2271 specimens and numerous single valves, in 23–360 m.

RECORDS: *Pleistocene*—Merklin et al. 1962:26, pl.1, f.13–16 (Chukotsk Peninsula); Richards 1962:52, pl.1, f.23, 24 (James Bay to Maine); Troitskiy 1974:265 (Siberia) *Recent*—Hägg 1904:13 (Greenland); Jensen 1905:320 (Greenland); Odhner 1915:64 (Spitzbergen); Massy 1930:239 (North Atlantic); Soot-Ryen 1939:8 (Franz Josef Land); Gorbunov 1946a:46 (Siberian Arctic); Filatova 1957b:52 (Eurasian Arctic); Ockelmann 1958:30, pl.1, f.13 (Greenland); Soot-Ryen 1958:9 (Greenland); Clarke 1961:8, pl.1, f.4 (Laurentian Basin); Richards 1962:52, pl.1, f.23, 24 (Arctic Canada to Maine); Petrov 1967:184 (Northern Bering Sea); Petersen 1968:6 (Faroe Islands); Clarke 1974:9 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and widely distributed throughout the Northern Atlantic and along the American coast as far south as Maine. It occurs sporadically in the northernmost Bering Sea, but not in the Pacific Ocean.

REMARKS: The taxon *P. lenticula ambliata* (Verrill and Bush 1898) is merely a thicker shelled form typical of coarser sediments and occurs throughout the range.

Genus *Yoldia* Møller 1842

Figure 24

Type species (subsequent designation ICZN 1966): *Yoldia hyperborea* Torell 1859. *Recent*. Arctic.

DESCRIPTION: Shell thin, subovate to elongate, posterior produced, sometimes distinctly rostrate, with a posterior gape. Surface smooth or with predominantly concentric lirae. Periostracum brilliantly polished, thin and dehiscent. Interior porcelaneous, margins always smooth. Hinge line with large subumbonal resilifer, taxodont dentition in two subequal series. Pallial line feebly impressed, pallial sinus well developed.

RANGE: Cretaceous to Recent. Recent distribution cosmopolitan in temperate and cold waters, from the high subtidal level to abyssal environments. Inhabiting a wide range of substrates, but usually with a high proportion of fine sediments. Long siphons permit the group to be deeply infaunal.

DEVELOPMENT: Ova large, development lecithotrophic with a very abbreviated planktonic phase.

REMARKS: This genus includes the most developed proto-branches, all are active burrowers, rapidly moving through the substrate, or using the bifurcated foot to move the unburied animal. Three species are represented in the collection, but all are

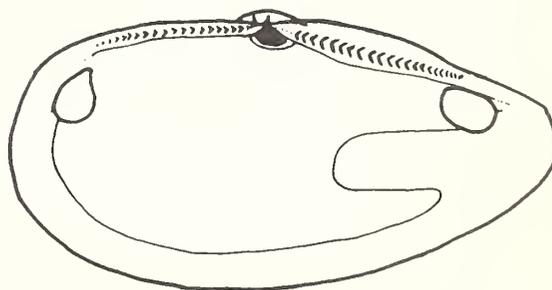


FIGURE 24. Interior of right valve of *Yoldia hyperborea* Torell.

scarce, as were those listed by MacGinitie (1959). It should be noted that *Y. thraciaeformis* (Storer 1838) was not found; it is circumboreal and abundantly represented in the Chukchi Sea and in Dolphin and Union Strait.

KEY TO THE SUBGENERA OF *YOLDIA*

Surface smooth, or with concentric lirae *Yoldia* s. str.
Surface with oblique incised lirae *Cnesterium*

Subgenus *Yoldia* s. str. *Yoldia (Yoldia) hyperborea* Torell (Loven MS) 1859

Figures 25, 26

Yoldia hyperborea Torell (Loven MS) 1859:142, pl.2, f.6a–b; Filatova 1948:421, pl.106, f.8; Ockelmann 1954:8, pl.1, f.1, 2, pl.2, f.1–4; Cowan 1968:58, pl.5, f.6, 7.

Yoldia limatula hyperborea. Gorbunov 1946a:46.

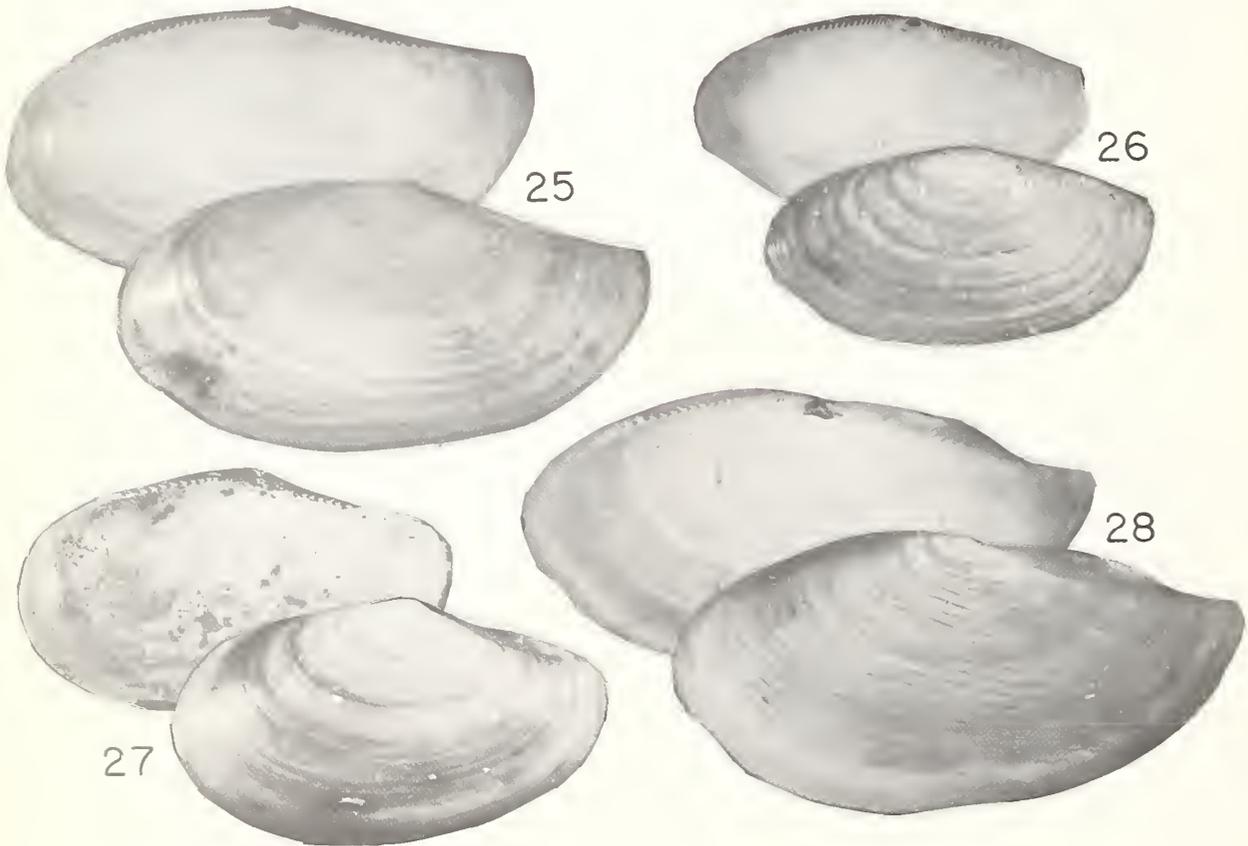
DESCRIPTION: Shell thin, compressed, total length to 45

mm. Surface smooth, sometimes with feeble incremental striae. Periostracum light brown to yellow, brilliantly polished and strongly adherent. Interior porcelaneous to chalky, shell margins smooth. Pedal and siphonal regions with pronounced gapes. Hinge line with large resilifer and taxodont dentition in two sub-equal series. Pallial line impressed, pallial sinus large.

COMPARISONS: This species is similar to the circumboreal *Y. amygdalea* Valenciennes 1846, but the posterior region is longer, more tapering and not pointed. The other representative of the genus also present in the Beaufort Sea is *Y. myalis* (Couthouy 1838) which is easily separated from *Y. hyperborea* by its more ovate outline, dull periostracum, and more posterior placement of the beaks.

COLLECTION: *Y. hyperborea* occurred at 13 stations for a total of 22 specimens and several single valves in a depth of 30–360 m.

RECORDS: *Pleistocene*—Merklin et al. 1962:24, pl.1, f.3 (Chukotsk Peninsula); Petrov 1966:188, pl.10, f.18–20 (Chukotsk Peninsula); Gladenkov 1972:207 pl.3, f.1–8 (Kamchatka). *Recent*—Leche 1883:444, pl.33, f.16, 17 (European Arctic); Krause 1885:25 (Bering Sea); Stuxberg 1886: 147 (Novaya Zemlya); Hägg 1904:10 (Greenland and Spitzbergen); Odhner 1910:18, pl.1, f.23 (Iceland); Odhner 1915:51 (Spitzbergen); Filatova 1957b:52 (Arctic); Ockelmann 1958:21 (Green-



FIGURES 25–28. 25, *Yoldia (Yoldia) hyperborea* (Torell), length 31.0 mm; 26, *Y. (Y.) hyperborea*, abbreviated form, length 24.8 mm; 27, *Yoldia (Yoldia) myalis* (Couthouy), length 17.1 mm; 28, *Yoldia (Cnesterium) scissurata* Dall, length 22.9 mm.

land); MacGinitie 1959:152, pl.18, f.5 (Point Barrow); Ellis 1960:38 (Baffin Island and Greenland); Sparks & Pereyra 1966:834 (Chukchi Sea); Petrov 1967a:184 (Northern Bering Sea); Gladenkov 1972:207, pl.3, f.1-8 (Kamchatka); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic, with discontinuous distribution. It is abundant in the Canadian Arctic Archipelago and Greenland and throughout the North Atlantic; also in the Chukchi and Northern Bering seas.

REMARKS: Ockelmann (1954) in a review of the various species proposed separation of North Atlantic more attenuated forms as *Y. hyperborea limatuloides* Ockelmann 1954. Cowan (1968) considered this stock distinct and conspecific with the circumboreal *Y. amygdalea* Valenciennes 1846.

Yoldia (Yoldia) myalis (Couthouy 1838)

Figure 27

Nucula myalis Couthouy 1838:62, pl.3, f.7.

Yoldia myalis (Couthouy), Oldroyd 1925:30, pl.5, f.8; Ockelmann 1954:18, pl.1, f.1, pl.2, f.5, 10.

DESCRIPTION: Shell inflated, ovate, anterior evenly rounded, posterior prolonged, subtriangular, maximum length to 30 mm. Surface with irregular concentric ridges. Periostracum olive green to dark brown, dull and dehiscent. Interior porcelaneous, margins smooth with prominent posterior and pedal gapes. Hinge line developed, taxodont dentition in two nearly equal series of short solid teeth. Resilifer large, shallow, and laterally produced. Pallial line deeply impressed, pallial sinus large.

COMPARISONS: Although the shell outline of this species tends to be variable, the more oval shape, posterior placement of the umbones, the full periostracum, and large elongated resilifer, readily distinguish this species from all other species of *Yoldia*.

COLLECTION: The species is represented by three specimens from one station in 79 m.

RECORDS: *Pleistocene*—Wood 1851:90, pl.10, f.17 a-c (Britain); Richards 1962:52, pl.1, f.26 (Maine); Petrov 1966:189, pl.10, f.21 (Chukotsk Peninsula). *Recent*—Gould 1841:99 (Massachusetts); Gould 1870:160 (Massachusetts); Crosse 1877:120 (Bering Sea); Johnson 1934:17 (Labrador to Massachusetts); Filatova 1957b:52 (Eurasian Arctic); MacGinitie 1959:152, pl.18, f.1 (Point Barrow, Alaska); Hulsemann 1962:71 (Beaufort Sea); Richards 1962:52, pl.1, f.26 (Labrador to Cape Cod); McLaughlin 1963:25 (Bering Sea); Filatova and Barsanova 1964:20 (Western Bering Sea); Sparks and Pereyra 1966:834 (Chukchi Sea); Bernard 1970:86 (British Columbia); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Limited Arctic distribution. The species is present along the North Atlantic American coast from Maine to Hudson Strait, but it is not found off Greenland. On the Pacific side it occurs from Washington State to Alaska and throughout the Bering Sea. It enters the Chukchi Sea and occurs sporadically on the adjacent continental margins as far west as the Siberian Sea and along the American coast to Point Barrow and the western Beaufort Sea.

REMARKS: Ockelmann (1954) is correct in regarding the distribution of this species as discontinuous, though Hulsemann (1962) extended the range some 250 km east of Point Barrow. There are consistent differences between the Pacific and Atlantic

stocks, with Arctic representatives more closely connected to the Atlantic form. It is possible that living Arctic specimens are relicts of an earlier holoarctic distribution.

Subgenus *Cnesterium* Dall 1898

Type species (original designation): *Yoldia scissurata* Dall 1897. Recent. Northeast Pacific.

Yoldia (Cnesterium) scissurata Dall 1897

Figure 28

Yoldia scissurata Dall 1897:8, [new name for *Yoldia arctica* Broderip and Sowerby 1829 not Gray 1824]; Oldroyd 1925:31, pl.5, f.2.

Yoldia (Cnesterium) scissurata Dall, Filatova 1957b:52.

Yoldia ensifera Dall 1897a:9, pl.2, f.4; Oldroyd 1925:32, pl.5, f.3, pl.37, f.6.

Yoldia ensifera plena Dall 1908:256; Oldroyd 1925:33.

Yoldia (Cnesterium) strigata Dall 1909:18, 104, pl.14, f.9, a; Grant and Gale 1931:131.

DESCRIPTION: Shell compressed, elongate, maximum length to 40 mm. The anterior end is evenly rounded, posterior end with slightly recurved small rostrum. Posterior dorsal margins produced to form blade-like crest. Surface with feeble concentric lirae, crossed by oblique incised lines. Periostracum brilliantly varnished, adherent, color light brownish-yellow to black, frequently with concentric bands of different colors. Interior polished, shell margins smooth, with small pedal and siphonal gapes. Taxodont dentition in two series, the anterior rather more numerous than the posterior teeth. Resilifer wide, deeply set. Pallial line feebly impressed, pallial sinus deep and rounded.

COMPARISONS: This species is easily distinguished by the oblique sculpture which involves the shell layers and may carry through into the interior, in some specimens it may be more easily observed in transmitted light.

COLLECTION: Represented by four specimens only from one station in 64 m.

RECORDS: (?) *Miocene*—Dall 1909:104, pl.14, f.9, a (Oregon); Arnold and Hannibal 1913:590 (Oregon); Weaver 1916:32 (Washington). *Pliocene*—Grant & Gale 1931:131 (Oregon). *Pleistocene*—Grant and Gale 1931:131 (California); Zhidkova et al. 1972:97, pl.10, f.12-18 (Kurile Islands). *Recent*—Packard 1918:249, pl.14, f.6 (California); Grant & Gale 1931:131 (Arctic Ocean to British Columbia); Eyerdam 1938:100 (Aleutian Archipelago); Kuroda and Habe 1952:35 (Northern Japan); MacGinitie 1959:154 (Point Barrow, Alaska); McLaughlin 1963:25 (Bering Sea); Parker 1964:157 (Gulf of California, Mexico); Sparks and Pereyra 1966:834 (Chukchi Sea); Bernard 1970:86 (British Columbia).

DISTRIBUTION: Present throughout the Bering Sea, this species extends along the American coast possibly as far south as the Gulf of California, Mexico. It is present in the Sea of Okhotsk to Northern Japan. It passes through the Bering Strait into the Chukchi Sea as far west as the Siberian Sea and to the east including Point Barrow and the present range extension.

REMARKS: There is little doubt *Y. ensifera* Dall is the southern representative of this species and identical to *Y. strigata* Dall of the Miocene of Oregon. It is possible that *Y. vasiljevskii* Slodkevitch 1935 from Franz Josef Land is closely related. They may all have originated from *Y. (Cnesterium) yakatagensis* Kanno 1971 from the Alaskan Tertiary.

Family ARCIDAE Lamarck 1809

Genus *Bathyarca* Kobelt 1891

Figure 29

Type species (original designation): *Arca pectunculoides* Scacchi 1833.
Eocene. Europe.

DESCRIPTION: Shell oval to elongate, inflated. Surface with incremental striae or small concentric riblets. Periostracum thick, dehiscent, hirsute, frequently with radial rows of short bristles. Interior porcelaneous, margins smooth. Hinge line with central edentulous space separating posterior and anterior series of pseudotoxodont teeth. In some species the hindermost teeth tend to be oblique and sometimes parallel the hinge margin. Ligament external, with small strands inserted in chevron-shaped grooves below the beaks. Pallial line entire, slightly impressed, no pallial sinus.

RANGE: Eocene to Recent. Recent distribution cosmopolitan, generally in deep and abyssal water, but may occur in 20 m or less in cold waters. The preferred habitat is gravel mixed with fine sediments and byssally attached to pebbles or other hard object. The habitat is superficially infaunal or nesting, often with only the anterior end buried, frequently resulting in the attachment to the shell of ascidians, actinians, and other small epizoa.

DEVELOPMENT: Ova are large, it is probable that development is lecithotrophic with a reduced, or absent planktonic phase (Thorson 1936, Ockelmann 1958).

REMARKS: Species presently included within *Bathyarca* fall into three distinct groups. The first comprise small, rather compressed types with few teeth that have a tendency to assume an oblique, or even horizontal, position. The shell is of medium thickness and the periostracum hirsute. The second group includes thin-shelled, highly inflated forms with concentric ribbing and overlying radial striae. The periostracum is thin and the teeth are more numerous. The last group is characterized by a thick chalky shell with irregular concentric striae and a thick very hirsute periostracum rather reminiscent of *Limopsis*. The interior between the adductor muscle scars is frequently colored red or

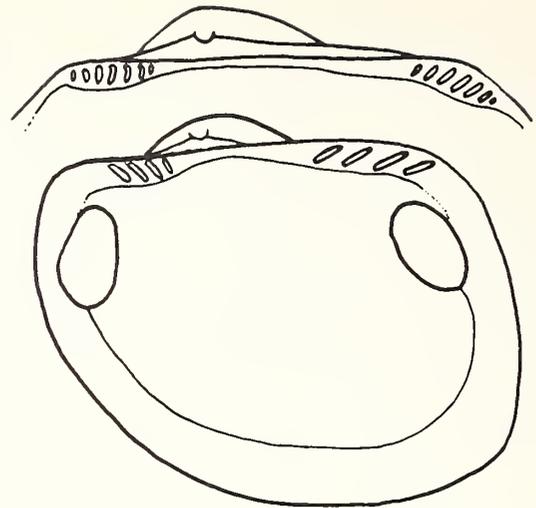


FIGURE 29. Interior of right valve of *Bathyarca pectunculoides* (Scacchi), inset, hinge of *B. glacialis* (Gray).

brown. It is likely that careful comparison, particularly of the soft anatomy, will show that separate genera or subgenera should be erected. Two species are present in the collection.

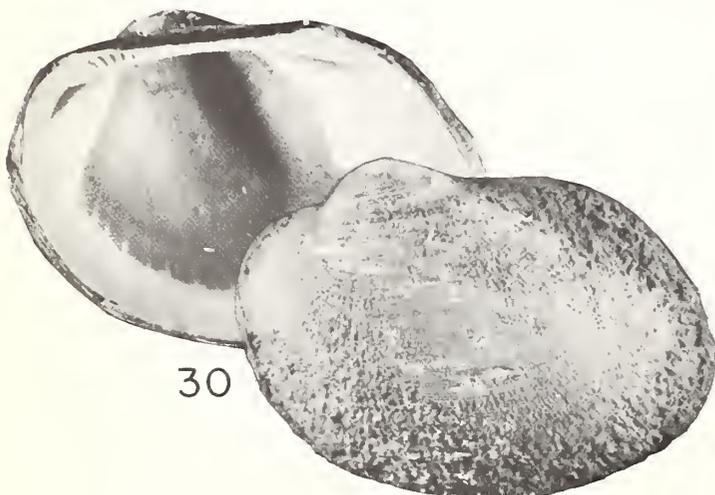
Bathyarca glacialis (Gray 1824)

Figure 30

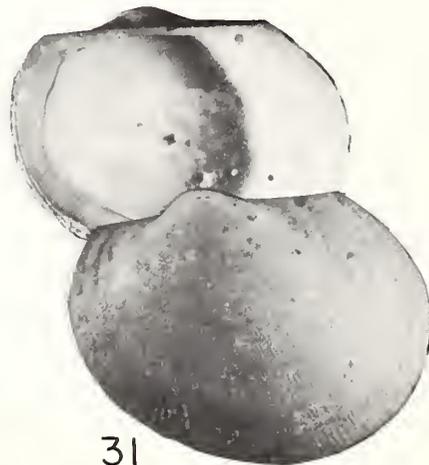
Arca glacialis Gray 1824:244 (Appendix); G. Sars 1878:43, pl.4, f.1 a-c.

Arca (Bathyarca) glacialis Gray, Filatova 1948:422, pl.106, f.10.

DESCRIPTION: Shell thick, chalky, inflated, length to 25 mm. Outline elongate to ovate. Surface with feeble concentric striae. Periostracum thick, light brown, very hirsute. Beaks usually eroded and periostracum absent from most of the disc. Interior dull to chalky, except for marginal band. Region between the



30



31

FIGURES 30-31. 30, *Bathyarca glacialis* (Gray), length 19.9 mm; 31, *Bathyarca raridentata* (Wood), length 7.9 mm.

adductor muscles often deeply stained, either brown or reddish. Hinge line straight and narrow with central edentulous space separating two series of a few pseudotaxodont teeth, the exterior ones tending to be oblique, particularly in the posterior region. Ligament elongated, duplivincular, periligamental chevron-shaped grooves poorly developed. Pallial line feebly impressed, but pallial attachment point crenulated, no pallial sinus.

COMPARISONS: The massive chalky shell, hairy periostracum, and inflated shape distinguish this species.

COLLECTION: Specimens were found at 20 stations for a total of 60 specimens, and some single valves in 23–455 m.

RECORDS: *Pleistocene*—Merklin et al. 1962:27, pl.1, f. 19–24 (Chukotsk Peninsula); Richards 1962:52 (Maine); Troitskiy 1974:265 (Siberia). *Recent*—Leche 1878:29 (Novaya Zemlya); D'Urban 1880:253 (Barents Sea); Leche 1883:448 (Arctic); Stuxberg 1886:147 (Novaya Zemlya); Hägg 1904:17 (Greenland); Dautzenberg and Fischer 1910:15 (Novaya Zemlya); Odhner 1915:73 (Greenland); Massy 1930:248 (North Atlantic); Mesjatev 1931:56 (Barents Sea); Soot-Ryen 1932:8, pl.1, f.12 (European Arctic); Johnson 1934:21 (Gulf of St. Lawrence); Gorbunov 1946a:46 (Arctic); Madsen 1949:22 (Iceland); Filatova 1957b:52 (Eurasian Arctic); Filatova and Zenkevich 1957:63 (Kara Sea); Ockelmann 1958:44, pl.1, f.18 (Greenland); Soot-Ryen 1958:11 (Greenland); Ellis 1960:38 (Baffin Island); Richards 1962:52 (Greenland to Gulf of St. Lawrence); Allen 1965:978 (Northwest Atlantic); Clarke 1974:9 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and boreal in the Atlantic. It is abundant from Baffin Island and Greenland, at least as far south as the Gulf of St. Lawrence and across the Atlantic to the Faroe Islands and Norway, though early reports that it is present in the Mediterranean are certainly erroneous. It is not present in the Pacific or Bering seas.

REMARKS: Several authors have taken the view that this species is closely allied to *B. raridentata* (Wood) through *B. pectunculoides* Scacchi 1834. Jeffreys (1863) rejected this, and it has not been accepted by the majority of workers.

Batharca raridentata (Wood 1840)

Figure 31

Arca pectunculoides, auctt., [not Scacchi 1834:82, pl.1, f.12a, b]; Philippi 1844:44, pl.15, f.3a–d.

Arca (*Batharca*) *pectunculoides* ("Scacchi"), Filatova 1948:422, p.106, f.12, 13.

Arca glacialis pectunculoides grandis Leche 1878:30, pl.1, f.9a–c.

Arca glacialis pectunculoides ("Scacchi"), Leche 1883:449; Gorbunov 1946a:46

Arca pectunculoides crenulata Verrill 1882:575; Lamy 1907:279.

Arca raridentata Wood 1840:232, pl.13, f.4; Forbes and Hanley 1848:241, pl.45, f.8; Jeffreys 1863:171, pl.5, f.3.

DESCRIPTION: Shell thin and delicate, outline ovate to rhomboidal, total length to 5 mm, usually rather smaller. Surface ornamented by radial and concentric riblets resulting in a reticulate appearance. Periostracum thin, light grey in color, hirsute and produced into concentric folds, especially in the ventral regions. Interior porcelaneous, sometimes with feeble radial striae, shell margins smooth, with projecting fringe of periostracum. Hinge lines straight, central portion edentulous, pseudotaxodont teeth few and weak, anterior series oblique, posterior series nearly parallel to hinge margin. Ligament duplivincular. Pallial line deeply impressed, no pallial sinus.

COMPARISONS: This species may be confused with *B. glacialis*, but the more delicate shell, smaller size, fewer teeth, and periostracum with concentric folds easily separate it.

COLLECTION: The species occurred at one station only represented by six specimens in 55 m.

resented by six specimens in 55 m.

RECORDS: *Pliocene*—Wood 1851:79, pl.10, f.3a, b (Britain) *Recent*—Loven 1846:34 (Greenland); Forbes and Hanley 1848:241, pl.45, f.8 (Hebrides); Wood 1852:79, pl.10, f.3a, b (Britain); M. Sars 1859:55 (European Arctic); Jeffreys 1863:171, pl.30, f.3 (Hebrides and Shetland Islands); G. Sars 1878:43 (Greenland); D'Urban 1880:253 (Barents Sea); Stuxberg 1886:146 (Novaya Zemlya); Hägg 1904:19 (Greenland); Jensen 1905:309 (Greenland); Dautzenberg and Fischer 1910:15 (Novaya Zemlya); Soot-Ryen 1925:5 (Spitzbergen); Massy 1930:247 (North Atlantic); Soot-Ryen 1939:9 (Franz Josef Land); Filatova 1957b:52 (Arctic); Filatova and Zenkevich 1957:67 (Kara Sea); Ockelmann 1958:39, pl.1, f.16 (Greenland); Allen 1965:978 (Northwest Atlantic); Soot-Ryen 1966:6 (North Atlantic); Petersen 1968:51 (Faroe Islands); Clarke 1974:9 (Baffin Bay).

DISTRIBUTION: Widely distributed in the North Atlantic from Greenland to Franz Josef Land and Novaya Zemlya, and south to Portugal and Canary Islands in deep water. Mediterranean records are probably in error. In the west Atlantic the species occurs from Baffin Island to Maine and possibly the Gulf of Mexico. It is probably panarctic with sporadic distribution. The species does not occur in the Bering Sea or Pacific Ocean.

REMARKS: I do not consider the Italian Miocene fossil *P. pectunculoides* Scacchi synonymous with the contemporary northern species. Scacchi's description is not adequate and the illustrations poor. However, they certainly do not represent the living Arctic and Atlantic bathyarcid so often referred to this species. I have examined several series of Wood's *Arca raridentata* from the Pliocene Coralline Crag of Britain presently in the British Museum (Natural History) Paleontological Collection, and conclude that it is identical to living material. Wood (1851) synonymized his *A. raridentata* with *A. pectunculoides* probably on the basis of Philippi's (1844) paraphrased and altered original description of the latter and his illustration which is not of Scacchi's species but most probably is *Arca pteroessa* E. A. Smith (1885). I consider *B. pectunculoides* a distinct species, essentially Mediterranean in distribution and extending to Belgium and Denmark. My examination of material from the Miocene of Belgium convinces me it is a markedly ovate form with three or four teeth on each side of the hinge, it is also more inflated than *B. raridentata* and the hinge appears to have a number of small denticles. It is with some reluctance that I reinstate Wood's taxon, but the conchological evidence supports this action. Clarke (1960, 1963) recognized *B. frielei* Jeffreys MS 1877 from the Laurentian Basin, and suggested this is the species recorded as *A. pectunculoides* by Scarlato in Brodskii and Nikitin (1955). Wagner (1977) identified *B. frielei* from the eastern Beaufort Sea. In my opinion *B. frielei* will prove to be a synonym of *B. raridentata*. *B. anomala* Verrill and Bush 1898, from the Atlantic coast of North America, is probably a gerontic specimen of *B. raridentata* with the dentition largely obliterated. *Arca pectunculoides orbiculata* Dall 1881 is not this species and I do not consider it closely related to *A. pectunculoides*.

Family MYTILIDAE Rafinesque 1815

This family is well represented throughout the Arctic, the present collection boasts three genera, but *Mytilus edulis* Linné was not collected. The latter is typically circumboreal and only sporadically panarctic. Its absence from the collection is probably attributable to the fact that no suitable inter- to subtidal habitat, protected from ice-scour, was sampled. Wagner (1977) recorded *Modiolus modiolus* (Linné 1750) from the eastern Beaufort Sea.

KEY TO THE GENERA OF MYTILIDAE

1. Shell with radial sculpture, reduced on shell posterior ...
 2
 Shell sculpture absent, or evenly distributed
 *Musculus*
- 2.(1) Shell with strong radial ribs
 *Dacrydium*
 Shell not sculptured, transparent
 *Crenella*

Genus *Crenella* Brown 1827

Figure 32

Type species (monotypy): *Mytilus decussatus* Montagu 1808. Recent. North Atlantic.

DESCRIPTION: Shell oval, inflated, surface with numerous radial ribs which may bifurcate. Periostracum thin, polished, strongly adherent. Interior polished, shell margins crenulate. Hinge line weak, resilifer small, elongated. Two small groups of tiny dysodont teeth are present. Ligament internal. Pallial line almost invisible, no pallial sinus.

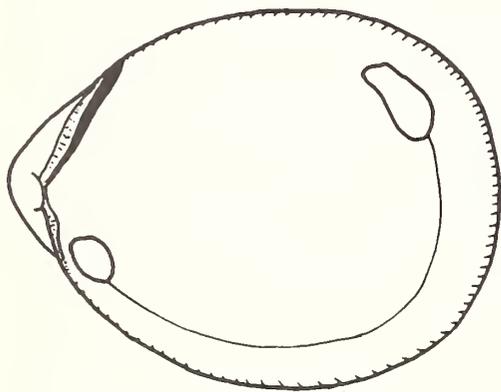


FIGURE 32. Interior of right valve of *Crenella decussata* (Montagu).

RANGE: Cretaceous to Recent. Recent distribution cosmopolitan, from Arctic to tropical seas, and the low intertidal zone to 4500 m. The preferred habitat is fine sediment mixed with larger rock fragments, where individuals usually are byssally attached epifaunal nestlers.

DEVELOPMENT: Egg size varies widely, but the Arctic species have large ova, and lecithotrophic development (Ockelmann 1958).

REMARKS: The most striking feature of the soft anatomy is the vermiform foot with thickened end. It is protruded from the shell and actively moves the animal when not byssally anchored. Nutrition is entirely by suspension-feeding.

Crenella decussata (Montagu 1808)

Figure 33

Mytilus decussatus Montagu 1808:69; Lamarck 1819:120.

Crenella decussata (Montagu), Odhner 1915:80; Oldroyd 1925:79; Soot-Ryen 1955:81, pl.8, f.43, 45; Petrov 1966:204, pl.12, f.11-13.

DESCRIPTION: Shell subglobular to ovate, maximum diameter 5 mm. Beaks prominent, incurved and prosogyrous with a distinct smooth prodissoconch. Surface sculptured by numerous minute radial ribs and weaker concentric striae, producing a decussated surface. Ribs on central portion of disc bifurcated. Periostracum thin, translucent ash grey to light brown, strongly adherent. Interior nacreous, shell margins minutely denticulated. Hinge line thickened, with fine nearly vertical ridges giving the appearance of small denticles. A long narrow, deeply set resilifer accommodates the internal ligament. Pallial line feebly impressed, no pallial sinus.

COMPARISONS: The bifurcated sculpture and the inflated shell distinguish this species from other mytilids.

COLLECTION: *C. decussata* was present at one station only; one specimen and a single valve was collected in 27 m.

RECORDS: *Pleistocene*—Grant and Gale 1931:254 (California). *Recent*—Middendorff 1849:530, pl.11, f.22-24 (Siberia); Jeffreys 1863:133, pl.28, f.6 (Britain); Leche 1878:34 (Novaya Zemlya); G. Sars 1878:31, pl.3, f.4a, b (Greenland); Dunker 1882:225 (Northern Japan); Krause 1885:21 (Bering Sea); Stuxberg 1886:150 (*Novaya Zemlya*); Whiteaves 1887:120 (British Columbia); Massy 1930:250 (North Atlantic); Grant and Gale 1931:254 (Bering Sea to California); Mesjatsjev 1931:68 (Barents Sea); Johnson 1934:29 (Greenland to North Carolina); Soot-Ryen 1939:10 (Franz Josef Land); Madsen 1949:24 (Iceland); Kuroda and Habe 1952:18 (Northern Japan); Filatova 1957b:52 (Eurasian Arctic); Ockelmann 1958:51 (Greenland); Ellis 1960:38 (Baffin Island); Kuznetsov 1963:109 (Kamchatka); Filatova and Barsanova 1964:34 (Eurasian Arctic); Petersen 1968:10 (Faroe Islands); Bernard 1970:87 (British Columbia).

DISTRIBUTION: Circumboreal and probably panarctic. This species occurs throughout the North Atlantic and sporadically in the Arctic. It has been recognized in the Bering Sea, the Sea of Okhotsk to Japan, and along the American Pacific coast as far south as California.

REMARKS: It is particularly significant finding a typical "European" morphotype in the Alaskan Arctic, as the Pacific representatives tend to have finer sculpture and more ponderous hinge than Atlantic *C. decussata*. Although Montagu's name has been applied to specimens from as far south as Baja California, it is probable that the circumboreal species only is found in the Pacific to northern Japan and central California.

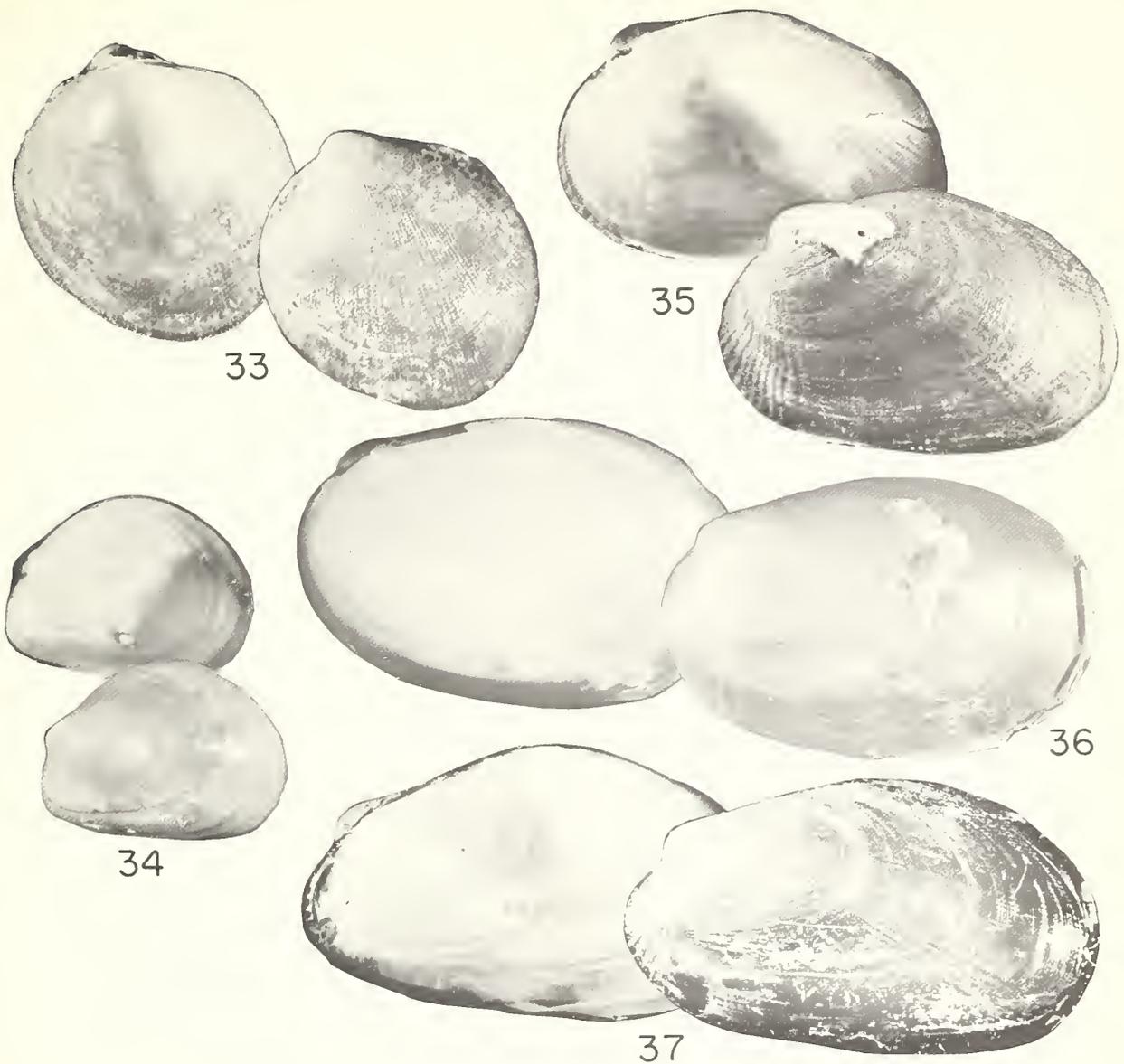
Genus *Dacrydium* Torell 1859

Figure 38

Type species (monotypy): *Mytilus vitrea* Møller [Hölboll ms] 1842. Recent. Arctic.

DESCRIPTION: Shell hyaline, thin, very inflated, outline ovate. Surface smooth. Periostracum thin, adherent, sometimes with attached sand particles. Hinge edentulous, but with one or more areas of vertical striations on the thickened hinge margins.

RANGE: (?) Pliocene to Recent. Recent distribution cosmopolitan in cold waters, generally bathyal to abyssal and extending to hadal depths. The genus is a member of the superficial infauna of fine sediments mixed with boulders and gravel.



FIGURES 33-37. 33, *Crenella decussata* (Montagu), length 5.0 mm; 34, *Dacrydium (Dacrydium) vitreum* (Møller), length 4.1 mm; 35, *Musculus (Musculus) corrugatus* (Stimpson), length 13.1 mm; 36, *Musculus (Musculus) discors* (Linné), length 22.6 mm; 37, *Musculus (Musculus) niger* (Gray), length 15.0 mm.

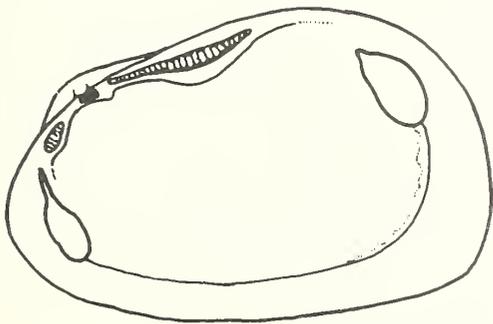


FIGURE 38. Interior of right valve of *Dacrydium vitreum* (Møller).

Though a developed byssal groove is present, there are no records of byssal attachment.

DEVELOPMENT: According to Ockelmann (1958) and Knudsen (1970), the ova of the species they examined are large, indicating lecithotrophic development, with a reduced or absent planktonic stage.

REMARKS: This genus displays a true amphiboreal distribution, being found in shallow water in the Arctic and Antarctic, but in deep water in the seas occupying lower latitudes. It is poorly represented in the Pacific by only two species, both in deep water. Ockelmann (1958) considers that further research will show the North Atlantic to possess several species presently lumped in *D. vitreum* (Møller). The subgenus *Quendreda* Iredale 1936, used by Soot-Ryen (1955) for a small species from the

Galapagos Islands, with vertical crenulations more pronounced than in *Dacrydium* s. str., probably deserves full generic separation.

Subgenus *Dacrydium* s. str.
Dacrydium (Dacrydium) vitreum
(Møller [Hölboll MS] 1842)

Figure 34

Mytilus vitrea Møller [Hölboll ms] 1842:19.
Dacrydium vitreum (Møller), G. Sars 1878:28, pl.3, f.2a, b.

DESCRIPTION: Shell translucent and fragile with beaks on anterior end, total length to 6 mm. Anterior reduced, inflated, posterior region high and compressed. Surface smooth, with an oily iridescence in fresh specimens. Periostracum thin, polished, sometimes with adhering particles. Interior polished. Hinge dorsally thickened, with small rectangular resilifer below beaks. The hinge is edentulous, but two series of small vertical crenulations occur, more abundantly posterior to the resilifer. Anterior adductor muscle is attached to a thickened support. Pallial line feebly impressed, no pallial sinus.

COMPARISONS: This species cannot be confused with any other Arctic bivalve, as no other mytilid displays the hyaline shell and striated hinge line of *D. vitreum*.

COLLECTION: The species occurred at 19 stations for a total of 60 specimens in 34–455 m.

RECORDS: *Recent*—Torell 1859:139, pl.1, f.2 (Spitzbergen); Leche 1878:34 (Novaya Zemlya); Stuxberg 1886:151 (Novaya Zemlya); Jensen 1905:325 (Greenland); Dautzenberg and Fischer 1910:13 (Novaya Zemlya); Jensen 1912:53 (Greenland, Iceland, Faroes); Odhner 1915:80 (Spitzbergen); Massy 1930:249 (North Atlantic); Mesjatsev 1931:69 (Barents Sea); Soot-Ryen 1939:10 (Franz Josef Land); Gorbunov 1946a:46 (Arctic); Filatova 1948:430, pl.108, f.10 (East Siberian Sea, Kara Sea); Madsen 1949:22 (Iceland); Filatova 1957b:52 (Arctic); Filatova and Zenkevich 1957:63 (Kara Sea); Ockelmann 1958:48 (Greenland); Soot-Ryen 1958:14 (Greenland); Clarke 1960:3 (Arctic); Clarke 1963:101 (Arctic); Clarke 1974:9 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea).

DISTRIBUTION: Possibly panarctic, this species is present along the Eurasian coasts, and widely distributed in the North Atlantic, south to the Faroe Islands and doubtfully the Azores. It is present in the Bering Sea and the Gulf of Alaska (Bernard MS). Clarke (1963) published the initial record for this species in the Laurentian Basin.

REMARKS: The present collection comprises large specimens which tend towards *D. pacificum* Dall 1916 in outline. I have no hesitation at including them with *D. vitreum*, which displays some variability in shell proportions, but is possible that further research will show Dall's Pacific representative to be synonymous.

Genus *Musculus* Röding 1798

Figure 39

Type species (subsequent designation Iredale 1915): *Mytilus discors* Linné 1767. *Recent*. North Atlantic.

DESCRIPTION: Shell modioliform, surface ornamented with radial ribs in the anterior and posterior parts while the central portion is smooth, or with concentric striae and wrinkles. Periostracum dark, polished and strongly adherent. Interior iridescent, shell margins at least partly crenulated. Hinge edentulous, but with distinct small irregular crenulations, particularly on posterior

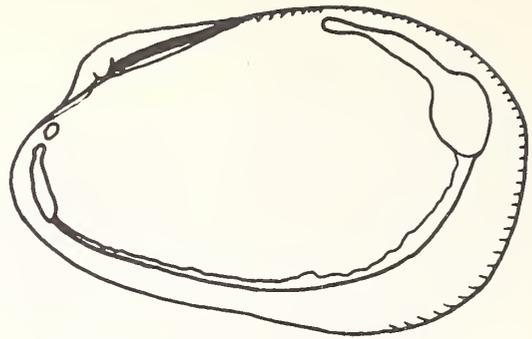


FIGURE 39. Interior of right valve of *Musculus discors* (Linné).

portion. Anterior adductor scar set well forward of the umbones and below large anterior pedal retractor muscles scar. Posterior adductor muscle scar subcircular, joined to elongated posterior retractor muscle scars. Pallial line not impressed, wide. No pallial sinus.

RANGE: Jurassic to Recent. Recent distribution cosmopolitan, in cold and temperate seas, and particularly in Arctic regions. Occurring from the intertidal zone to more than 1500 m, the genus is a member of the byssally attached epifauna, generally nestling in cavities or under rocks. Individuals may also attach to buried particles, becoming partially infaunal.

DEVELOPMENT: Eggs are large and attached within the byssal "nest" of the parent. Development continues within the gelatinous egg-mass and the planktonic stage is omitted (Ockelmann 1958).

REMARKS: The anatomy is typically mytilid, but the pallial current is anterior-posterior. Water is taken in through a funnel-like extension of the anterior mantle and expelled through a posterior extension forming an excurrent siphon. Nutrition is entirely by filter-feeding. The genus is notable for the construction of a "nest" or cylinder of byssus threads used as an egg-case. All species appear to be gregarious to some degree, generally being found in small groups mutually attached by byssal threads. Arctic representatives all belong to *Musculus* s. str. Three species are present.

Subgenus *Musculus* s. str.
Musculus (Musculus) corrugatus
(Stimpson 1851)

Figure 35

Mytilus corrugatus Stimpson 1851:12.
Modiolaria corrugata (Stimpson), Dall 1874:250; Jensen 1912:62, pl.3, f.7 a–d; Oldroyd 1925:25.
Crenella corrugata (Stimpson), Stuxberg 1886:151.
Musculus corrugatus (Stimpson), Scarlato 1955:188, pl.5, f.1.
Musculus (Musculus) corrugatus (Stimpson), Scarlato 1960:86, pl.4, f.5, text-fig. 45.

DESCRIPTION: Shell irregularly ovate, inflated, total length to 20 mm, usually rather less. Surface ornamented with large rounded radial ribs on the anterior third of the shell. The central portion is not ribbed, but may display fine radial striae. The posterior part of the shell has finer and more numerous ribs. Periostracum greenish yellow to black, polished and strongly adherent. The periostracum may have fine concentric wrinkles on the cen-

tral portion of the shell. Beaks inflated, posterior hinge margin drawn out into a keel. Interior of shell iridescent, margins crenulated. Hinge edentulous, but irregular vestigial denticles may be present.

COMPARISONS: There is some doubt of the validity of this species, some workers regarding it as a form of *M. discors* (Linné). It displays coarser ribbing than either of the other two American Arctic species, and the shell is more robust, the beaks more inflated, and the smooth central portion slightly inset along the ventral margins.

COLLECTION: Eleven specimens were present at five stations in 27–70 m.

RECORDS: *Pleistocene*—Richards 1962:57, pl.5, f.5, 6 (Quebec and Maine); Petrov 1966:201, pl.12, f.8–9 (Chukotsk Peninsula). *Recent*—Crosse 1877:120 (Bering Sea); G. Sars 1878:30, pl.19, f.2a, b (Greenland); Krause 1885:19 (Bering Sea); Hägg 1904:22 (Greenland and Spitzbergen); Dautzenberg and Fischer 1910:14 (Novaya Zemlya); Soot-Ryen 1939:9 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Filatova 1948:429, pl.108, f.6 (Arctic); Filatova 1957b:53 (Arctic); MacGinitie 1959:158, pl.4, f.11, pl.18, f.7, pl.21, f.4 (Point Barrow, Alaska); Ellis 1960:39 (Baffin Island and Greenland); Kotaka 1962:146, pl.34, f.17 (Okhotsk Sea); Richards 1962:57, pl.5, f.5, 6 (Greenland to North Carolina); Filatova and Barsanova 1964:20 (Eurasian Arctic); Petrov 1967a:184 (Bering Sea); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Possibly panarctic. The species is recorded from the Canadian Archipelago, Hudson Bay and south to Maine, possibly to South Carolina. It is doubtful that it occurs in the Atlantic segment of the Arctic, but is present throughout the East Siberian Sea, the Chukchi Sea, and into the Bering Sea to Kamchatka and along the coast of Alaska. There are no substantiated records south of the Aleutian Islands.

REMARKS: The identity and distribution of this species remains uncertain. It is frequently considered a transitional form or subspecies of other *Musculus*, but Jensen (1915) thought the general outline and microscopic wrinkling of the periostracum of the central portion of the shell to be a constant feature. Ocklemann (1958) did not record *M. corrugatus* from Greenland, and believed it not to be present at Jan Mayen Land, but Jensen (1915) recorded it from Greenland, Spitzbergen, and the Kara Sea. A case may possibly be made to consider *M. corrugatus* a *nomen dubium*, as Stimpson (1851) gave no description or illustration, but merely equated it to the "*Modiola discors* Linné" of Gould 1841, recognizing that it differed from *M. discors* Linné of European authors.

Musculus (Musculus) discors (Linné 1767)

Figure 36

Mytilus discors Linné 1767:1159, Fabricius 1780:418; Dillwyn 1817:319.

Modiola discors (Linné), Lamarck 1819:114.

Musculus discors (Linné), Filatova 1948:429, pl.108, f.8; Scarlato 1955:189, pl.50, f.2.

Modiola laevigata Gray 1824:244.

Modiolaria laevis Beck 1851:208, pl.17, f.3a–f.

Modiolaria discors laevigata (Gray), Jensen 1912:57, pl.3, f.4a, b.

Modiolaria nigra laevigata (Gray), Gorbunov 1946a:46.

Modiola substriata Gray 1824:245.

Modiolaria substriata (Gray), Oldroyd 1925:76.

Modiolaria discors substriata (Gray), Jensen 1912:58, pl.3, f.5a, b.

DESCRIPTION: Shell ovate to elongate, thin and fragile, maximum length to 40 mm. Anterior and posterior thirds of shell ornamented with faint radial ribs and lirae. The central section is smooth, but may display irregular concentric growth lines. Peri-

ostracum ash yellow to dark brown, polished and strongly adherent. Interior brilliantly iridescent, shell margins crenulated, more prominently in the anterior and posterior ends. Hinge line and dentition as in genus.

COMPARISONS: This species may be confused with *M. corrugatus* (Stimpson) and it may be difficult to separate them during immature stages. Adult *M. discors* are characterized by the thin inflated shell, the much finer and sometimes absent radial ribbing, and the smooth central periostracum. Jensen (1912) showed that *M. laevigatus* and *M. substriatus*, both of Gray 1824 are merely varieties of *M. discors*. As the supposedly distinguishing characters form a continuous series, little purpose is served by retaining separate names.

COLLECTION: This species is represented at 16 stations in 27–101 m, with a total of 26 specimens.

RECORDS: *Pliocene*—Wood 1851:63, pl.18, f.5 (Britain); Wood 1874:111 (Britain); Petrov 1966:202, pl.12, f.10 (Siberia). *Pleistocene*—Knipowisch 1900:382 (Spitzbergen); Merklin et al. 1962:30, pl.2, f.7 (Chukotsk Peninsula). *Recent*—Montagu 1803:167 (Britain); Gould 1841:130, f.84 (Massachusetts); Møller 1842:19 (Greenland); Middendorff 1849:531, pl.12, f.11, 12 (Novaya Zemlya); Torell 1859:133 (Spitzbergen); Crosse 1877:120 (Bering and Arctic seas); Leche 1878:32 (Novaya Zemlya); G. Sars 1878:29, pl.3, f.3a, b (Greenland); D'Urban 1880:253 (Barents Sea); Krause 1885:18 (Bering Sea); Melvill and Standen 1900:3 (Franz Josef Land); Hägg 1904:23 (Greenland and Spitzbergen); Soot-Ryen 1932:9 (Greenland); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:27 (Iceland); Kuroda and Habe 1952:25 (Northern Japan); Filatova 1957b:52 (Arctic); MacGinitie 1959:159, pl.18, f.10, pl.21, f.5 (Point Barrow, Alaska); Ellis 1960:39 (Baffin Island and Greenland); Clarke 1961:7 (Gulf of St. Lawrence); McLaughlin 1963:25 (Bering Sea); Allen 1965:980 (Northwest Atlantic); Sparks and Pereyra 1966:834 (Chukchi Sea); Golikov and Scarlato 1967:88, f.77 (Sea of Japan); Petrov 1967:184 (Bering Sea); Habe and Igarashi 1967:31 (Northern Japan); Petersen 1968:51 (Faroe Islands); Bernard 1970:87 (British Columbia); Clarke 1974:9 (Baffin Bay); Scarlato and Ivanova 1974:301 (Kurile Islands); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. This species is widely distributed through the North Atlantic from Greenland to the Kara Sea and south to Britain, Ireland and Norway. It is present in the Canadian Arctic Archipelago, Hudson Bay and south at least to New England. It is also represented in the Bering and Okhotsk seas south to Japan and along the American coast to Washington State and possibly Oregon.

REMARKS: *M. discors* is almost invariably collected with remnants of the byssal thread "nest" attached and with adhering epizoa and small nestling bivalves. Thorsen (1935) showed it to be a protandric hermaphrodite.

Musculus (Musculus) niger (Gray 1824)

Figure 37

Modiola nigra Gray 1824:244.

Crenella nigra (Gray), M. Sars 1859:55.

Modiolaria nigra (Gray), Crosse 1877:120.

Musculus nigra (Gray), Scarlato 1955:189, pl.50, f.5.

Musculus niger (Gray), Petrov 1966:203, pl.12, f.14–18.

Musculus niger obesus Dall 1916a:19 [nom. nud. not *Mytilus obesus* Reeve 1858]; Dall 1916b:405.

Musculus niger protractus Dall 1916a:19 (nom. nud.); Dall 1916b:405.

Modiola nexa Gould 1841:128, f.86.

DESCRIPTION: Shell modioliform, compressed, maximum length to 45 mm. Surface ornamented with 10–15 strong radial

ribs on the anterior end, the central portion of the shell is not ribbed but may have obscure radial and concentric wavy lines and small tubercles. Anterior part of shell with radial ribs, smaller and more numerous than on the posterior end. Periostracum polished, strongly adherent, color olive green to black. Interior nacreous, often colored purple or reddish-brown. Shell margins with irregular crenulations. Hinge as in genus. Pallial line wide, feebly impressed.

COMPARISONS: This species is distinguished from other Arctic members of the genus by the generally more compressed shell, and the coarser ribbing on the anterior end. The ribs on both ends of the shell tend to be decussate.

COLLECTION: This species occurred at seven stations, for a total of 51 specimens collected between 27–64 m. Two small specimens were with a station label indicating 2560 m, probably the result of a collecting or labelling error as MacGinitie (1959) records this species to 200 m and Ockelmann (1958) gives 376 m as depth maximum.

RECORDS: *Pleistocene*—Slodkevitch 1938:94, pl.54, f.9–12 (Kamchatka); Merklin et al. 1962:30, pl.2, f.4–6 (Chukotsk Peninsula); Richards 1962:57, pl.5, f.12 (Quebec to Maine); Ilyina 1963:118; pl.51, f.10 (Kamchatka); Wagner 1970:38 (Northeastern Canada). *Recent*—Middendorff 1849:533 (Arctic); Torell 1859:130 (Spitzbergen); Jeffreys 1863:128, pl.28, f.4 (Britain); Gould 1870:190, f.487, 488 (Massachusetts); G. Sars 1878:31 (Greenland); Leche 1883:451 (European Arctic); Krause 1885:20 (Bering Sea); Stuxberg 1886:151 (Novaya Zemlya); Whiteaves 1887:120 (British Columbia); Melvill and Standen 1900:3 (Franz Josef Land); Hagg 1904:26 (Greenland); Dautzenberg and Fischer 1910:14 (Novaya Zemlya); Jensen 1912:63 (Arctic); Odhner 1915:75 (Greenland); Mesjatsjev 1931:65 (Barents Sea); Soot-Ryen 1932:8 (European Arctic); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:28 (Iceland); Kuroda and Habe 1952:25 (Northern Japan); Filatova 1957b:53 (Eurasian Arctic); MacGinitie 1959:157, pl.18, f.6, pl.21, f.6 (Point Barrow, Alaska); Ockelmann 1958:58 (Greenland); Ellis 1960:39 (Baffin Island and Greenland); Scarlato 1960:78, pl.3, f.1, text-fig. 40 (Bering and Arctic seas); Clarke 1961:7 (Gulf of St. Lawrence); Kotaka 1962:140, pl.34, f.15, 16 (Okhotsk Sea); Richards 1962:57, pl.5, f.12 (Arctic Ocean to North Carolina); McLaughlin 1963:25 (Bering Sea); Filatova & Barsanova 1964:21 (Bering Sea); Sparks and Pereyra 1966:834 (Chukchi Sea); Hulsemann 1967:71 (Beaufort Sea); Petrov 1967b:150 (Northern Bering Sea); Habe and Igarashi 1967:31 (Northern Japan); Petersen 1968:11 (Faroe Islands); Bernard 1970:87 (British Columbia); Clarke 1974:9 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. The species is widely distributed throughout the North Atlantic and along the entire shallow bathyal zones of the Arctic Sea. It is well established in the Bering, Okhotsk and Sea of Japan. It is abundant off British Columbia and Washington and occurs sporadically as far south as Santa Barbara, California, from the low intertidal zone to 60 m.

REMARKS: This is the largest member of the genus and the shell morphology is fairly constant, although some variability in rib size and degree of shell inflation is present. The shell is frequently found with the anterior end only buried in the substrate. It does not construct a byssus "nest" like that of *M. discors* (R. Baxter pers. comm.).

Family PECTINIDAE Rafinesque 1815

The family is poorly represented in the collections. *Arctinula*

greenlandica (Sowerby) is abundant, the other material present consists of a worn, probably fossil, fragment of a chlamid, and one recently dead *Chlamys pseudislandica* (MacNeil). *Hyalopecten frigidus* (Jensen 1912) was reported by Clarke (1962) from the central part of the Laurentian Basin, so it probably occurs in the deeper zones of the Beaufort Sea.

KEY TO THE GENERA OF PECTINIDAE

- Shell with strong radial ribs, both valves convex
 *Chlamys*
 Shell sculpture weak, margins of right valve reflected ...
 *Arctinula*

Genus *Arctinula* Thiele 1935

Figure 40

Type species (monotypy): *Pecten greenlandicus* Sowerby 1842. Recent. Arctic.

DESCRIPTION: Shell very thin, generally transparent, tightly closing. Auricles nearly symmetrical. Left valve may be unsculptured, but usually with radial rows of pustules or scales. Right valve smooth or with concentric lamellae; margins reflected against left valve. Byssal notch large, pectinidial teeth few and vestigial. Hinge line straight, resilifer triangular and deeply sunk. Interior smooth, monomyarian adductor scar hardly visible. Pallial attachment line wide, but difficult to see.

RANGE: Miocene to Recent. Recent distribution Arctic and boreal Atlantic to north Africa in deep water. Habitat preference is for fine sediments, often with mixture of boulders and large siliceous sponges. The genus is a member of the byssally attached epifauna occurring in 10 m to abyssal depths.

DEVELOPMENT: Ova large, development is lecithotrophic with a reduced planktonic phase (Thorson 1936).

REMARKS: The anatomy is typically pectinid, but the foot is particularly large, vermiform in shape with a flattened tip. The

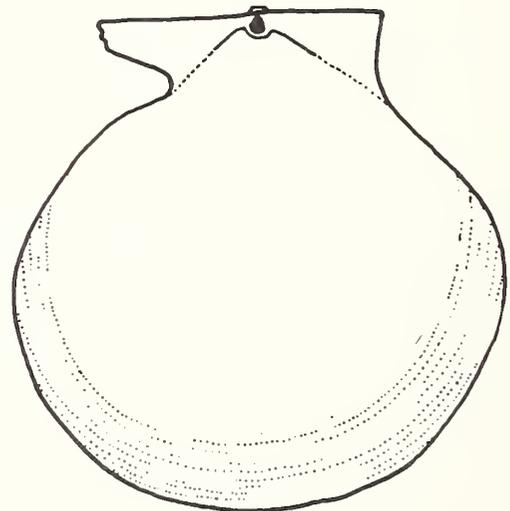


FIGURE 40. Interior of right valve of *Arctinula greenlandica* (Sowerby).

byssal apparatus is well developed; however, shells are attached by a few threads which are readily broken, the scallop moving actively prior to re-attachment. Nutrition is by filter feeding, but there are anatomical modifications for macrophagy. There is no agreement on the systematic placement of the small, thin-shelled pectinids. Several workers have identified American *Pseudamussium*, auctt., not Mörch 1853, with *Pallioluu* Monterosato 1884. The type species of the latter is the Mediterranean *Pecten incomparabilis* Risso 1826, a species with small but well developed cardinal crura and a pigmented shell pattern. *Arctinula*, originally proposed in *Propeamussium* Gregorio 1883, was first considered a genus by Soot-Ryen (1958) and so utilized by MacNeil (1967). The developed anterior auricles and reflected margin of the right valve distinguish it from *Cyclopecten* and *Delectopecten*.

Arctinula greenlandica (Sowerby 1842)

Figure 42

- Pecten vitreus* Gray 1824:245 [not *Ostrea vitrea* Dillwyn 1817]
Pecten greenlandicus Sowerby 1842:57, pl.3, f.40.
Pecten groelandicus (Sowerby), Middendorff 1849:529 (invalid emend.)
Pecten grönlandicus (Sowerby), G. Sars 1859:53 (invalid emend.)
Propeamussium (Arctinula) groenlandicum (Sowerby), Filatova 1948:425, pl.107, f.4.
Cyclopecten (Delectopecten) greenlandicus (Sowerby), Grau 1959:53, pl.20.
Arctinula greenlandica (Sowerby), MacNeil 1967:8, pl.4, f.6.
Pseudamussium andersoni Dall 1919:19A, pl.12, f.7, 8, [not *Pecten (Plagiocentium) andersoni* Arnold 1906.]
Pecten binominatus Hanna 1924:175, [new name for *P. andersoni* Dall 1919.]

DESCRIPTION: Shell very thin, transparent, outline ovate to circular, maximum length to 35 mm. Left valve ornamented with numerous minute irregular concentric striae with occasional fine radial threads. Right valve the smaller, with sporadic radial striae, but concentric growth checkmarks may be present. Prodissoconch and early shell often concentrically corrugated. Periostracum not visible, the shell surface with an oily violet iridescence when fresh. Hinge line straight, resilifer small and delicate. Auricles poorly developed, byssal notch deep, pectinidial teeth vestigial or absent. Interior polished, pallial or adductor muscle scars not visible.

COMPARISONS: This hyaline pectinid cannot be confused with any other Arctic species and is easily separated from *Hyalopecten frigidus* (Jensen 1912) by the latter's strong concentric undulations and pronounced radial striae.

COLLECTION: This species is extremely abundant in the Western Beaufort Sea, more than 50,000 specimens occurred at 42 stations in 19–2560 m.

RECORDS: *Miocene*—MacNeil 1957:104, pl.11, f.17, 18 (North Alaska). *Pliocene*—MacNeil 1957:104, pl.11, f.17, 18 (North Alaska). *Pleistocene*—Richards 1952:55, pl.3, f.15, 16 (Maine); Troitskiy 1974:265 (Siberia). *Recent*—Loven 1847:186 (Norway); Hanley 1856:274 (Greenland); Whiteaves 1872:348 (Gulf of St. Lawrence); Leche 1878:35 (Novaya Zemlya); G. Sars 1878:23, pl.2, f.4a–c (Greenland); D'Urban 1880:253 (Barents Sea); Stuxberg 1886:152 (Novaya Zemlya); Dautzenberg and Fischer 1910:12 (Novaya Zemlya); Jensen 1912:30 (Greenland); Soot-Ryen 1932:9 (Arctic); Johnson 1934:25 (Newfoundland); Soot-Ryen 1939:10 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:36 (Iceland); Richards 1952:55, pl.3, f.15, 16 (Greenland to Newfoundland); Filatova 1957b:53 (Eurasian Arctic); Filatova and Zenkevich 1957:68 (Arctic); Ockelmann 1958:68, pl.2, f.2 (Greenland); Soot-Ryen 1958:12 (Greenland); MacNeil 1967:8, pl.4, f.6 (Arctic Alaska); Clarke 1974:9 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic. The species is abundant off eastern Greenland and widely distributed throughout the boreal Atlantic. It does not occur in the Bering Sea or Pacific Ocean.

REMARKS: The original spelling "greenlandicus" is acceptable and emendations by latter authors to the nordic diacritical form, or its diphthong approximation, are invalid. Sowerby was a British writer using the English form for the country of origin. Ockelmann (1958) has shown that specimens from more southerly parts of the Atlantic, considered a subspecies by Locard (1898), have anatomical differences and should be separated. It is intriguing that this most abundant species in the OSU collection was not recorded by Hulsemann (1967).

Genus *Chlamys* Röding 1798

Figure 41

Type species (subsequent designation Herrmannsen 1847): *Pecten islandicus* Müller 1776. Recent. North Atlantic.

DESCRIPTION: Valves convex. Auricles large, the anterior longer than posterior. Both valves with strong radial ribs. Byssal notch large, pectinidial teeth well developed. Hinge line straight. Adductor muscle scar clearly visible, pallial attachment scars obscure.

RANGE: Triassic to Recent. Recent distribution cosmopolitan, from the low intertidal zone to 500 m, but most abundant in warm shallow waters.

DEVELOPMENT: The larvae of a number of chlamids have been described and literature summarized by Thorson (1946). Ockelmann (1958) examined mature eggs and recently-settled *C. islandica* (Müller), in all cases the evidence points to a fully planktotrophic development.

REMARKS: The genus contains a large number of superficially similar species distinguished by minor sculptural details, which may represent several separate phylogenetic lines (MacNeil 1967). It is poorly represented and sporadic in Arctic waters, but contains the most brightly colored northern shells.

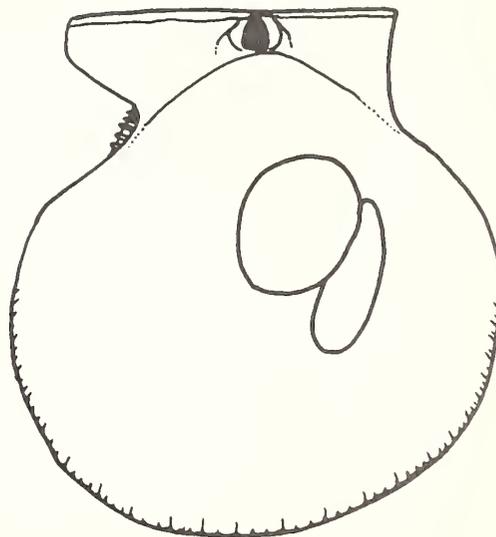


FIGURE 41. Interior of right valve of *Chlamys islandica* (Müller).

Subgenus *Chlamys* s. str.
Chlamys (Chlamys) pseudislandica
 MacNeil 1967

Figures 43, 44

Chlamys (Chlamys) pseudislandica MacNeil 1967:31, pl.19, f.7, pl.20, f.8, pl.23, f.1, 2.

DESCRIPTION: Shell subcircular to ovate, valves inflated. Maximum height 75 mm. Both valves ornamented with prominent radial ribs, wider and less prominent on the right valve. Ribs with sparse concentric scales, particularly on the left valve. Ribs divergating in mature specimens. Interspaces with one prominent interstitial riblet. Interspace of right valve with minute latticed microsculpture. Left valve with latticed sculpture on early shell, replaced by concentric ridges on mature shell. Left valve mottled, reddish-brown to dark purple, frequently rayed with white or pink. Right valve white to light yellow-grey. Auricles broad and short. Byssal notch deep, pectinidial teeth strong, 6–8 in number. Interior polished, with radial plications conform-

ing to external ribs. Adductor muscle scar and pallial line clearly impressed.

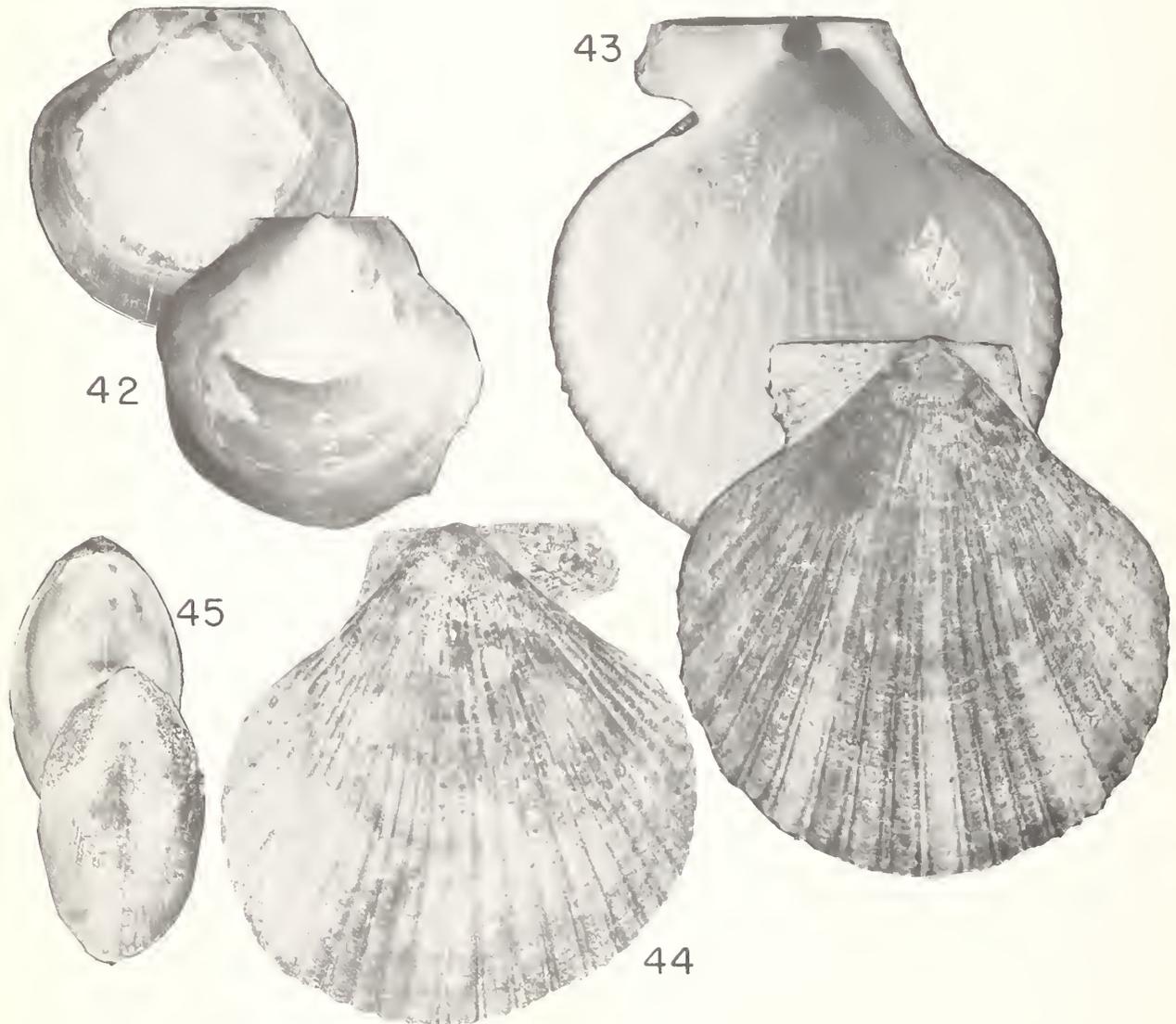
COMPARISONS: The species may be confused with *C. islandica* (Müller) which has more numerous and finer ribs that rarely divaricate near the shell margins. *C. rubida* (Hinds 1845) and its subspecies comprise thinner and less inflated shells.

COLLECTION: Represented by one recently dead and still articulated specimen, collected in 55 m at 71°18.1'N, 152°32.2'W.

RECORDS: *Pleistocene*—Wood 1851:40, pl.5, f.1 (Scotland). *Recent*—MacGinitie 1959:155, pl.19, f.4 (Point Barrow, Alaska); MacNeil 1967:31, pl.19, f.7, pl.20, f.8, pl.23, f.1, 2 (Arctic Alaska and Northern Bering Sea).

DISTRIBUTION: This species has the most restricted range of any Arctic shallow water form: Point Barrow, Alaska to St. Lawrence Island, Northern Bering Sea.

REMARKS: Grau (1959) concluded that *C. islandica* (Müller) is not living in the Pacific or Bering Sea, but did occur in the Arctic. MacGinitie (1959) referred 19 specimens from Point Bar-



FIGURES 42–45. 42, *Arctiunula greenlandica* (Sowerby), length 20.6 mm; 43, *Chlamys (Chlamys) pseudislandica* MacNeil, length 56.7 mm; 44, *C. (C.) pseudislandica*, exterior of right valve, length 41.7 mm; 45, *Limatula hyperborea* Jensen, length 6.8 mm.

row to *C. islandica*, citing a range south through the Bering Sea to the Aleutian and Shumagin Islands. These southern records should be assigned to *C. rubida* (Hinds 1845). I follow MacNeil (1967) in separating the Arctic from the European stock, though this may be subject to revision following a comprehensive comparative study. Although the *islandica*-group had a Pacific origin, there are no American fossil records for *C. pseudislandica*, so it is probable that this form as well as the typical developed in the Atlantic. MacNeil (1967) identified *C. pseudislandica* in the late Pleistocene of Scotland. It is possible that further work will find living specimens in the Atlantic and the Canadian Arctic archipelago.

Family LIMIDAE Rafinesque 1815 Genus *Limatula* Wood 1839

Figure 46

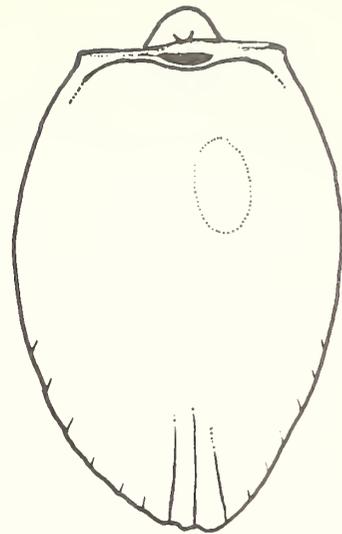


FIGURE 46. Interior of right valve of *Limatula subauriculata* (Montagu).

Type species (subsequent designation Gray 1847): *Pecten subauriculata* Montagu 1808. Recent. North Atlantic.

DESCRIPTION: Shell ovate to elongate; maximum diameter dorsoventral. Surface with fine to coarse radial ribs. Periostracum thin, dehiscent. Interior polished. Hinge line straight, edentulous, and with small central resilifer.

RANGE: Triassic to Recent. Recent distribution cosmopolitan, generally in cold and temperate seas. Habitat preference is for coarse sediments, but includes fine substrates mixed with coarser particles. The genus is a member of the byssally temporarily attached epifauna.

DEVELOPMENT: Little information is available, but Thorson (1946) discussed the closely related *L. loscombi* (Sowerby 1824) and reported normal planktonic development.

REMARKS: The genus includes medium to small-sized shells most often found in deep and cold waters. Individuals are able to move and sometimes swim, by pulsating the extremely long tentacular fringe of the mantle edges. More usually, species are byssally attached, often in a 'nest' of matted byssal threads that may serve as a protection for the exposed tissues and delicate shell.

It is probable that the genus requires separation at the generic or subgeneric level, as it presently includes nearly equilateral to markedly oblique species, some with tightly closing valves and others with large gapes. Many species are superficially alike and the external ornamentation may vary with habitat. Useful distinguishing characters are found in the comparative height of the umbones and the length of the cardinal area just below the beaks.

L. subauriculata (Montagu 1803), though recorded in the early literature, does not occur in the high Arctic. It is widely distributed in the north Atlantic and also in the north Pacific. It is probable that research will result in separation of the Pacific representative.

Limatula hyperborea Jensen 1905

Figure 45

Limatula hyperborea Jensen 1905:329, f. 1a-d.
Lima hyperborea (Jensen), Jensen 1912:41, pl. 2, f. 5a-e.

DESCRIPTION: Shell oval, very inflated, total height to 20 mm. Surface with numerous sharp elevated radial ribs, the two central ones larger and with a wider interspace than the others, which tend to become indistinct on the lateral shell margins. Periostracum brown, dehiscent. Interior polished, subnacreous. Shell margins crenulated by the larger ribs, the two prom-

inent central ribs cause a corresponding furrow in the shell interior. Hinge line straight, edentulous, with a small central triangular resilifer. Pallial and adductor muscle attachment scars not obvious.

COMPARISONS: It is with some reservation that I assign this material to *L. hyperborea*, though it agrees well with Jensen's description and with specimens from east Greenland. The genus is poorly understood and probably overnamed, the last comprehensive published study of the North Atlantic-boreal species being by Jensen (1912). The present material is most easily confused with *L. subauriculata* (Montagu 1808) which is proportionately narrower and with more rounded ribs. It is also similar to the North Atlantic *L. subovata* Jeffreys 1876 (probably a synonym of *L. ovata* Wood 1848), which is more inflated and has more numerous radial ribs.

COLLECTION: Six specimens and 11 valves were collected from two stations in 79 and 455 m.

RECORDS: Recent—Gorunov 1946a:46 (Eurasian Arctic); Filatova 1957b:53 (Arctic); Ockelmann 1958:72, pl. 2, f. 3 (Greenland); Clarke 1963:102, pl. 2, f. 13 (Chukchi Sea); Clarke 1974:10 (Baffin Bay); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: The species is widely distributed in the north Atlantic from Greenland to Spitzbergen and the Kara Sea, and eastwards to the New Siberian Islands. Clarke (1963) first reported the species from the Laurentian Basin, the present collection extends the range approximately 1100 km south.

REMARKS: The relationship of this species, together with the two mentioned in the "comparisons" paragraph, to other North Atlantic species is not clear. A minority of authors have treated *L. hyperborea* as a subspecies of *L. gwyni* (Sykes 1903), a new name for *L. elliptica* Jeffreys 1863, not Whiteaves 1861. A review will have to consider at least 12 North Atlantic limatulids, several of them belonging to the *L. ovata* Jeffreys 1876 complex. At least two species occur in the Bering Sea and Eastern Pacific, the group is also well developed in the Subantarctic Region, with several species scarcely different from *L. subauriculata* (Montagu).

Family THYASIRIDAE Dall 1901

The family is cosmopolitan, but more abundantly represented in boreal waters where representatives may be found in often oxygen-poor environments with little other bivalve fauna. The family is a member of the eulamellibranch superfamily Lucinacea, that has adapted to an infaunal habitat without the development of long siphons. To provide communication with the surface, the long vermiform foot is thrust through the sediments and mucus-producing regions on the tip of the foot consolidate the particles to form a cohesive tube. Ventilation through the pallial cavities has been modified to utilize the pedal tube. Nutrition too, has been modified, the family tending to macrophagy as evidenced by the large mouth, reduced or vestigial labial palps, and only two, very large, ducts leading to the digestive diverticula. While identification of the family is readily made using shell structure, a useful cross-check is supplied by the very distinct digestive diverticula and gonad which form an arborescent mass connected to the body by a narrow band of tissue. A similar structure is only present in the septibranchs.

The three genera present in the collection are easily separable using external shell characters, but specific identification may be difficult due to a lack of strongly developed dentition and the marked variability of external proportions.

KEY TO THE GENERA OF THYASIRIDAE

1. Shell with concave lunule 2
 Shell without concave lunule
 *Axinulus*
- 2.(1) Posterior of shell separated by radial fold
 *Thyasira*
 Posterior area not separated by radial fold
 *Axinopsida*

Genus *Axinopsida* Keen and Chavan in Chavan 1951

Figure 47

Type species (original description): *Axinopsis orbiculata* G. Sars 1878.
 Recent. North Atlantic.

DESCRIPTION: Shell suborbicular, lunule deeply concave. Surface smooth, sometimes with obscure concentric growth lines. Periostracum very thin, adherent. Interior dull to porcelaneous, shell margins smooth. Hinge line weak, edentulous, but with subumbonal internal shell margin upturned in each valve to form a peg-like pseudocardinal tooth. Adductor muscle scars elongated, pallial line wide.

RANGE: Pliocene to Recent. Recent distribution is limited to north boreal temperate and cold waters, and possibly the Mediterranean. The genus is a member of the deeply buried infauna, occurring in fine sediments.

DEVELOPMENT: Ockelmann (1958) found the type of the genus, *A. orbiculata* (G. Sars 1878) from Greenland, to have large ova, indicating lecithotrophic development.

REMARKS: The genus is closely related to *Thyasira*, and the mode of existence similar. The pallial current is modified to an anterior-posterior passage, and the vermiform foot is utilized to construct a mucus-lined inhalant tube, allowing burial to a depth generally limited to the long-siphoned bivalves.

Axinopsida orbiculata (G. Sars 1878)

Figure 49

Axinopsis orbiculata G. Sars 1878:63, pl.19, f.11a-d; Filatova 1948:438, pl.110, f.16.

Axinopsida orbiculata (G. Sars), Keen and Chavan in Chavan 1951:211.

DESCRIPTION: Shell orbicular, inflated, length to 5 mm. Surface smooth, brightly polished, sometimes with incremental striae and growth checks. Periostracum thin, varnished, adherent, but umbones frequently eroded. Beaks small, lunule deeply impressed, escutcheon obsolete. Shell interior polished, porcelaneous, margins smooth. Hinge edentulous, but with a subumbonal thickening to form a peg-like pseudocardinal tooth in each valve. Ligament attached to a small ill-defined groove. Adductor muscle scars elongated, subequal. Pallial line weakly impressed, no pallial sinus.

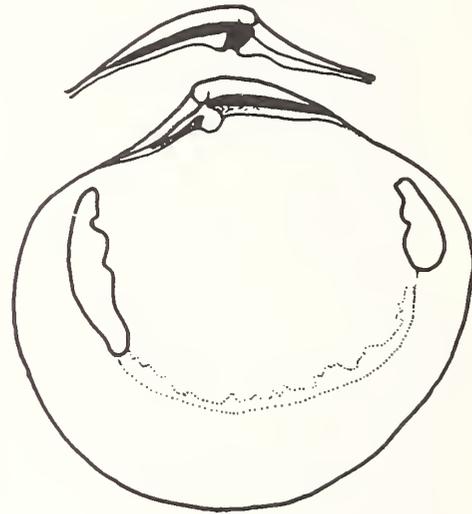


FIGURE 47. Interior of right valve and hinge of left valve of *Axinopsida orbiculata* (Sars).

COMPARISONS: The genus is readily recognized by the bilateral single pseudocardinal tubercle, and no other Atlantic-Arctic species resembles *A. orbiculata*. There is doubt as to the status of *A. viridis* (Dall 1901) from Alaska, which tends to have a deeper lunule and a more elongate outline. The other Pacific species is the Californian *A. serricata* (Carpenter 1864), which may be a senior synonym of *A. viridis*. It is possible that a careful review may unite these taxa and *A. orbiculata inaequalis* (Verrill and Bush 1898) into one polymorphic unit.

COLLECTION: This species occurred at 27 stations for a total of 206 specimens and numerous single valves, in 32–270 m.

RECORDS: *Pleistocene*—Merklin et al. 1962:39, pl.6, f.6 (Chukotsk Peninsula); Wagner 1970:40, pl.3, f.18a, b (Northeastern Canada). *Recent*—Hägg 1904:44 (Greenland); Jensen 1905:342 (Greenland); Odhner 1915:104 (Spitzbergen); Mesjatsjev 1931:97 (Barents Sea); Johnson 1934:40 (Greenland to Maine); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:55 (Iceland); Filatova 1957b:55 (Arctic); Ockelmann 1958:111, pl.2, f.7, 8 (Greenland); Soot-Ryen 1958:23 (Greenland); MacGinitie 1959:172, pl.20, f.2 (Point Barrow, Alaska); Ellis 1960:39 (Baffin Island and Greenland); Clarke 1974:10 (Baffin Bay); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic. Abundant in the North Atlantic from Greenland to Norway and south at least to the Faroe Islands. In the western Atlantic it occurs from the Canadian Arctic Archipelago to Massachusetts. The species is not found south of Bering Strait, and records such as Petrov (1967a) should be referred to *A. viridis* (Dall).

REMARKS: In common with other thyasirids, this species is most easily assigned to family and genus by examination of the soft anatomy. The elongated adductors, vermiform bulb-ended foot, and arborescent digestive diverticula and gonad are all diagnostic.

Genus *Axinulus* Verrill and Bush 1898

Figure 48

Type species (original designation): *Axinulus brevis* Verrill and Bush 1898. Recent. North Atlantic.

DESCRIPTION: Shell ovate to elongate, without a radial sulcus setting off the posterior end. Surface smooth, but with obscure concentric striae and growth checks. Periostracum very thin, often coated with ferruginous material. Shell interior polished, margins smooth. Hinge weak, edentulous, but with slight thickening of central part. Adductor muscle scars elongate, the posterior rather smaller. Pallial line wide, indistinct.

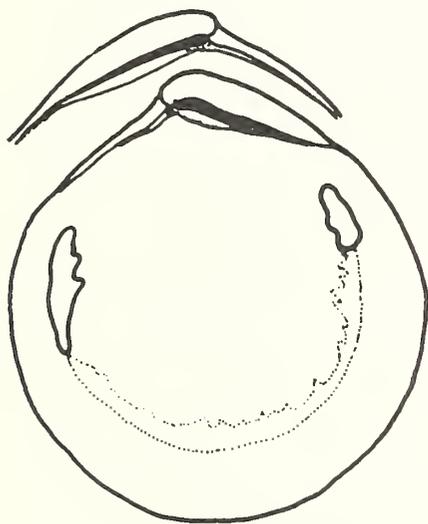


FIGURE 48. Interior of right valve and hinge of left valve of *Axinulus brevis* Verrill and Bush.

RANGE: Recent and possibly Pliocene. Recent distribution limited to North Atlantic and Arctic oceans and also the Mediterranean. The taxon is a member of the shallow infauna of fine sediments.

DEVELOPMENT: No observations.

REMARKS: The genus is close to *Thyasira*, displaying the same vermiform foot and arborescent gonad and digestive diverticula. Verrill and Bush (1898) proposed *Axinulus* as a new subgenus separated from *Thyasira* by the lack of the posterior radial plication and smaller posterior adductor muscle scar. The appearance of deposits cemented to the shell, and the frequently eroded umbones, suggest a superficially infaunal habitat.

Axinulus careyi NEW SPECIES

Figure 50

ORIGINAL DESCRIPTION: Shell minute, inflated, outline ovate. Umbones prosogyrous, not prominent. Surface earthy, white, with irregular concentric striae visible under high magnification. Periostracum thin, adherent. Shell coated with strongly cemented mud and debris, particularly in posterior and anterior portions. Interior smooth, polished. Hinge weak, edentulous, with a small thickening just below the umbone of each valve. Ligament small and external except for anterior end which occupies an obscure groove just behind the beaks. Adductor scars elongate, subequal. No pallial sinus.

TYPE LOCALITY: Western Beaufort Sea, Arctic Alaska. Oregon State University Station No. SMG 950 at 71°14.3'N, 149°22.9'W in 695 m. Collected by Smith-McIntyre Grab on September 5, 1971.

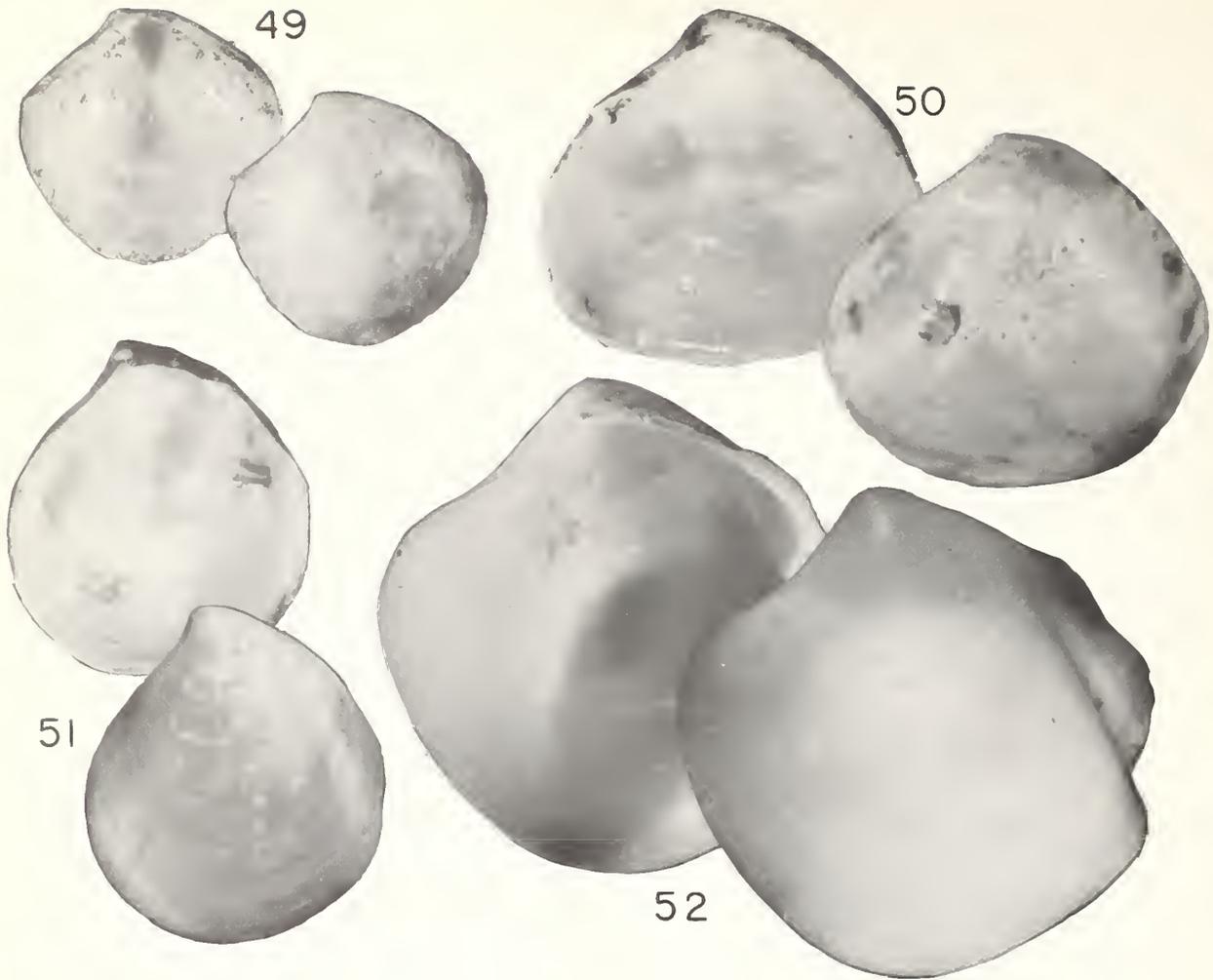
DIAGNOSIS: Shell to 3 mm, inflated, outline ovate. No depressed lunule, no radial sulcus, otherwise as in *Thyasira*. Separated from the related genus *Leptaxinus* Verrill and Bush 1898 by the rounded posterior margins.

ETYMOLOGY: This species is named for A.G. Carey, Jr. of Oregon State University in recognition of his important contributions to the study of Arctic benthic ecology.

Collection: This new species occurred at 12 stations for a total of 216 specimens in 585–2195 m.

MEASUREMENTS AND TYPE DEPOSITION:

Type	Measurements (mm)			Depository
	L	H	W	
Holotype	2.6	2.1	1.3	LACM No. 1900
Paratype 1	2.4	2.1	1.5	LACM No. 1901
Paratype 2	2.7	2.2	1.4	USNM No. 771436
Paratype 3	2.4	2.0	1.3	NMC No. 77001
Paratype 4	2.5	2.2	1.4	OSU No. 01047
Paratype 5	2.2	1.9	1.1	CAS No. 58994



FIGURES 49-52. 49, *Axinopsida orbiculata* (Sars), length 4.1 mm; 50, *Axinulus careyi* new species, HOLOTYPE, Length 2.6 mm; 51, *Thyasira* (*Thyasira*) *equalis* (Verrill and Bush), length 5.0 mm; 52, *Thyasira* (*Thyasira*) *gouldii* (Philippi), length 7.3 mm.

REMARKS: The generic assignment of this deep water species is difficult and possibly a new genus could be proposed to contain it. The new species appears intermediate between *Leptaxinus* and *Axinulus*, both of Verrill and Bush 1898, combining the external characteristics of one and the hinge of the other. It is closest to *A. brevis* Verrill and Bush 1898, the type of the genus, but this species is proportionately higher and there is a small, but distinct radial posterior sulcus. Other related species include *A. ferruginosus* (Forbes 1844), characterized by a large posterior pseudocardinal process, and *A. pygmaeus* Verrill and Bush 1898, which has distinct posterior and anterior hinge tuberosities. There are several more related boreal Atlantic species, all distinguishable by shell outline or peculiarities of the pseudodental tuberosities, it is probable that *Axinulus* has been overnamed and the various sizes and shape of the hinge structures are a function of maturity.

Genus *Thyasira* Lamarck (Leach MS) 1818

Figure 53

Type species (original designation): *Tellina flexuosa* Montagu 1803.
Recent. Mediterranean.

DESCRIPTION: Shell subglobular to oblique, posterior area set off by one or more radial sulci. Surface polished or chalky, smooth but sometimes with incremental concentric striae. Periostracum very thin, dehiscent in some species. Interior polished, shell margins smooth. Hinge line weak, edentulous, a small pseudocardinal tubercle may be present on left valve. Adductor muscle scars nearly equal, very elongated. Pallial line feebly impressed, wide. No pallial sinus.

RANGE: Cretaceous to Recent. Recent distribution cosmopolitan especially in cold and deep waters. The group is deeply infaunal in fine sediments.

DEVELOPMENT: Published works on various species (Thorson 1936; Ockelmann 1958; Bernard 1972) indicate large ova with lecithotrophic development. Blacknell and Ansell (1974) report that the eggs of *T. gouldii* (Philippi) are large, sticky and attach to the substrate close to the parent. Development is direct within the capsule, a benthic juvenile hatching after a period of up to 2 months.

REMARKS: The anatomy of this group has been described by various authors, the points of interest including the long vermiform foot with a terminal bulb, the arborescent digestive diverticula, and the rotation of the body in the vertical plane, leading to elongation of the adductor muscles and their associated scars. The pallial current is anteroposterior, a secondary modification from the normal posterior exchange of most bivalves. A mucus-lined tube is formed through the substrate by the foot, permitting burial to a far greater depth than the respiratory apertures would allow. The genus is filter-feeding, but shows some modifications towards macrophagy. Arctic representatives are all assignable to *Thyasira* s. str.

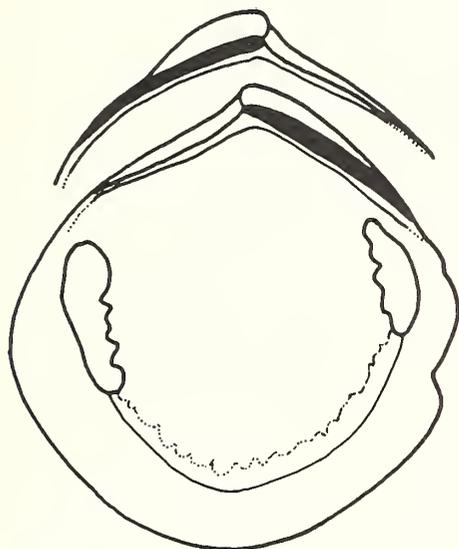


FIGURE 53. Interior of right valve and hinge of left valve of *Thyasira flexuosa* (Montagu).

Subgenus *Thyasira* s. str.
Thyasira (*Thyasira*) *equalis*
(Verrill and Bush 1898)

Figure 51

Cryptodon equalis Verrill and Bush 1898:788, pl.91, f.5, 6.
Thyasira equalis (Verrill and Bush), Soot-Ryen 1966:27, pl.1, f.11.
Cryptodon croulinensis altus Verrill and Bush 1898:787, pl.88, f.1, 2.

DESCRIPTION: Shell thin, inflated, maximum length to 10 mm, but usually not more than 5 mm. Surface smooth, chalky or polished, with faint incremental striae only. Periostracum thin, colorless, adherent. Posterior part of shell set off by a broad shallow radial flexure. Umbones prominent and markedly prosogyrous. Lunule not deeply impressed, forming a flat surface below the erect umbones. Ligamental marginal area sunken, circumscribed with an incised line. Interior of shell polished, margins smooth. Hinge weak and narrow, with an obscure subumbonal swelling, but no pseudocardinal tooth in either valve. Adductor muscle scars subequal, elongate but not deeply impressed. Pallial line not apparent.

COMPARISONS: This species may be confused with *T. croulinensis* (Jeffreys 1847), which is similar in hinge morphology

and valve inflation, but has a greatly produced anterior region, and the posterior is set off by two radial plications forming a prominent ridge. There is also some resemblance to *T. gouldii* (Philippi 1845), which is rather more compressed and proportionately longer. Furthermore, the hinge of *T. equalis* is not as developed and lacks the pseudodental tubercle. *T. dunbari* Lubinsky 1976 from the central Canadian Arctic is more elongated and oblique.

COLLECTION: The species is represented at seven stations for a total of 95 specimens, collected between 923–1926 m. The majority of the delicate shells have been damaged by storage in formaldehyde solution.

RECORDS: *Recent*—Jensen 1905:341 (Greenland); Ockelmann 1958:104 Text-fig. 7 (Greenland); Clarke 1974:10 (Baffin Bay).

DISTRIBUTION: Probably panarctic in the deeper bathyal and abyssal regions. The species occurs frequently from northeastern America to Greenland and Massachusetts, then extends eastward to Iceland and the Kara Sea. This is the first record from the Beaufort Sea.

REMARKS: This is another Arctic Alaskan species identified with some doubt that only a full revision of the genus will remove. I am very grateful to K.W. Ockelmann who kindly examined representative specimens and agreed that they are close to *T. equalis* (Verrill and Bush), but pointed out that the prodissoconch is slightly larger. This certainly cannot be a sole differential feature, and is to be expected in specimens from separated populations at different latitudes. I find the OSU material so close to east American examples of *T. equalis* that it is best relegated to this taxon.

Thyasira (*Thyasira*) *gouldii*
(Philippi 1845)

Figure 52

Thyasira flexuosa, auctt., in part, [not *Tellina flexuosa* Montagu, 1803, new name for *Venus sinuosa* Donovan 1802 not Pennant, 1777].
Bernard 1972:382, f.5, 6, 12.

Lucina gouldii Philippi 1845:74, pl.2, f.7.

Axinus gouldii (Philippi), G. Sars 1878:60, pl.19, f.6a, b.

Thyasira flexuosa gouldii (Philippi), Soot-Ryen 1932:15, pl.2, f.7.

Thyasira wajampolkana Kristofovich 1936:44, pl.3, f.3a, pl.6, f.3a.

Thyasira tokunagai Kuroda and Habe 1951:86.

DESCRIPTION: Shell subcircular to nearly trigonal, thin, often translucent. Maximum length 15 mm, usually smaller. Surface smooth with irregular concentric incremental striae. Periostracum very thin, dehiscent. Umbones prominent, beaks prosogyrous. Lunular area concave. Posterior region of shell set off by a deep radial groove. Interior polished, often with minute radiating lines inside the pallial line. Hinge considerably thickened, with a pseudocardinal tubercle in the left valve. Adductor muscle scars elongate, well defined. Pallial line wide and irregular. No pallial sinus.

COMPARISONS: This species has long been combined with *T. flexuosa* (Montagu), but Ockelmann (1958) considered it distinct, limiting *T. flexuosa* to the North Atlantic, a view supported by Miloslaskaja (1970). *T. gouldii* is separated from *T. flexuosa* by a larger prodissoconch (> 215 μ across), a more shallow posterior radial fold, less inflated valves, and smaller size.

COLLECTION: This species occurred at 23 stations with a total of 60 specimens collected in 23–270 m. Thyasirid material from 11 other stations may be *T. gouldii*, but are too damaged to be identified with certainty.

RECORDS: *Pliocene*—Dall 1874b:297 (California); Cooper 1888:237 (California); Slodkevich 1938:952, pl.70, f.5a, b, (Kamchatka); Petrov 1966:217, pl.16, f.6, 7 (Chukotsk Peninsula); Hertlein and Grant 1972:255, pl.43, f.17, 21 (California); *Pleistocene*—Arnold 1903:135 (California); Richards 1962:60, pl.7, f.6, 7 (Newfoundland to Maine); Wagner 1970:40, pl.3, f.17a, b (Eastern Canada). *Recent*—G. Sars 1878:51, pl.19, f.4a, b (Greenland); Krause 1885:33 (Bering Sea); Stuxberg 1886:143 (Novaya Zemlya); Odhner 1915:103 part (Greenland); Oldroyd 1925:120, pl.34, f.5 (Bering Sea to California); Grant and Gale 1931:282 (Bering Sea to California); Johnson 1934:39 (Greenland to Connecticut); Gorbunov 1946a:46 (New Siberian Islands); Filatova 1957b:55 (Eurasian Arctic); Ockelmann 1958:100, pl.2, f.4, 5 (Greenland); MacGinitie 1959:171, pl.4, f.12 (Point Barrow, Alaska); Richards 1962:60, pl.7, f.6, 7 (Labrador to North Carolina); Kuznetsov 1963:96 (Kamchatka); Petersen 1968:19 (Faroe Islands); Bernard 1970:88 (British Columbia); Clarke 1974:10 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and probably circumboreal. The species occurs from northern Greenland and south to at least North Carolina, and eastwards to Iceland and Norway. It is abundant along the entire Arctic coast of America, the Bering Sea, and extends to the Sea of Okhotsk and northern Japan. On the Pacific coast it is present to southern California.

REMARKS: Gould (1841) in his *Invertebrata of Massachusetts* identified a small thyasirid with the European *T. flexuosa* (Montagu). Philippi (1845), in a paper reviewing this work, expressed the opinion that the species merited separation and proposed calling it *T. gouldii*. Jeffreys (1863) questioned its validity, but it was fully accepted by Binney (1870) in the revised edition of Gould's work. The status of *T. gouldii* has never been clear, and for nearly a century it has been considered a subspecies or junior synonym of *T. flexuosa* (Jeffreys 1877; Soot-Ryen 1932; MacGinitie 1959). Ockelmann (1958), followed by Miloslavskaja (1970) considered *T. flexuosa* a boreo-lusitanian species, distinct from the panarctic and amphi-american *T. gouldii*. The entire taxon is in need of a full review to elucidate distribution, particularly in the Western Pacific as *T. gouldii* was recorded from the Japanese Tertiary by Yabe and Nomura (1925), but latter renamed *T. tokunagai* by Kuroda and Habe (1951). I believe this species to be identical to *T. wajampolkana* Kristofovich 1936, from the Pliocene of Kamchatka, and clearly a synonym of *T. gouldii*.

Family UNGULINIDAE H. and A. Adams 1857

This family is not represented in the collections, although MacGinitie (1959) reported a single specimen of *Diplodonta aleutica* Dall 1901 from Point Barrow. This species, originally proposed as a subspecies of *D. torelli* Jeffreys 1876, is distinct from the North Atlantic representatives and probably the same as *D. orbellus* (Gould 1852) distributed throughout the North Pacific and Bering Sea, with Point Barrow the easternmost location.

Family MONTACUTIDAE Clark 1885

MacGinitie (1959) recognized a single specimen of *Pseudopythina compressa* Dall 1899 in the Point Barrow material. This species, presently placed in the genus *Neaeromya* Gabb 1873, is commensal with burrowing invertebrates and found in the North

Pacific Ocean and Bering Sea ranging to the Chukchi Sea. It appears that Point Barrow is the eastern limit on the American coast.

KEY TO THE GENERA OF MONTACUTIDAE

1. Resilifer small, vertical *Montacuta*
Resilifer developed, not vertical 2
- 2.(1) Resilifer deep, oblique *Mysella*
Resilifer shallow, wide and horizontal *Boreacola*

Genus *Boreacola* NEW GENUS

Figure 54

Type species (original designation): *Boreacola vadosa* new species.

ORIGINAL DESCRIPTION: Shell minute, thick, ovate, inflated; posterior truncated, anterior rounded. Surface with fine regular concentric lirae. Periostracum thin, adherent, highly polished. Umbones not prominent; prodisoconch large, white, clearly separable from later shell. Left valve with long anterior lamella bent ventrally to form small subumbonal pseudocardinal tooth. Posterior lamella vestigial, not hooked. Right valve with smaller anterior lamella, not hooked; posterior lamella absent. Resilifer wide and shallow. Shell interior lustrous, partially punctate. Adductor muscle scars elongated, subequal. Pallial line narrow, no pallial sinus.

RANGE: Arctic Alaska in shallow water.

ETYMOLOGY: The name is derived from the Latin northern (*Borealis*) and the suffix a dweller in (*-cola*).

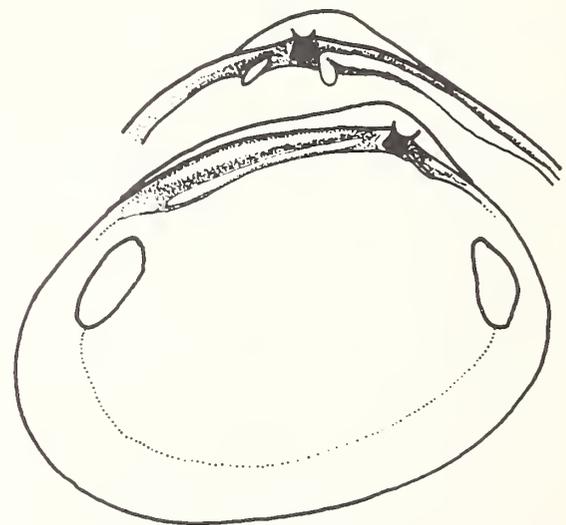


FIGURE 54. Interior of right valve and hinge of left valve of *Boreacola vadosa* N.GEN., N.SP.

REMARKS: The thick translucent shell is quite different from the opaque and chalky shells of *Montacuta* and *Mysella*. The prominent ventrally flexed umbonal end of the anterior lamina in the left valve, the vestigial dentition of the right valve, and the wide resilifer contrasts to the two stout lateral teeth in the right valve and edentulous left valve of *Mysella*. In *Montacuta* the hinge is weaker and the umbonal hooks, though small, are present on both the anterior and posterior lamella of the right valve.

I have no hesitation in proposing this new genus of Montacutidae. The dentition of the group, although small and difficult to observe, is perfectly consistent and unlike other genera. There is little doubt that several separate phylogenies are included in the family. The new genus is closest to *Montacuta*, but in this group the subumbonal hooks are formed by the lateral flexure of a vertical lamella, whereas in *Boreacola* it is formed by the rotation of a horizontal ridge.

Boreacola vadosa NEW SPECIES

Figure 56

ORIGINAL DESCRIPTION: Shell thick, minute, inflated, ovate to elliptical. Maximum length 3 mm. Anterior produced, rounded; posterior truncated. Surface smooth, with regular concentric lirae. Periostracum pale yellow to grey, adherent, highly polished. Umbones prominent, prodisoconch nearly horizontal in adult specimens, frequently coated by dark deposits. Interior pol-

ished, translucent. Right valve with obscure dentition, left valve with long anterior lamella and subumbonal pseudocardinal tooth. Resilifer wide and shallow. Ligament entirely internal. Muscle and pallial scars clearly impressed; no pallial sinus.

TYPE LOCALITY: Western Beaufort Sea, Arctic Alaska. Western Washington State College station M12 at Pitt Point, 70°55'44"N, 153°12'44"W, Collected in 0.5 m with the Smith-McIntyre Grab.

DIAGNOSIS: Shell to 3 mm, thick, subhyaline. Anterior produced, posterior truncated. Left valve with two teeth-like lamellae and subumbonal pseudocardinal. Right valve with corresponding vestigial dentition.

ETYMOLOGY: The specific name is derived from *vadosus*, the Latin for shallows and refers to the shallow water habitat.

COLLECTION: 354 specimens from 15 stations in 0.5–30 m.

MEASUREMENTS AND TYPE DEPOSITION:

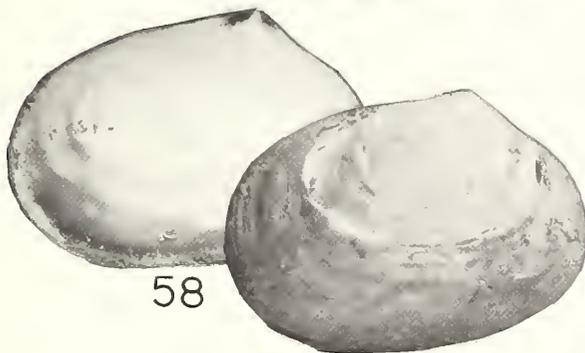
Type	Measurements (mm)			Depository
	L	H	W	
Holotype	2.3	2.0	1.3	LACM No. 1902
Paratype 1	1.9	1.6	1.1	LACM No. 1903
Paratype 2	2.3	1.9	1.2	USNM No. 771437
Paratype 3	2.1	1.7	1.3	NMC No. 77002
Paratype 4	1.9	1.7	1.1	OSU No. 01048
Paratype 5	2.0	1.5	1.0	CAS No. 58995



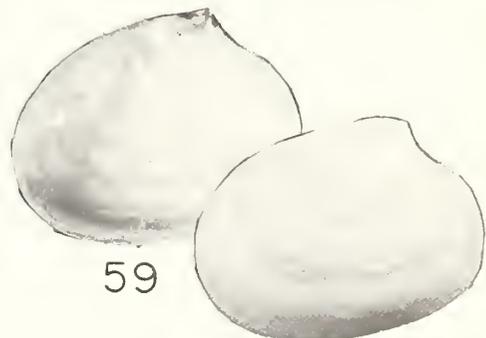
56



57



58



59

FIGURES 56–59. 56, *Boreacola vadosa* new genus, new species, HOLOTYPE, length 2.3 mm; 57, *Montacuta dawsoni* Jeffreys, length 1.9 mm; 58, *Mysella (Mysella) planata* (Dall in Krause), length 4.4 mm; 59, *Mysella (Rochefortia) tumida* (Carpenter), length 2.6 mm.

COMPARISONS: The salient differences are given under the generic discussion. This species may only be confused with *Mysella tumida* (Carpenter), but the two large divergent teeth of the right valve of the latter species clearly separate it.

REMARKS: The species is very abundant in favored areas, particularly the extremely shallow subtidal regions that have had little sampling effort. A number of specimens of a montacutid turned up in the shallow (< 30 m) stations of the 1970–72 OSU collections, but I was unable to assign to genus due to extensive formaldehyde damage. Examination of the Western Washington State College material collected at Pitt Point, Alaska (<1 m), revealed abundant representatives in excellent preservation.

Genus *Montacuta* Turton 1822

Figure 55

Type species (subsequent designation Herrmannsen 1846): *Ligula substriata* Montagu 1808. Recent. North Atlantic.

DESCRIPTION: Shell thin, ovate to subquadrangular, inflated. Surface usually with concentric lirae and growth checkmarks, occasionally with fine radial threads. Periostracum thin and polished. Interior of shell chalky, margins smooth. Hinge weak, with anterior lamina terminating in a minute cardinal hook in each valve, but larger in the right valve. Posterior lamina weak, sometimes vestigial. Ligament mostly internal, resilifer a small oblique channel posterior to the umbones. Adductor muscle scars irregular, elongated. Pallial line wide. No pallial sinus.

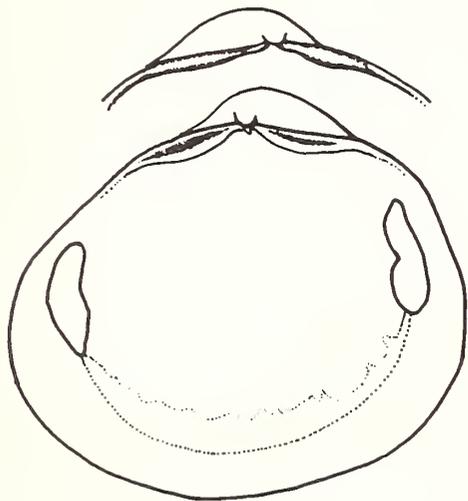


FIGURE 55. Interior of right valve and hinge of left valve of *Montacuta substriata* (Montagu).

RANGE: Eocene to Recent. Recent distribution Arctic and circumboreal. Commensal with larger burrowing invertebrates, particularly echinoderms and polychaetes.

DEVELOPMENT: Eggs are retained in the mantle cavity in at least some species and released for a short planktonic phase (Oldfield 1961; Thorson 1946; Loven 1848). The planktonic larva has been described by Lebour (1938).

REMARKS: Nutrition in the genus is by filter feeding. The anatomy points to a shallow infaunal existence, but specimens

are usually collected in the deeper sediments. Most are commensals byssally attached to their infaunal partners, or to the walls of burrows, allowing existence at a greater buried depth.

Montacuta dawsoni Jeffreys 1863

Figure 57

Montacuta dawsoni Jeffreys 1863:216; Jeffreys 1869:178, pl.31, f.7
Mysella sovaliki MacGinitie 1959:173, pl.4, f.10.

DESCRIPTION: Shell obliquely triangular to subelliptical, maximum length 3 mm. Surface smooth with occasional concentric incremental striae and growth checks. Periostracum thin, light brown, dehiscent. Umbones not prominent, usually eroded. Interior polished, with faint radiating lines, margins smooth. Hinge with an anterior and smaller posterior lamina in each valve, but obscure in left valve. Resilifer triangular, subumbonal. Adductor muscle scars and pallial line not apparent.

COMPARISONS: The species is readily separated from others in the genus by the triangular outline that is due to the extension of the anteroventral margins. The low beaks separate it from the New England species *M. elevata* Stimpson 1851.

COLLECTION: *M. dawsoni* occurred at three stations for a total of five specimens collected in 23–29 m.

RECORDS: Recent—Johnson 1934:44 (Greenland to Newfoundland); Gorbunov 1946a:46 (New Siberian Islands); Filatova 1957b:55 (Arctic). MacGinitie 1959:173, pl.4, f.10 (Point Barrow, Alaska); Clarke 1962:66 (North Atlantic and Mediterranean).

DISTRIBUTION: Probably panarctic, the species is widely distributed through the North Atlantic from Greenland to Norway, south to Britain, and along the American eastern seaboard from Baffin Island to New Brunswick; and from the Canadian Arctic Archipelago to Point Barrow, Alaska. It does not occur in the Bering Sea or Pacific Ocean.

REMARKS: I consider *Mysella sovaliki* MacGinitie 1959 a synonym. MacGinitie gave an abbreviated description, comparing it only to the northeast Pacific *Tellinya tumida* Carpenter 1864, and stated that three specimens (USNM 170490) labelled *Montacuta dawsoni* should be referred to the new species. After examination of the type of *M. sovaliki* and numerous specimens of *M. dawsoni*, I conclude that MacGinitie's species falls within the expected variation of high Arctic bivalves. I have been unable to arrive at a firm conclusion, but am of the opinion that *Mysella maltzani* Verkrüzen 1876 is also a probable synonym. This species is sporadically distributed from Norway to the Siberian Sea (Filatova 1948), Novaya Zemlya (G. Sars 1878), and Spitzbergen (Odhner 1915), thus completing the panarctic distribution of *M. dawsoni*.

Genus *Mysella* Angas 1877

Figure 60

Type species (original designation): *Mysella anomala* Angas 1877. Recent. Australia.

DESCRIPTION: Shell subtriangular to elliptical. Surface smooth or with obscure concentric lirae. Periostracum polished, light to dark brown, dehiscent. Umbones prominent, beaks small. Interior glossy, shell margins smooth. Hinge well developed, with two stout teeth bordering the central resilifer in the right valve. Left valve edentulous, but with shell margins inserted into a

groove above teeth of right valve. Adductor muscle scars weakly developed. Pallial line irregular and obscure. No pallial sinus.

RANGE: Miocene to Recent. Recent distribution cosmopolitan, generally in fine sediments and commensal with burrowing echinoderms, polychaetes, sipunculids, and mollusks (Boss 1965).

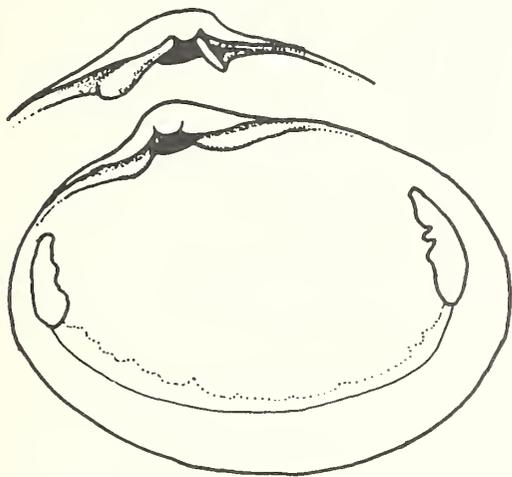


FIGURE 60. Interior of right valve and hinge of left valve of *Mysella anomala* (Angas).

DEVELOPMENT: Thorson (1946) observed the species *M. bidentata* (Montagu 1803) brooding its eggs, which are released at an advanced stage of development.

REMARKS: The genus contains filter feeding bivalves that attach directly to larger invertebrates, or affix the byssus to the burrow wall of deep infauna, probably benefiting from the water circulation generated by the host. A review of the many species currently placed within *Mysella* will probably show that the northern boreal representatives should be placed in several genera and separated from the antipodal *Mysella*.

KEY TO THE SUBGENERA OF *MYSELLA*

Resilifer narrow, oblique *Mysella* s. str.
Resilifer wide, vertical *Rochefortia*

Subgenus *Mysella* s. str. *Mysella (Mysella) planata* (Dall in Krause 1885)

Figure 58

Tellimya planata Dall in Krause 1885:34, pl.3, f.6a-d.
Mysella planata (Dall in Krause), Dall 1899:892, pl.88, f.12.
Rochefortia planata (Dall in Krause), Oldroyd 1925:132.
Montacuta planata (Dall in Krause), MacGinitie 1959:974, pl.20, f.1, 3-7, 9-11.

DESCRIPTION: Shell compressed, subquadrate to ovate, maximum length 10 mm, usually less than 5 mm. Surface smooth, sometimes with incremental lirae. Periostracum dark brown, dehiscent, with concentric wrinkles and folds. Umbones situated nearer the posterior end of shell, not prominent and usually

eroded. Interior polished, frequently with faint radial lines. Shell margins smooth. Hinge developed, with two prominent diverging teeth on either side of the resilifer of the right valve. Left valve edentulous, but dorsal margins of shell slightly produced to fit into corresponding grooves in the right valve. Adductor muscle scars subequal, narrow and irregular. Pallial line wide and indistinct. No pallial sinus.

COMPARISONS: This species may be confused with *M. tumida* (Carpenter 1864) a species with a more triangular outline, weaker dentition, and a polished periostracum.

COLLECTION: *M. planata* occurred at six stations for a total of 39 specimens and a few single valves from 270-717 m.

RECORDS: *Pliocene*—Durham and MacNeil 1967:331 (North Pacific). *Recent*—Paetel 1890:134 (Bering Sea); Dall 1921:37 (Arctic Ocean to Southern Alaska); Filatova 1957b:55 (Siberian Arctic); MacGinitie 1959:174, pl.20, f.1, 3-7, 9-11 (Point Barrow, Alaska); Eyerdam 1960:37 (Aleutian Islands); Scarlato and Ivanova 1974:306 (Kurile Islands); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: The species is limited to the Chukchi Sea and adjacent Arctic Ocean from the Beaufort to the Siberian Sea, and south to include the Bering Sea and the Kurile Islands. It has not been identified south of the Aleutian Archipelago, or in the Atlantic segment of the Arctic.

REMARKS: MacGinitie (1959) following Dall (1899) identified *M. planata* with *M. elevata* Mörch in Jones 1875 (not Stimpson, 1851), and with *M. moelleri* Mörch (Holboll MS) in Jones 1875. According to Dall, the latter was not validly proposed, so the taxon dates from Posselt 1898, and therefore falls into the synonymy of *M. planata*. However, I believe the Mörch taxon to be valid; furthermore, it is a distinct species synonymous with *M. elevata* Mörch in Jones 1875. Rejection of Dall's (1899) synonymy removes the North Atlantic records of *M. planata* cited by MacGinitie (1959).

Subgenus *Rochefortia* Velain 1877

Type species (monotypy): *Rochefortia australis* Velain 1877. Recent. Indian Ocean.

Mysella (Rochefortia) tumida (Carpenter 1864)

Figure 59

Tellimya tumida Carpenter 1864:602, 611, 643; Tryon 1872:229.
Mysella tumida (Carpenter), Dall 1899:881, pl.87, f.7; Palmer 1958:88, pl.7, f.8-12.
Rochefortia tumida (Carpenter), Oldroyd 1925:132, pl.54, f.11-14.

DESCRIPTION: Shell ovate to subtriangular, compressed, maximum length 5 mm. Surface smooth, with irregular incremental striae. Periostracum dark brown, sometimes with bands of darker color. The surface of the periostracum is polished, but microscopic concentric wrinkles are present. Umbones inflated, eroded, placed near truncated posterior margins. Interior glossy, shell margins smooth, very tightly closing. Hinge strong, two large teeth in right valve, left valve with hinge margins produced into two laminar pseudolaterals, otherwise edentulous. Adductor muscle scars elongated. Pallial line wide, indistinct. No pallial sinus.

COMPARISONS: The subtriangular outline and truncated posterior end of the shell, and the heavy dentition of the hinge distinguish this species from *M. planata* (Dall in Krause 1885).

COLLECTION: Eight specimens from two stations were collected in 29 and 71 m.

RECORDS: *Pliocene*—Hertlein and Grant 1972:239, pl.44, f.2–5, 7, 8, 12, pl.45, f.5, 8, 9, 12 (California). *Pleistocene*—Grant and Gale 1931:301, pl.14, f.16, 17 (Lower California, Mexico); Kanakoff and Emerson 1959:24 (California); Addicott 1966:4, pl.4, f.12, 13 (California); Allison 1973:20 (Aleutian Islands, Alaska). *Recent*—Krause 1885:36 (Bering Sea); Newcombe 1893:4 (British Columbia); Baker 1910:47 (Alaska); Willett 1918:68 (Alaska); Grant and Gale 1931:301, pl.14, f.16, 17 (Alaska to California); Eyerdam 1960:44 (Aleutian Islands, Alaska); Bernard 1970:88 (British Columbia); Wacasey 1975:27 (Beaufort Sea).

DISTRIBUTION: Widely distributed in the Bering Sea and the American coast as far south as Tillamook, Oregon and possibly California.

REMARKS: This species was not recorded by MacGinitie (1959), however, I have no hesitation assigning the few OSU specimens to *M. tumida*. I have not seen material collected south of central Oregon.

Family CARDITIDAE Fleming 1828

Genus *Cyclocardia* Conrad 1867

Figure 61

Type species (subsequent designation Stoliczka 1871): *Cardita borealis* Conrad 1831. Recent. North Atlantic.

DESCRIPTION: Shell rounded to trigonal, thick and solid. Surface ornamented with strong radial ribs, which may be beaded. Periostracum dark brown to black, frequently velvety. Beaks prosogyrous, not prominent. Interior porcelaneous, shell margins coarsely crenulated. Hinge ponderous, with peg-like, often bifid, anterior cardinal tooth and curved elongate posterior cardinal in the left valve. Right valve with large central cardinal and narrow laminar subligamental posterior cardinal tooth.

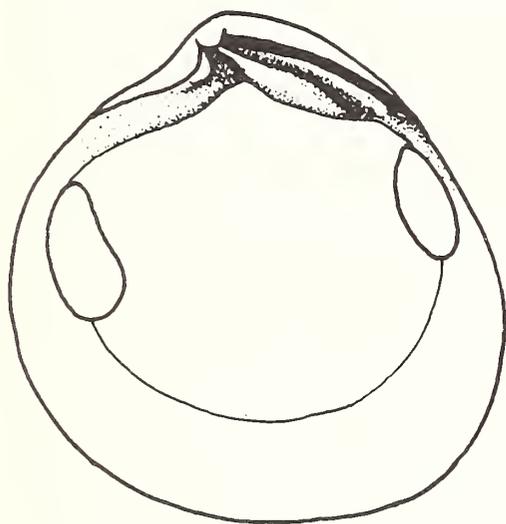


FIGURE 61. Interior of right valve of *Cyclocardia borealis* (Conrad).

Adductor muscle scars nearly equal in size, deeply impressed. Pallial line width irregular. No pallial sinus.

RANGE: Cretaceous to Recent. Recent distribution cosmopolitan in temperate and boreal waters. The genus is a member of the shallow infauna of coarse sediments. Large specimens frequently have sessile invertebrates attached to the posterior end of the shell.

DEVELOPMENT: The family is generally incubatory with the young released as benthic juveniles (Dall 1903; Jones 1963).

REMARKS: MacGinitie (1959) obtained a number of specimens of *C. crassidens* (Broderip and Sowerby 1829), at Point Barrow and Coan (1977) recorded the species at Cape Simpson (CAS 35058). It is not represented in the present collection, so it is possible this northeastern Pacific species is not firmly established in the Arctic. The anatomy of *Cyclocardia* has been reported by Pelseneer (1911) and Pacific species were examined by Yonge (1969) who also summarized the salient features of the superfamily. Coan (1977) published a review of the Northwest American species.

Subgenus *Cyclocardia* s. str. *Cyclocardia* (*Cyclocardia*) *crebricostata* (Krause 1885)

Figures 63, 64

Cardita borealis crebricostata Krause 1885:70, pl.3, f.4.

Venericardia crebricostata (Krause), Oldroyd 1925:114, pl.13, f.12.

Venericardia (*Cyclocardia*) *crebricostata* (Krause), Kotaka 1962:150, pl.35, f.5–7.

Cyclocardia crebricostata (Krause), Coan 1977:378, f.6–7.

Venericardia (*Cyclocardia*) *alaskana* Dall 1903a:710, 715; Dall 1903b: pl.63, f.7.

DESCRIPTION: Shell circular to nearly ovate, inflated, thick, maximum length 40 mm. Surface ornamented with 18–30 rounded ribs with equal interspaces crossed by numerous small concentric folds resulting in a scalariform appearance. Periostracum dark brown, velvety. Beaks small, erect, usually eroded. Interior polished, shell margins crenulated. Hinge delicate for the genus. Left valve with large central bifid cardinal and curved, elongated posterior cardinal tooth. Right valve with large central cardinal and thin laminar posterior cardinal tooth. External ligament placed on well-developed nymphs. Adductor muscle scars equal, deeply impressed. Pallial line impressed. No pallial sinus.

COMPARISONS: This species is allied to the North Atlantic *C. borealis* (Conrad 1831) but is distinguishable by the thinner shell, more delicate ribs, and weaker hinge.

COLLECTION: This species occurred at 19 stations for a total of 29 specimens from 30–101 m.

RECORDS: *Pliocene*—MacNeil et al. 1943:75, pl.14, f.16, 17 (Alaska); Hopkins and MacNeil 1960:B341 (Northwest Alaska); Petrov 1966:215, pl.10, f.3 (Chukotsk Peninsula); Zhidhova et al. 1968:94, pl.23, f.4, 5 (Sakhalin Islands). *Pleistocene*—Miller 1953:29 (Alaska); Barth 1956:119 (Pribiloff Islands, Alaska); Merklin et al. 1962:36, pl.15, f.7 (Chukotsk Peninsula); Hopkins et al. 1972:126 (St. Lawrence Island). *Recent*—Kinoshita and Isaka 1934:15, pl.11, f.81 (Northern Japan); Kuroda and Habe 1952:34 (Northern Japan); Habe and Igarashi 1957:35 (Northern Japan); Filatova 1957b:54 (South Chukchi Sea); MacGinitie 1959:169 (Point Barrow, Alaska); Merklin et al. 1962:36, pl.5, f.7 (Chukotsk Peninsula); McLaughlin 1963:26 (Bering Sea); Bernard 1970:88 (British Columbia).

DISTRIBUTION: Widely distributed throughout the Bering Sea, the species extends westward into the Okhotsk Sea and to Northern Japan. Along the American coast it is found from Point

Barrow to central Oregon (Bernard MS) and has been recorded from the Chukchi Sea.

REMARKS: This is a northern species and records south of central Oregon are in error. It appears to have originated in the Western Bering Sea and only recently entered the high Arctic, probably after the Pleistocene Kotzebuan Transgression (Hopkins et al. 1972). *C. alaskana* (Dall 1903) is certainly this species which Dall separated from the Atlantic *C. borealis* auctt (in part Conrad 1890). Localized high-count rib populations, identified as *C. crebricostata nomensis* MacNeil 1943, are present in both the Bering and Chukchi seas (D.M. Hopkins, pers. comm.), and may be considered morphs of the typical form. The relationship to *Venericardia granulata rjabiniinae* Scarlato 1955 from the Chukotsk Peninsula is unresolved. The latter appears to be more elongated and with wider interspaces between the ribs.

Family ASTARTIDAE d'Orbigny 1844
Genus *Astarte* J. Sowerby 1816

Figure 62

Type species (original designation): *Pectunculus sulcatus* Da Costa 1778.
Recent. North Atlantic.

DESCRIPTION: Shell trigonal, quadrangular, or rounded. Surface smooth or with concentric lirae or ribs. Periostracum thick, varnished, adherent. Interior porcelaneous, shell margins smooth or finely crenulated. Hinge well developed, with three teeth in the left valve. Adductor muscle scars subequal, deeply impressed. Pallial line uniform. No pallial sinus.

RANGE: Jurassic to Recent. Recent distribution cosmopolitan, especially in boreal and cool waters, extending to low latitudes in deeper water. The genus is a member of the superficial infauna, with the shell frequently covered with various small sessile invertebrates.

DEVELOPMENT: Reproduction is non-pelagic according to the species examined by Thorson (1946). Ova are large and adhesive, attaching to the substrate or shell near the parent (Oeckelmann 1958).

REMARKS: The limited distribution of juveniles may be the primary cause of the great polymorphism displayed by the genus. All observed species are active movers over the substrate, espe-

cially at night, they are shallow burrowers, often leaving the posterior end of the shell, with its small pallial aperture, exposed. It is interesting to note that Stanley (1970) reported an exception in *A. castanea* (Say 1822), which exposes the anterior end. As it is commonly present in coarse sediments, it is probable that this species utilizes the interstitial water for respiration and nourishment.

KEY TO THE SUBGENERA OF *ASTARTE*

1. Shell smooth, or with regular concentric ribs 2
Shell with broad irregular, sometimes broken concentric ribs *Rictocyma*
- 2.(1) Lunule rounded, depressed, ligamental nymph narrow *Astarte* s. str.
Lunule elongate, superficial, ligamental nymph broad *Tridonta*

Subgenus *Astarte* s. str.
Astarte (Astarte) crenata (Gray 1824)

Figure 65

Nicania crenata Gray 1824:119.

Astarte crenata (Gray), Smith 1881:23; Jensen 1912:113, pl.4, f.5a-m; Soot-Ryen 1932:14, pl.1, f.15-18.

Astarte crenata inflata Hägg 1904:f.4-6; Jensen 1912:113, pl.4, f.5h-i.
Astarte crenata quadrata Filatova 1957b:54 [nom. nud.].

Crassina elliptica Brown 1827:96, pl.38, f.3 [not *Astarte elliptica* Sibirgokova, 1961].

Astarte elliptica (Brown), Smith 1881:204.

Astarte semisulcata Möller 1842:19 [not *Crassina semisulcata* Leach in Ross 1819].

DESCRIPTION: Shell ovate to rhomboidal, posterior end truncated. Surface ornamented with strong rounded equidistant concentric ribs. Periostracum with a silken sheen, yellow to brown. Umbones prominent, beaks usually eroded. Interior porcelaneous, polished, shell margins finely crenated in mature specimens, smooth in immature individuals. Hinge delicate for the genus. Right valve with three cardinal teeth. Left valve with posterior cardinal obsolete. Ligamental nymph vestigial, ligament in sunken groove. Adductor muscle scars subequal. Pallial line impressed. No pallial sinus.

COMPARISONS: The regular and equidistant concentric ribbing of most of the disc and the wide lunule distinguish this species from all other Arctic representatives of the genus. The crenulation of the shell margins is age-dependent and can not be used as a basis for identification.

COLLECTION: This species occurred at two stations for a total of 56 specimens from 357 and 455 m.

RECORDS: *Pliocene*—Wood 1853:181, pl.16, f.7 (Britain); Schlesch 1924:11 (Iceland); Glibert and Van De Poel 1970:74 (Scotland). *Pleisto-*

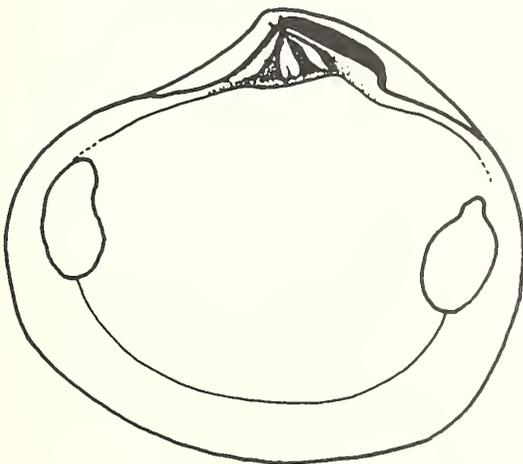


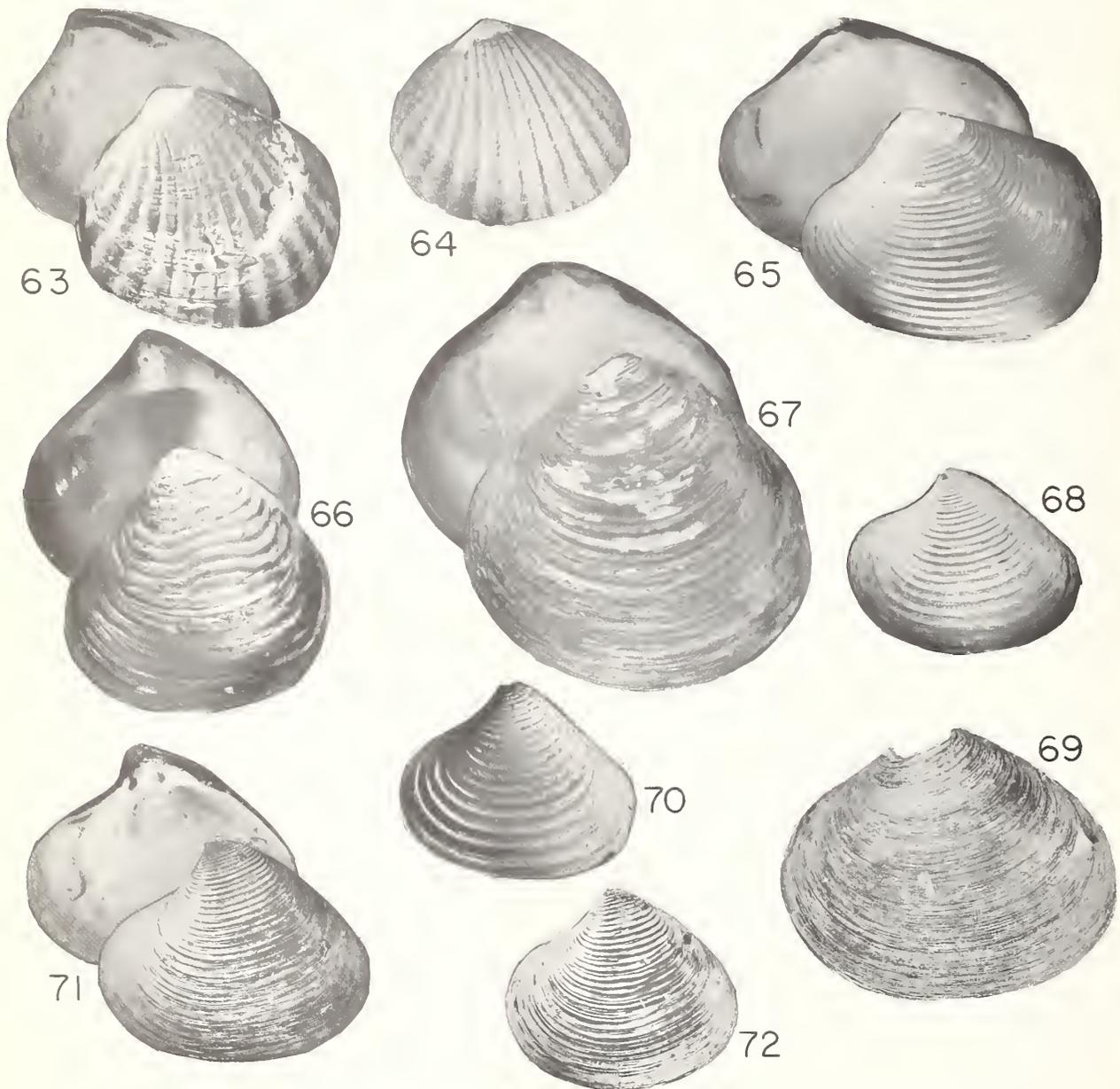
FIGURE 62. Interior of right valve of *Astarte sulcata* (Da Costa).

cene—Richards 1962:58, pl.6, f.6, 7 (Labrador to Massachusetts). *Recent*—D'Urban 1880:253 (Barents Sea); Petersen 1893:75 (Denmark); Melville and Standen 1900:4 (Franz Josef Land); Hägg 1904:36 (Greenland); Mesjatsev 1931:84 (Barents Sea); Johnson 1934:36 (Greenland to Gulf of St. Lawrence); Soot-Ryen 1939:14 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Filatova 1948:434, pl.109, f.5–8 (Arctic); Madsen 1949:48 (Iceland); Filatova 1957b:65 (Kara Sea); Filatova and Zenkevich 1957:66 (Kara Sea); Ockelmann 1958:89 (Greenland); Soot-Ryen 1958:20 (Greenland); Richards 1962:58, pl.6, f.6, 7 (Arctic to Massachusetts); Kuznetsov 1963:66 (Kamchatka); Petersen 1968:52 (Faroe Islands); Clarke 1974:10 (South Greenland); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Probably panarctic, the species is widely distributed from Greenland eastwards to Norway and south to the

Faroe Islands. It occurs in the Canadian Arctic Archipelago, Hudson Bay, and south to Massachusetts. It is present in the Siberian Sea, but does not extend into the Eastern Bering Sea or Pacific Ocean.

REMARKS: This is a highly polymorphic species, with numerous varietal and subspecific forms, a selection of the more important ones are presented in the systematic citation section above. It is easily distinguishable in its "typical form" but varieties may be confused, particularly with *A. borealis* (Schumacher 1817). Distinguishing points are the comparative thinness of the shell, the regular concentric ribbing over most of the disc, and the light colored periostracum which is thin and never fibrous or decorticated as in *A. borealis*. Under the microscope the peri-



FIGURES 63–72. 63, *Cyclocardia (Cyclocardia) crebricostata* (Krause), length 16.5 mm; 64, *C. (C.) crebricostata*, length 18.4 mm; 65, *Astarte crenata* (Gray), length 21.0 mm; 66, *Astarte (Rictiocyma) esquimalti* (Baird), length 11.2 mm; 67, *Astarte (Tridonta) borealis* (Schumacher), length 29.2 mm; 68, *A. (T.) borealis*, length 24.0 mm; 69, *A. (T.) borealis*, length 33.1 mm; 70, *A. (T.) borealis*, juvenile, length 10.9 mm; 71, *Astarte (Tridonta) montagui* (Dillwyn), length 17.2 mm; 72, *A. (T.) montagui*, juvenile, length 4.1 mm.

ostracal folds are more regular and less numerous than in the latter species. Care must be exercised in utilizing the fine structure of the periostracum as an identification aid suggested by Ockelmann (1958). Although useful, microscopic appearance is not absolutely consistent.

Subgenus *Rictocyma* Dall 1872

Type species (monotypy): *Rictocyma mirabilis* Dall 1872. Recent. North-east Pacific.

Astarte (Rictocyma) esquimalti (Baird 1863)

Figure 66

Crassatella esquimalti Baird 1863:70.

Astarte esquimalti (Baird), Oldroyd 1925:108 [not pl.13, f.19].

Rictocyma zenkevitchi Filatova 1957a:300 f.4.

DESCRIPTION: Shell quadrate to subtrigonal, compressed, maximum length 20 mm. Surface with numerous irregular concentric ribs. In large individuals ribs may be absent from ventral part of disc. Periostracum light to dark brown, with microscopic striae and wrinkles. Umbones prominent. Beaks erect and generally eroded. Lunule long and flat. Escutcheon elongated. Interior porcelaneous, sometimes with pearly luster, margins smooth. Hinge carved, left valve with prominent anterior tooth, a central laminar and a vestigial subligamental tooth. Right valve with three teeth, the central one large. Adductor muscle scars equal, deeply impressed. Pallial line narrow. No pallial sinus.

COMPARISON: *A. esquimalti* is the only Arctic representative of the subgenus and is easily separated from the inflated trigonal *A. mirabilis* (Dall 1871), of the Bering Sea, by the more numerous and narrower concentric ribs.

COLLECTION: Twelve specimens from six stations were collected in 34–270 m.

RECORDS: *Pleistocene*—Miller 1953:29 (Alaska). *Recent*—Lord 1866:368 (Vancouver Island); Whiteaves 1887:121 (Queen Charlotte Islands to Vancouver Island); Paetel 1890:138 (Vancouver Island); Newcombe 1893:4 (Vancouver Island); Taylor 1895:35 (British Columbia); Willett 1918:67 (Alaska); Eyerdam 1960:43 (Alaska); Bernard 1970:88 (Alaska to Puget Sound, Washington).

DISTRIBUTION: The species occurs throughout the Bering Sea and south to Puget Sound, Washington. Dall (1885) reported this species from Cape Franklin, but this is the first record from the Beaufort Sea.

REMARKS: Dall (1871) proposed *Rictocyma* as a subgenus to contain his new species *A. mirabilis*. The description is diagnostic, but the illustration is poor, and Dall was apparently unaware of Baird's *Crassatella esquimalti*, although it was included in the catalogue of West American mollusks by Carpenter (1864) and Lord (1866). In 1885 Dall, without explanation, synonymized his species with Baird's, and in 1903 Dall stated that *A. mirabilis* was a juvenile *A. esquimalti* and illustrated (Dall 1903b, pl.63, f.11, 12) a large specimen from the Shumagin Islands, reproduced by Oldroyd (1925, pl.13, f.19). I consider *A. mirabilis* a valid species as Dall apparently based his concept of Baird's species entirely upon the brief Latin diagnosis because the holotype (BM[NH] no number) has not been figured. Dall's difficulty is apparent from his MS name *A. esquimalti limata* on the specimen label (USNM 169565) that I consider to be *A. esquimalti* s. str. I hold *R. zenkevitchi* Filatova 1957a, from the Western Bering Sea and Kamchatka to be synonymous to *A. esquimalti* as Filatova based her comparison upon Dall's illustration of "*A. esquimalti*" which in fact is *A. mirabilis*. *A. (Gonilia?) diversa*

Dall 1920 from the Alaskan Pliocene is probably also a synonym of *A. mirabilis*.

Subgenus *Tridonta* Schumacher 1817

Type species (monotypy): *Tridonta borealis* Schumacher 1817 ex *Venus borealis* Chemnitz 1784. Recent. Arctic.

Astarte (Tridonta) borealis (Schumacher 1817)

Figures 67, 68, 69, 70

Venus borealis Chemnitz 1784 (of "Linné") invalid binom. ICZN [not *Venus borealis* Linné 1767].

Tridonta borealis Schumacher 1817:47, pl.17, f.1.

Astarte borealis ("Chemnitz"), Jensen 1912:92, pl.4, f.1a, b; Oldroyd, 1925:106; Scarlato, 1955:192, pl.51, f.8.

Astarte (Tridonta) borealis (Linné), Filatova 1948:435, pl.109, f.11.

Astarte borealis ovata Filatova 1957b:54 [not *Crassina ovata* Brown 1827].

Astarte (Tridonta) borealis pseudoactis Merklin and Petrov in Petrov et al. 1962:33, pl.4, f.1–3.

Crassina semisulcata Leach in Ross 1819 [not *Astarte semisulcata* Møller 1842].

Crassina withami J. Smith 1839:105, pl.1, f.21.

DESCRIPTION: Shell ovate to quadrangular, compressed, total length to 55 mm. Surface sculptured with concentric ribs usually limited to first 6–8 mm of the disc. Periostracum thick, yellow to black, adherent. In some individuals the periostracum is compact and polished with microscopic concentric striae, in others it is fibrous and decorticated. Umbones subcentral, not prominent. Interior polished, margins smooth, valves tightly closing. Hinge strong, right valve with two diverging teeth, left valve with large central cardinal and two smaller lateral teeth. Ligament supported by prominent nymphs. Adductor muscle scars deeply impressed, anterior pedal retractor scar prominent. Pallial line narrow. No pallial sinus.

COMPARISONS: This species is very variable, the proportions and the appearance of the periostracum are not consistent, but it is separated from other astartids by the always uncrenulated shell margins, the nearly central umbones, and the concentric ribs limited to the umbonal region.

COLLECTION: Twenty-six specimens and numerous single valves were collected from 16 stations between 28–270 m.

RECORDS: *Pliocene*—Wood 1853:175, pl.16, f.3a–d (Britain); Yokoyama 1922:163 pl.10 f.11a, b (Northern Japan); Nomura and Hatai 1935:85 (Japan); Slodkevich 1938:759, pl.59, f.5a, b (Chukotsk Peninsula); Petrov 1966:206 (Chukotsk Peninsula); Glibert and Van De Poel 1970:73 (Belgium); Zhidkova et al. 1972:119, pl.23, f.2 (Kurile Islands). *Pleistocene*—Knipowisch 1900:379 (Spitzbergen); Filatova 1957b:59 (Eurasian Arctic); Merklin et al. 1962:32, pl.2, f.8–13 (Chukotsk Peninsula); Richards 1962:59, pl.6, f.10, 11 (Labrador to Maine); Glibert and Van De Poel 1970:73 (Belgium); Hopkins et al. 1972:126 (St. Lawrence Island); Allison 1973:20 (Aleutian Islands). *Recent*—M. Sars 1850:170 (Norway); Crosse 1877:123 (Arctic and Bering seas); G. Sars 1878:50, pl.5, f.8a, b (Greenland); Melvill and Standen 1900:4 (Franz Josef Land); Mesjatsjev 1931:71 (Barents Sea); Soot-Ryen 1932:12 (Greenland); Johnson 1934:37 (Greenland to Massachusetts); Soot-Ryen 1938:10, pl.1, f.1–3 (Franz Josef Land); Gorbunov 1946a:46 (Arctic); Madsen 1948:43 (Iceland); Kuroda and Habe 1952:14 (Northern Japan); Ockelmann 1958:74 (Greenland); Soot-Ryen 1958:19 (Greenland); MacGinitie 1959:166, pl.22, f.1–6 (Point Barrow, Alaska); Clarke 1960:11 (Arctic); Ellis 1960:39 (Baffin Island); Hulsemann 1962:71 (Beaufort Sea); Kotaka 1962:148, pl.34, f.24, 25, 28, 29 (Okhotsk Sea); Richards 1962:59, pl.6, f.10, 11 (Arctic Ocean to Massachusetts); Kuznetsov 1963:6 (Kamchatka); Sparks and Pereyra 1966:834 (Chukchi Sea); Petrov 1967a:184 (Bering Sea); Golikov and Scarlato 1967:99, pl.9, f.4 (Northern Japan);

Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal, this species is widely distributed throughout the North Atlantic from the Canadian Arctic Archipelago to Norway and Denmark, and south to Massachusetts. It is not represented in the Pacific south of Prince William Sound, but is abundant in the Bering Sea and extends into the Sea of Okhotsk and the Sea of Japan. It is essentially a shallow water species, but drift shells have been recorded in more than 1600 m (Clarke 1960).

REMARKS: The shell outline and proportion of the hinge teeth are of little use in identification, but the microscopic appearance of the periostracum is constant for this particular species. Ockelmann (1958) showed it to be plain with fine concentric folds that may be prolonged into a fibrous mat, particularly on the ventral part of the disc. MacGinitie (1959) has pointed out that the dentition of high Arctic specimens may be rather coarser than that found on individuals from lower latitudes.

Astarte (Tridonta) montagui (Dillwyn 1817)

Figures 71, 72

Venus compressa Montagu 1808:43, pl.26, f.1 [not Linné 1767].

Venus montagui Dillwyn 1817:167.

Astarte montagui (Dillwyn), Jensen 1912:97, pl.4, f.2a, b; Filatova 1948:435, pl.110, f.5–8; Filatova and Barsanova 1964:20.

Nicania banksii Leach in Ross 1819: Appendix 62.

Nicania banksii (Leach in Ross), Gray 1839:152, pl.44, f.10.

Nicania striata Leach in Ross 1819: Appendix 62.

Astarte striata (Leach in Ross), Gray 1839:152, pl.44, f.9.

Astarte multicostata MacGillivray 1843:211 [not *Crassina multicostata* J. Smith 1839; not *Astarte multicostata* Filatova 1957a].

Astarte warhami Hancock 1846:336, pl.5, f.15, 16.

Astarte fabula Reeve in Belcher 1855:398, pl.33, f.5a, b; Oldroyd 1925:107, pl.19, f.4a.

DESCRIPTION: Shell trigonal to ovate, occasionally elongate. Maximum length 25 mm, rarely more than 15 mm. Surface with numerous concentric narrow sharp riblets, evenly spaced on the early shell, and tending to become irregular in the ventral regions. Periostracum thick, straw-yellow to maroon. The polished surface covered with numerous microscopic wrinkles. Umbones prominent, beaks usually eroded. Lunule wide, deeply impressed. Escutcheon flattened, not demarcated. Interior polished, translucent. Hinge well developed, curved. Right valve with prominent cardinal, posterior and anterior teeth vestigial. Left valve with two large, and one small tooth. Ligament on a large nymph. Adductor muscle scars and anterior and posterior pedal muscle scars deeply impressed. Pallial line wide. No pallial sinus.

COMPARISONS: This is one of the most variable members of the genus as testified by its numerous synonyms. It may be distinguished from other Arctic astartids by the wide and deeply concave lunule, the elongated shallow escutcheon and the slight protuberance of the ligament, which does not project as far as in *A. borealis* (Schumacher 1817). The interior of *A. montagui* is more polished than in other species and may display a bluish alabasterine depth, particularly on the adductor muscle scars. The region above the pallial line and between the adductor scars is generally opaque and less polished.

COLLECTION: This is the most abundant astartid in the collection, 641 specimens and many single valves occurred at 129 stations between 10–455 m.

RECORDS: *Pleistocene*—Fielden 1877:489 (Greenland); Knipovich 1900:379 (Spitzbergen); Laursen 1950:86 (Iceland); Merklin et al. 1962:34, pl.4, f.4, 8 (Chukotsk Peninsula); Richards 1962:58, pl.6, f.14, 15 (Arctic); Petrov 1966:210, pl.15, f.8–15 (Eurasian Arctic); Glibert and Van De Poel 1970:76 (Belgium); Wagner 1970:39, pl.3, f.14a, b, 15a, b, (Eastern Canada); Troitskiy 1974:265 (Siberia). *Recent*—Mørch 1869:233 (Iceland); Crosse 1877:123 (Bering and Arctic seas); Leche 1878:17 (Novaya Zemlya); D'Urban 1880:256 (Barents Sea); Krause 1885:31 (Bering Sea); Melvill and Standen 1900:4 (Franz Josef Land); Dall 1903b:942, 945 (Arctic and Bering seas); Odhner 1915:96 (Spitzbergen); Soot-Ryen 1925:5 (Spitzbergen); Spärck 1929:13 (Iceland); Grant and Gale 1931:268 (Herschel Island, Arctic and Bering Sea); Mesjatev 1931:76 (Barents Sea); Soot-Ryen 1939:11, pl.1, f.4 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:44 (Iceland); Filatova 1957b:54 (Arctic); Ockelmann 1958:80 (Greenland); Soot-Ryen 1958:19 (Greenland); MacGinitie 1959:167, pl.22, f.11, 12 (Point Barrow, Alaska); Clarke 1960:2, 11, pl.1, f.5 (Arctic); Hulsemann 1962:68 (Beaufort Sea); Richards 1962:58, pl.6, f.14, 15 (Arctic); McLaughlin 1963:26 (Bering Sea); Kuznetsov 1963:66 (Kamchatka); Sparks and Pereyra 1966:834 (Chukchi Sea); Clarke 1966:11, pl.1, f.5 (Arctic); Petrov 1967:167, 184 (Bering and Chukchi seas); Golikov and Scarlato 1967:100, f.84 (Northern Japan); Bowden and Heppell 1968:248 (Britain); Petersen 1968:52 (Faroe Islands); Clarke 1974:10 (Baffin Bay); Wacasey 1974:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. The species is widely distributed in the North Atlantic from Greenland to Norway and Sweden and south to Faroe and Shetland islands and Northern Britain. It occurs along the American coast from Nova Scotia through the Arctic shores and into the Bering Sea. It does not occur south of the Aleutian Islands. It is the most common astartid present on the Eurasian Arctic coast from the Kara Sea to Siberia and extends into the Sea of Okhotsk to Northern Japan.

REMARKS: A number of authors have retained form names such as *warhami* Hancock, but as no geographic pattern is discernible and a continuous series of intergrades occur, there is little benefit in naming extremes. Jensen (1912) suggested the environment influences morphology, the shell becoming less tumid and more elongate in colder waters. This is the pattern for Greenland (Ockelmann 1958); however, it does not hold for the Pacific high latitudes, as the most elongated and tumid forms of *A. montagui* occur in the Bering Sea.

Family CARDIIDAE Lamarck 1809

The collection contained a few specimens belonging to genera *Clinocardium* and *Serripes*. Wagner (1977) recorded both *Cerastoderma echinatum* (Linné 1758) and *C. elegantulum* (Beck in Møller 1842) from the eastern Beaufort Sea, so it is possible that the low-salinity area of the Mackenzie estuary forms an effective barrier to westward penetration of the typically European Arctic genus.

KEY TO THE GENERA OF CARDIIDAE

- Shell with strong radial ribs, dentition developed
 *Clinocardium*
 Shell with obscure radial channels, dentition vestigial
 *Serripes*

Genus *Clinocardium* Keen 1936

Figure 73

Type species (original designation): *Cardium nuttallii* Conrad 1837.
Recent. Northeast Pacific.

DESCRIPTION: Shell elliptical to subtrigonal, surface with numerous uniform radial ribs, overlaid by fine concentric threads. Periostracum thin, ciliated in some species. Beaks recurved, prosogyrate. Interior porcelaneous, margins coarsely crenulate. Hinge strong, arched. Each valve with two cardinal and a posterior and anterior lateral teeth. Ligament on a short nymph. Adductor muscle scars nearly equal, not impressed. Pallial line shallow, uniform width. No pallial sinus.

RANGE: Miocene to Recent. Recent distribution Arctic circumboreal, intertidal to 500 m, not a typically high Arctic genus, but one or two species numerically abundant.

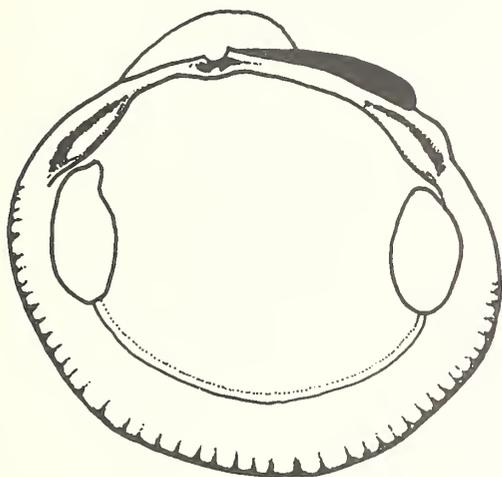


FIGURE 73. Interior of right valve of *Clinocardium nuttallii* (Conrad).

DEVELOPMENT: The type of the genus undergoes planktonic development (Bernard MS) and Ockelmann (1958) stated that *C. ciliatum* (Fabricius) also has a long pelagic phase.

REMARKS: Although widely distributed in the Arctic, the genus does not appear fully adapted, and is usually found only sporadically. It is probable that the requirement for a lengthy planktonic larval existence may hinder distribution.

Clinocardium ciliatum (Fabricius 1780)

Figure 75

Cardium ciliatum Fabricius 1780:410; Lamarck 1819:6 [as "ciliare"]; Jensen 1912:79, pl.3, f.10.

Cardium (*Cerastoderma*) *ciliatum* (Fabricius), Oldroyd 1925:142, pl.19, f.8, a; Filatova 1948:432, pl.109, f.1.

Clinocardium ciliatum (Fabricius), Keen 1936:120.

Cardium (*Clinocardium*) *ciliatum* (Fabricius), Clench and Smith 1944:15, pl.10.

Laevicardium (*Cerastoderma*) *ciliatum* (Fabricius), Grant and Gale 1931:310, pl.19, f.11.

Cardium arcticum Sowerby 1840:106.

DESCRIPTION: Shell subcircular to ovate, inflated, length to 70 mm, usually smaller. Surface with 28–40 radial triangular ribs, less prominent in the lateral part of disc. Periostracum yel-

low to greyish-brown, thin, adherent, with numerous concentric folds especially produced over the ribs, giving them a ciliated appearance. Umbones prominent, beaks prosogyrate. Lunule and escutcheon obscure. Interior porcelaneous, margins coarsely crenulate. Hinge plate arched. Two cardinal and two lateral teeth in each valve, but the posterior lateral and cardinal almost vestigial. Ligament weak, attached to small nymph. Adductor muscle scars nearly equal. Pallial line indistinct. No pallial sinus.

COMPARISONS: The species is easily distinguished by the thin shell, the numerous narrow sharp ribs, and the periostracal fringe on the radial ribbing which may, however, be absent from gerontic and abraded specimens. The dentition, particularly the lateral teeth, is weaker than in other members of the genus.

COLLECTION: Eight specimens and some fragments occurred at seven stations between 26–159 m.

RECORDS: *Pleistocene*—Meek 1923:414 (Alaska); Wagner 1959:5 (British Columbia); Merklin et al. 1962:38, pl.6, f.1 (Chukotsk Peninsula); Richards 1962:63, pl.8, f.8, 9 (Hudson Bay to Massachusetts); Petrov 1966:221, pl.17, f.1–3 (Eurasian Arctic). *Recent*—Montagu 1803:79 (England); Leche 1878:21 (Novaya Zemlya); G. Sars 1878:46, pl.5, f.4a, b (Greenland); Leche 1883:443 (Arctic); Hägg 1904:51 (Greenland and Spitzbergen); Mesjatsev 1931:107 (Barents Sea); Kinsoshita and Isaka 1934:15, pl.12, f.84 (Northern Japan); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:63 (Iceland); Soot-Ryen 1951:3 (Norway); Kuroda and Habe 1952:17 (Northern Japan); Filatova 1957b:55 (Arctic); Ockelmann 1958:118 (Greenland); MacGinitie 1959:176, pl.26, f.4 (Point Barrow, Alaska); Clarke 1961:7 (Gulf of St. Lawrence); Ellis 1960:39 (Baffin Island); Kotaka 1962:151, pl.35, f.4 (Sea of Okhotsk); Richards 1962:63, pl.8, f.8, 9 (Arctic to Massachusetts); McLaughlin 1963:26 (Bering Sea); Filatova and Barsonova 1964:34 (Bering Sea); Allen 1965:983 (Northwestern Atlantic); Sparks and Pereyra 1966:834 (Chukchi Sea); Habe and Igarashi 1967:36 (Northern Japan); Petrov 1967:184 (Bering Sea); Clarke 1974:11 (Baffin Bay); Kafanov 1974:1469 (North Atlantic and Arctic); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. The species is distributed throughout the North Atlantic from Greenland to Norway and south to England and Ireland. It is abundant from Cape Cod, Massachusetts to Hudson Bay and Baffin Island. It has been reported from all the Arctic coasts, the Bering Sea, Sea of Okhotsk and south to northern Japan. In the eastern Pacific it ranges into the northern portion of the Gulf of Alaska.

REMARKS: The species has been named several times, these synonyms, listed by Dall (1901) should be re-examined when the limits of variability have been established. Though the dentition is reduced there is no doubt that the species should be assigned to *Clinocardium*. Kafanov (1974) proposed the genus *Ciliocardium* with *C. ciliatum* as type species and sole living representative of the taxon, which apparently arose from Miocene *Clinocardium* stock. The value of this generic separation has not been established. Andrews (1972) discussed fossil and living growth rates.

Genus *Serripes* Gould 1841

Figure 74

Type species (monotypy): *Cardium groulaudicum* Bruguière 1789.
Recent. Arctic.

DESCRIPTION: Shell ovate, inflated and brittle. Surface with weak radial channels, especially on anterior and posterior slopes. Periostracum thin, adherent. Interior polished or dull, margins smooth. Hinge narrow and poorly developed. Right valve with two cardinals and anterior and posterior lateral teeth. Left valve with corresponding laterals and single cardinal tooth. Dentition is

evanescent and many specimens, irrespective of size, are edentulous. Ligament large, on wide nymph. Adductor muscle scars equal. Pallial line uniform. No pallial sinus.

RANGE: Miocene to Recent. Recent distribution includes the Arctic Ocean and northern circumboreal regions. Shallow and intertidal infauna of mixed sediments.

DEVELOPMENT: According to Thorson (1936) the ova of *S. groenlandicus* (Bruguère 1789) are small and poor in yolk, accordingly, development is planktotrophic.

REMARKS: This genus includes the largest high Arctic bivalves and the only one of major significance as food for walrus.

Serripes groenlandicus (Bruguère 1789)

Figures 76, 77

Venus islandica (of "Linné") Fabricius 1780:411 [not *Venus islandica* Linné 1767].

Cardium grönlandicum Chemnitz 1782:pl.19, f.198 [non binom. ICZN.]

Cardium grönlandicum Bruguère 1789:222; Gmelin 1791:3252; Jensen 1915:115.

Aphrodite groenlandica (of "Chemnitz"); Leche 1883:443.

Cardium (Serripes) groenlandicum (of "Chemnitz"), Jensen 1912:85, p.3, f.12a, b.

Serripes grönlandicus (of "Chemnitz"), Gould 1870:145, f.454; Oldroyd 1925:145, pl.8, f.3; Filatova 1948:431, pl.108, f.12.

Serripes groenlandicus (of "Chemnitz"), Soot-Ryen 1932:14; Clench and Smith 1944:28, pl.13, f.5-7; Scarlato 1955:143, pl.51, f.11; Petrov 1966:222, pl.17, f.4-9, pl.18, f.1-3.

Serripes grönlandicus protractus Dall 1900:1112.

DESCRIPTION: Shell thin, inflated, subquadrate with rounded anterior and truncated posterior, length to 95 mm, usually less than 45 mm in the high Arctic. Surface with narrow radial channels, absent from the central part of the disc. Concentric growth lines and checks may be present. Periostracum thin, light

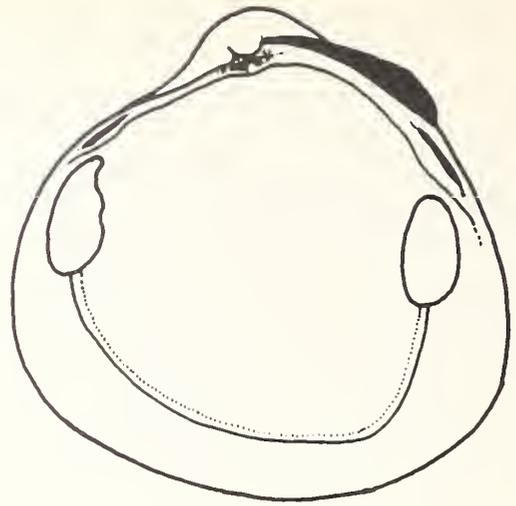
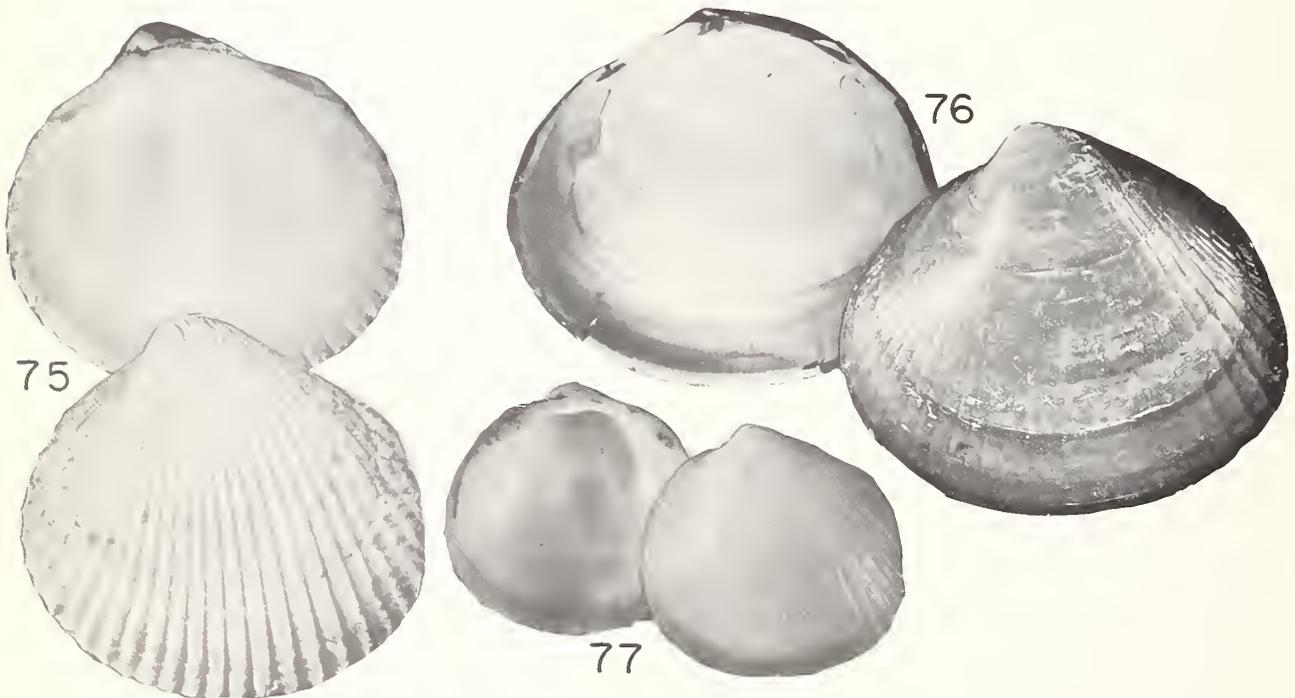


FIGURE 74. Interior of right valve of *Serripes groenlandicus* (Bruguère).

pinkish-brown to dark-brown, often with concentric bands of darker color. Interior polished, margins smooth except for lateral zones that may be obscurely crenulate. Hinge narrow, frequently edentulous with obscure tuberosities, but some specimens with a small central cardinal and weak anterior and posterior lateral teeth in each valve. Adductor muscle scars nearly equal. Pallial line weakly impressed. No pallial sinus.

COMPARISONS: Although this species is rather variable, it is easily distinguished by the thin, brittle shell, the obscure dentition, and the radial channels between the wide and shallow ribs confined to the anterior and posterior of the shell. It is surprising



FIGURES 75-77. 75, *Clinocardium ciliatum* (Fabricius), length 20.6 mm; 76, *Serripes groenlandicus* (Bruguère), length 27.7 mm; 77, *S. groenlandicus*, juvenile, length 2.9 mm.

that a number of synonyms have been proposed, most of them merged by Wood (1853). Another species, *S. laperousii* (Deshayes 1839), limited to the Gulf of Alaska, Bering, Okhotsk and Sea of Japan, is separable by the elongated posterior which has a marked gape, and the much heavier shell.

COLLECTION: Ten juvenile specimens and four larger valves occurred at 10 stations between 10–101 m.

RECORDS: *Pliocene*—Wood 1853:160, pl.13, f.1a–d (Britain); Hopkins and MacNeil 1960:B41 (Alaska); Zhidkova et al. 1968:104 (Sakhalin Islands); Zhidkova et al. 1972:127, pl.9, f.1 (Kurile Islands). *Pleistocene*—Wood 1853:160, pl.13, f.1a–d (Britain); Wagner 1959:5 (British Columbia); Merklin et al. 1962:38, pl.6, f.3–5 (Chukotsk Peninsula); Richards 1962:63, pl.8, f.12, 13 (Labrador to Maine); Hopkins et al. 1972:126 (St. Lawrence Island). *Recent*—Gould 1841:92 (Massachusetts); Middendorff 1849:557, pl.16, f.6–9 (Novaya Zemlya); Leche 1878:21 (Novaya Zemlya); G. Sars 1878:49, pl.5, f.3a–b (Greenland); Krause 1885:27 (Bering Sea); Melvill and Standen 1900:4 (Franz Josef Land); Dautzenberg and Fischer 1910:20 (Novaya Zemlya); Soot-Ryen 1939:15 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:59 (Iceland); Soot-Ryen 1951:2 (Norway); Kuroda and Habe 1952:31 (Northern Japan); Filatova 1957b:55 (Eurasian Arctic); Ockelmann 1958:113 (Greenland); MacGinitie 1959:176, pl.26, f.5 (Point Barrow, Alaska); Clarke 1961:7 (Gulf of St. Lawrence); Richards 1962:63, pl.8, f.12, 13 (Greenland to Massachusetts); McLaughlin 1963:27 (Bering Sea); Allen 1965:983 (Northwestern Atlantic); Golikov and Scarlato 1967:107 (Northern Japan); Petrov 1967:167 (Arctic); Bernard 1970:88 (British Columbia); Clarke 1974:10 (Baffin Bay); Scarlato 1976:103 (Bay of Peter the Great); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. This species is found throughout the north Atlantic from Greenland to Norway and south to Iceland, the Faroe Islands, and Britain. Along the American coast it occurs from Baffin Island to Cape Cod, Massachusetts. It has been reported from all regions of the shallow high Arctic, into the Bering Sea, west to northern Japan and along the Alaskan coast south to northern Oregon.

REMARKS: This is a shallow water species, but shells may be transported to great depths. Clarke (1960) reported fragments from 2200 m in the Laurentian Basin. It may be noted that the diacritic mark of the first vowel in the original combination is deleted in current nomenclature and the letter “e” inserted.

Family TELLINIDAE Blainville 1814

There were no representatives of *Tellina* in the collection. MacGinitie (1959) noted abundant fossil *Tellina lutea* Wood (Gray MS) 1828 (= *Tellina lutea alternidentata* Broderip and Sowerby 1829) at Point Barrow, and the species is recognized in the Pliocene and Pleistocene of Alaska. Living representatives, however, appear limited to the Chukchi, Bering and Okhotsk seas, and do not occur east of Cape Lisburne, Alaska. There is British Museum material (BM[NH] 1860. 1. 23.5) cited by Coan (1971) and labelled Cape Krusenstern, Arctic coast of Mackenzie, Canada (vicinity of Dolphin and Union Strait). I believe this locality to be mistaken for Cape Krusenstern (formerly spelled with a “z”) on the north side of Kotzebue Sound, Alaska, which is well within the known distribution of *T. lutea*. The species is not known to occur live in the Arctic, but does occur fossil at several locations in Arctic Alaska. The “*Herald*” (the vessel which collected the B.M. *Tellina*) did obtain material from the Canadian Arctic (Seemann 1853), but the majority of the described material originated in the Pacific and Bering seas. Forbes (1850) discussing American Pacific shells and lack of precise location data states “a few specimens of considerable

interest were taken by the “*Herald*” at Cape Krusenstern.” Wagner (1977) recorded an unidentified species of *Tellina* from the eastern Beaufort Sea.

Genus *Macoma* Leach 1819

Figure 78

Type species (monotypy): *Tellina calcarea* Gmelin 1791. Recent. North Atlantic.

DESCRIPTION: Shell ovate to subtrigonal, compressed. Surface white, chalky, smooth with faint incremental striae and growth checkmarks. Posterior of shell produced, frequently twisted to the right. Periostracum thin, light brown to colorless. Interior porcelaneous to chalky, shell margins smooth. Hinge weak, two cardinal teeth in each valve, lateral teeth absent. Ligament external, seated on nymph. Adductor muscle scars irregular. Pallial line narrow, not joining posterior adductor scar. Pallial sinus conjoined with pallial line, with a different configuration in each valve.

RANGE: Miocene to Recent. Recent distribution cosmopolitan, preferring fine sediments from the intertidal to the abyssal zones. The group is shallow to deeply infaunal, usually lying in the horizontal plane on the left valve (Stanley 1970).

DEVELOPMENT: There appears to be a range of developmental types within the genus. *M. moesta* (Deshayes 1854) produces large, adhesive ova undergoing a reduced, or totally absent, planktonic phase, while *M. calcarea* (Gmelin 1791) undergoes a normal planktonic development (Ockelmann 1958, 1962).

REMARKS: The genus has long been considered totally deposit feeding, as is *M. calcarea* (Reid and Reid 1969), but this is not universal, Braefield and Newell (1961) showed *M. balthica* may also function as a filter feeder. Four species are represented in the collection; however, there is a high probability that further exploration, particularly in sheltered nearshore environments, will yield additional species. As an aid to those using this text to identify macomids from the study area, the most likely additional species are listed below. Identifications of these and other species may be found in Coan (1971). I am most grateful to E.V. Coan for confirming my identifications.

Macoma brota Dall 1916b. This was proposed as a new name for *Tellina edentula* Broderip and Sowerby 1829 [not Spengler 1798]. It is widely distributed in the Chukchi and Bering seas and

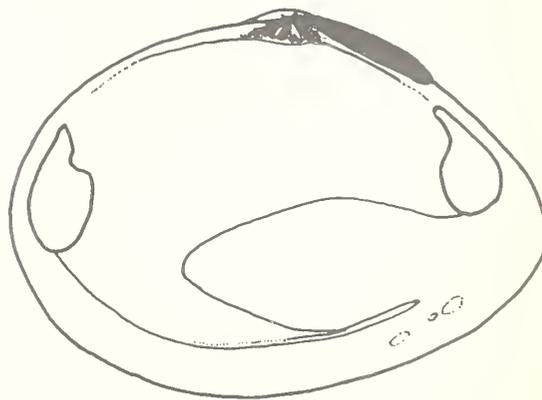


FIGURE 78. Interior of right valve of *Macoma calcarea* (Gmelin).

south to Washington State. In the North Atlantic it has been reported living from several locations in the Canadian Arctic Archipelago and in Bathurst Inlet. Though it is well represented in the Arctic Pleistocene, it is rare in the Beaufort Sea and probably may not occur east of Dease Inlet (USNM 363169).

Macoma crassula (Deshayes 1855). This is the *Macoma torelli* (Jensen [Steenstrup MS] 1905), a typically high Arctic species discussed and synonymized by Coan (1971). It occurs at Point Barrow and Nunivak Island, and Wacasey (1974) reported it from Mackenzie Bay and Wagner (1977) from the eastern Beaufort Sea. The distribution is probably panarctic.

Macoma lama Bartsch 1929. Together with its synonym, *M. planiuscula* Grant and Gale 1931, is represented in the northeastern Pacific, Bering and Chukchi seas, extending eastward to Point Barrow. The USNM contains material from Dease Inlet (USNM 363166) to the east of Point Barrow, so the species may extend some way into the Beaufort Sea.

Macoma middendorffi Dall 1884. This is the *Tellina edentula* auctt. not Broderip and Sowerby 1829. It is distributed throughout the Bering and Chukchi seas and along the Siberian coast. It has been collected at Point Barrow (USNM 207073), but is not recorded by MacGinitie (1959).

Macoma obliqua (Sowerby 1817). This is not *Tellina obliqua* Wood 1815 but ICZN Opinion 948:1971 (application by Coan and Sealey 1969) conserves the junior name. Coan (1969) showed that the common North Pacific *Tellina incongrua* (von Martens

1865) is conspecific with the British Coralline Crag (Pliocene) fossil *Tellina obliqua* Sowerby 1817, presently extinct in the North Atlantic. The species occurs throughout the Bering Sea and Japan and south along the American coast to Washington State. It was recorded living from Point Barrow by MacGinitie (1959), who found a single specimen, and Coan (1969) referred to material in the USNM (207073) from the same locality. Though distributed throughout the Pleistocene facies of Arctic America, it has not been found living in the Beaufort Sea.

Subgenus *Macoma* s. str.

Macoma (Macoma) calcarea (Gmelin 1791)

Figures 79, 80

Tellina calcarea Chemnitz 1782:140, pl.13, f.136 [not binom.]; Gmelin 1791:3236.

Tellina (Macoma) calcarea (of "Chemnitz"), Jensen 1905:342, f.2a, b. *Macoma calcarea* (Gmelin). Oldroyd 1925:173 [not pl.42, f.5]; Soot-Ryen 1932:15, pl.2, f.1-6; Filatova 1948:440, pl.111, f.2; Scarlato 1955:196, pl.53, f.1; Dunnill and Ellis 1969:10, f.4, 1a-d, 9e; Afshar 1969:78, pl.30, f.8-12.

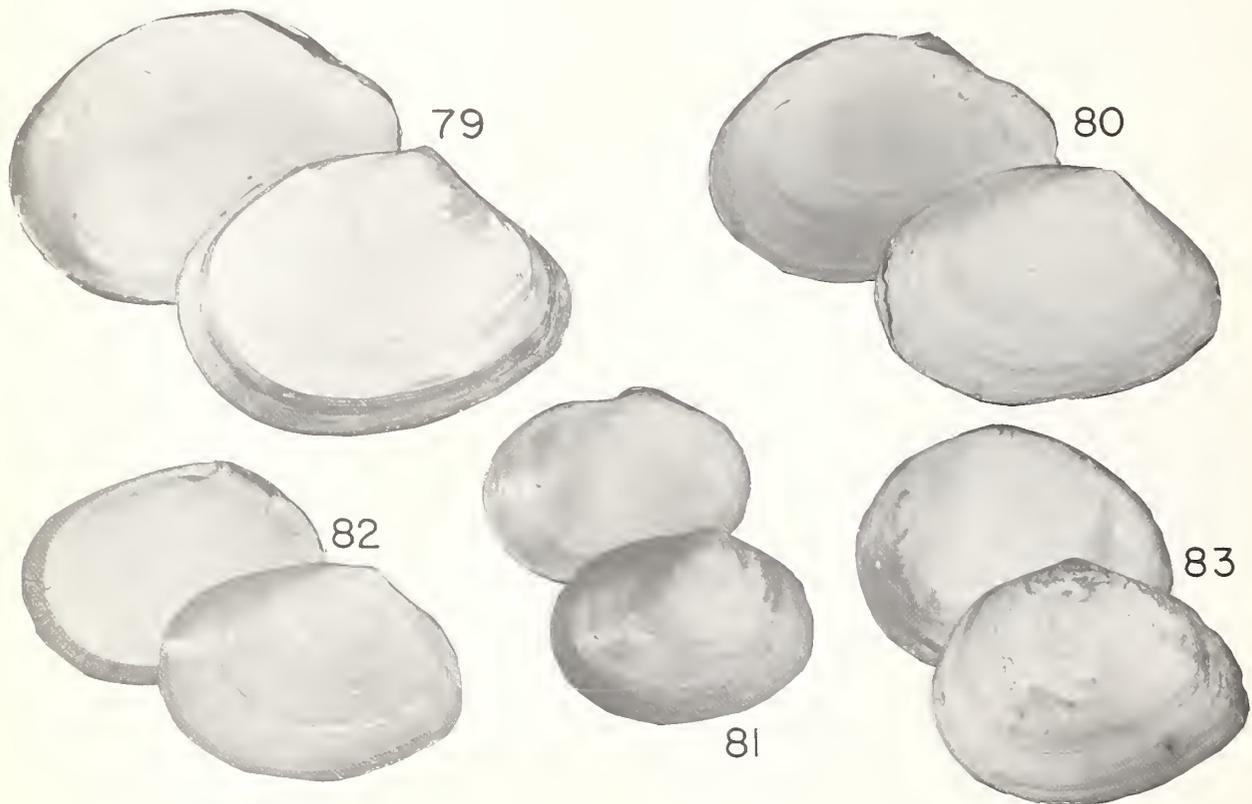
Macoma (Macoma) calcarea (Gmelin), Coan 1971:20, pl.3, f.20, pl.4, f.21-24, pl.5, f.25, text-fig. 9.

Macoma calcarea obliqua Soot-Ryen 1932:15, pl.2, f.4a, b [not *Tellina obliqua* Sowerby, 1817].

Macoma calcarea longisinuata Soot-Ryen 1932:17, pl.2, f.1, 3.

Macoma sitkana Dall 1900:307, 323, pl.4, f.6, 7.

DESCRIPTION: Shell ovate, posterior elongated, flexed to the right. Length to 54 mm, shell thin chalky. Surface smooth with incremental striae and growth checks. Periostracum thin,



FIGURES 79-83. 79, *Macoma (Macoma) calcarea* (Gmelin), length 37.2 mm; 80, *M. calcarea*, length 22.6 mm; 81, *Macoma (Macoma) loveni* Jensen, length 13.3 mm; 82, *Macoma (Macoma) moesta alaskana* Dall, length 20.7 mm; 83, *Macoma balthica* (Linné) length 17.6 mm.

dark grey, dehiscent, generally absent except for marginal band. Umbones not prominent, beaks usually eroded. Interior chalky to porcelaneous, shell margins smooth. Hinge weak, two small cardinal teeth in each valve. Ligament strong and elongate, partly buried in escutcheon. Adductor muscle scars subequal, irregular. Pallial line not distinct, not connecting adductor muscle scars. Pallial sinus large, partly conjoined with pallial line, of different size in each valve.

COLLECTION: 120 specimens and many single valves were found at 54 stations between 10 and 360 m.

COMPARISONS: Although this is a polymorphic species, the produced and rostrated posterior, with its characteristic flexure and weak dentition distinguish *M. calcarea*. Stocks of this species in the Arctic and Atlantic appear fairly stable, but in the Bering and Pacific areas there is a degree of plasticity. Dunnill and Coan (1968) showed that at least two species were included in northeastern Pacific populations previously assumed to be *M. calcarea*.

RECORDS: *Miocene*—Arnold and Hannibal 1913:590 (Oregon); Ilyina 1963:8, pl.24, f.8, pl.27, f.4, pl.49, f.2 (Kamchatka). *Pliocene*—Arnold and Hannibal 1913:590 (California); McNeil et al. 1943:75, pl.15, f.19 (Aleutian Islands); Petrov 1966:228, pl.19, f.3–11 (Siberia); Zhidhova et al. 1968:118, pl.11, f.4–6 (Sakhalin Islands); Zhidhova et al. 1972:132, pl.18, f.16 (Kuril Islands). *Pleistocene*—Wood 1857:229 (Britain); Arnold and Hannibal 1913:590 (Washington); Newcombe 1914:107 (British Columbia); Meek 1923:414 (Alaska); Grant and Gale 1931:369 (California); Slodkevich 1938:1273, pl.94, f.1–3 (Chukotsk Peninsula); Wagner 1959:5 (British Columbia); Richards 1962:66, pl.10, f.17–19 (Labrador to South Carolina); Merklin et al. 1962:41, pl.7, f.5–10 (Chukotsk Peninsula); Wagner 1970:42, pl.4, f.5a, b (Eastern Canada); Hopkins et al. 1972:126 (St. Lawrence Island); Troitskiy 1974:265 (Siberia). *Recent*—Møller 1842:120 (Greenland); D'Urban 1880:253 (Barents Sea); Hägg 1904:46 (Greenland and Spitzbergen); Dautzenberg and Fischer 1910:24 (Novaya Zemlya); Odhner 1915:111 (Greenland) Massy 1930:270 (North Atlantic); Johnson 1934:52 (Greenland to Long Island Sound); Slodkevich 1938:1273, pl.94, f.1–3 (Northern Japan); Soot-Ryen 1939:16 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Filatova 1957b:56 (Arctic); Filatova and Zenkevich 1957:64 (Kara Sea); Ockelmann 1958:125, pl.2, f.10 (Greenland); MacGinitie 1959:181, pl.24, f.5–7, pl.26, f.6–9 (Point Barrow, Alaska); Ellis 1960:39 (Baffin Island and Greenland); Clarke 1962:67 (Arctic); Hulsemann 1962:72 (Beaufort Sea); Richards 1962:66, pl.10, f.17–19 (Arctic to New Jersey); Kuznetsov 1963:66 (Kamchatka); McLaughlin 1963:27 (Bering Sea); Filatova and Barsanova 1964:31 (Bering Sea); Allen 1965:983 (Northwestern Atlantic); Sparks and Pereyra 1966:834 (Chukchi Sea); Okutani 1966:12 (Northern Japan); Golikov and Scarlato 1967:112, f.104 (Sea of Japan); Dunnill and Coan 1968:12 (British Columbia); Petersen 1968:53 (Faroe Islands); Ishikawa 1969:49 (Northern Japan); Bernard 1970:89 (British Columbia); Kuroda et al. 1971:457, pl.100, f.9 (Japan); Okutani 1972:96 (Northern Japan); Clarke 1974:11 (Baffin Bay); Scarlato and Ivanova 1974:311 (Kuril Islands); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. This species is found throughout the North Atlantic and Pacific. It is well represented in the Canadian Arctic Archipelago, Hudson Bay and south to New Jersey, and across the Atlantic from Greenland to Iceland, the Faroe Islands, and Britain. It may occur as far south as the Azores in deep water. The range includes the Bering and Okhotsk seas to Northern Japan, and along the coast of America as far as central Washington.

REMARKS: The species probably originated during the late Miocene in the North Pacific and is first recorded on the Atlantic side in the Pleistocene (Wood 1855), under the synonym *Tellina lata* Gmelin 1791.

Macoma (Macoma) loveni (Jensen [Steenstrup MS] 1905)

Figure 81

Tellina (Macoma) loveni Jensen (Steenstrup MS) 1905:45, pl.1, f.5a–h.
Macoma loveni (Jensen), Filatova 1948:440, pl.111, f.6.
Macoma (Macoma) loveni (Jensen), Coan 1971:31, pl.8, f.42, 43, text-fig. 19.

DESCRIPTION: Shell oval, inflated, thin and fragile. Maximum length 20 mm, usually smaller. Anterior rounded, posterior slightly truncated. Surface smooth with occasional checkmarks. Periostracum thin, light-brown with an iridescent sheen, dehiscent. Interior polished, shell margins smooth. Hinge weak, with two minute cardinals in each valve. Ligament short, projecting substantially on the exterior. Adductor muscle scars nearly equal. Pallial line deeply impressed. Pallial sinus deep, larger in the left valve.

COMPARISONS: This is the most inflated of Arctic macomids and is easily separable from *M. moesta* (Deshayes) on that basis, and from *M. calcarea* (Gmelin) by the lack of a posterior rostration, and the pallial sinus of the left valve is only slightly confluent with the pallial line.

COLLECTION: The species only occurred at one station (70°34.8'N, 144°23.1'W) in 71 m where 12 specimens were collected.

RECORDS: *Recent*—Soot-Ryen 1938:16, pl.1, f.10 (Franz Josef Land); Gorbunov 1946a:46 (Eurasian Arctic); Filatova 1957b:56 (Arctic); Ockelmann 1958:132, pl.2, f.11 (Greenland); Soot-Ryen 1958:25 (Greenland); Filatova and Barsanova 1964:31 (Bering Sea); Kuznetsov 1963:114 (Kamchatka); Golikov and Scarlato 1967:125, f.108 (Sea of Japan); Clarke 1974:11 (Baffin Bay); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Possibly panarctic in distribution. This species occurs from Baffin Island and Greenland across the Atlantic to the Kara Sea. It is present throughout the Bering Sea, extending to northern Japan and Siberia and has been collected from Point Barrow, Alaska.

REMARKS: It is with some doubt that I assign material to this species, but general characters conform to Greenland specimens. Coan (1971) showed that *M. inflata* Dawson 1872 is not a synonym.

Macoma (Macoma) moesta alaskana Dall 1900

Figure 82

Tellina moesta Deshayes 1855:361.
Tellina (Macoma) moesta (Deshayes), Jensen 1905:346, f.4a–c in part.
Macoma moesta (Deshayes), Filatova 1948:440, pl.111, f.4.
Macoma alaskana Dall 1900b:309, pl.3, f.5.
Macoma (Macoma) moesta alaskana (Dall), Coan 1971:29, pl.7, f.38, text-fig. 17.
Macoma krausei Dall 1900:322, pl.4, f.8 [in part *Tellina lutea* auctt. not Gray 1828].
Macoma oneilli Dall 1919:20A, pl.2, f.1.

DESCRIPTION: Shell thin, compressed, oval with rounded anterior and broadly truncated posterior. Maximum length 40 mm. Surface smooth, sometimes with minute concentric striae and growth checkmarks. Periostracum greenish-grey to yellow, polished and adherent. Umbones not prominent, beaks usually eroded. Interior chalky, more rarely polished. Shell margins smooth. Hinge poorly developed, two small cardinals in each valve, the anterior left cardinal bifid. Ligament external, on well developed nymph. Adductor muscle scars nearly equal. Pallial

line not deeply impressed. Pallial sinus of left valve largest.

COMPARISONS: This is the most oval and compressed of Arctic macomids and is easily separated from other species.

COLLECTION: This species occurred at 24 stations between 10–64 m for a total of 74 specimens.

RECORDS: *Pleistocene*—Smith 1919:138 (British Columbia). *Recent*—Odner 1915:112 (Spitzbergen); Grant and Gale 1931:370, pl. 20, f.3 (Arctic and Bering seas); Kuroda and Habe 1952:24 (Northern Japan); Filatova 1957b:56 (Eurasian Arctic); Filatova and Zenkevich 1957:67 (Kara Sea); Ockelmann 1958:129, pl.2, f.13 (Greenland); MacGinitie 1959:182, pl.21, f.1–3, pl.23, f.10, pl.24, f.1–3 (Point Barrow, Alaska); Ellis 1960:39 (Baffin Island); Hulsemann 1962:73 (Beaufort Sea); Kotaka 1962:153, pl.35, f.20, 21 (Okhotsk Sea); Kuznetsov 1963:107 (Kamchatka); McLaughlin 1963:28 (Bering Sea); Filatova and Barsanova 1964:20 (Bering Sea); Sparks and Pereyra 1966:834 (Chukchi Sea); Habe and Igarashi 1967:41 (Northern Japan); Clarke 1974:11 (Baffin Bay); Wacasey 1974:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. This species is found from the Canadian Arctic Archipelago to Greenland and east to Spitzbergen and the Kara Sea. It is abundant throughout shallow water of the Bering and Okhotsk seas to Northern Japan, and along the American coast as far south as Washington state.

REMARKS: Coan (1971) retained Dall's *M. alaskana* as a subspecies of *M. moesta* for specimens from Shelikof Strait and south to Puget Sound. He considered the nomenclatural question not solved and commented on the continuous nature of the variation. I am of the opinion that material in the OSU collection is similar to specimens from British Columbia, rather than the very compressed form of *M. moesta* from the north Atlantic and Arctic, so favor the use of Dall's taxon as a subspecies. However, a critical comparison, based on an adequate series of representatives is required, as the compressed form is widely distributed in the Arctic, the Bering Sea and along the Alaska Peninsula.

Macoma balthica (Linné 1758)

Figure 83

Tellina balthica Linné 1758:677; Gmelin 1791:3241; Dillwyn 1817:102.

Macoma balthica (Linné), G. Sars 1878:72; Oldroyd 1925:172, pl.44, f.1, 2, 9; Scarlato 1935:196, pl.52, f.12; Golikov and Scarlato 1967:126, f.109 [as "*baltica*"]; Coan 1971:44, pl.11, f.65, pl.12, f.66–69, text-fig. 30.

Tellina inconspicua Broderip and Sowerby 1829:363.

Macoma inconspicua (Broderip and Sowerby), Dunnill and Ellis 1969:20, f.6, 9.

DESCRIPTION: Shell ovate, irregularly inflated, anterior rounded, posterior produced. Maximum length 35 mm, usually not more than 20 mm. Surface smooth, chalky, with concentric checkmarks. The shell may be white or stained pink or yellow. Periostracum thin, brownish-red to grey, thrown into numerous small concentric wrinkles, strongly adherent, but usually eroded from most of the disc. Interior of shell dull, colored white to pink, shell margins smooth. Hinge weak, with two cardinal teeth in each valve, the left anterior and right posterior tooth bifid. Adductor muscle scars irregular. Pallial line deeply impressed. Pallial sinus large, confluent with pallial line for most of its length.

COMPARISONS: This species is readily distinguishable from other northern macomids by the large pallial sinus, of nearly equal size in each valve, which fuses with the pallial line near its anterior end. The tendency of the shell to pink or yellow coloration is unique, the lack of a lateral flexure of the posterior end is a further distinguishing character.

COLLECTION: The species is represented by nine specimens and some single values collected from six stations in 10–270 m.

RECORDS: *Pleistocene*—Henderson 1927:1 (Washington); Merklin et al. 1962:42, pl.8, f.1 (Chukotsk Peninsula); Richards 1962:66, pl.10, f.15, 16 (Labrador to South Carolina); Spaink and Norton 1967:39, pl.2, f.6a–e (Holland); Wagner 1970:41, pl.4, f.3a, b (Eastern Canada); Hopkins et al. 1972:127 (St. Lawrence Island). *Recent*—Krause 1885:36 (Bering Sea); Peterson 1888:147 (Denmark); Hägg 1904:45 (Spitzbergen) Yocum and Edge 1929:50 (Oregon); Massy 1930:270 (North Atlantic); Grant and Gale 1931:371, pl.4, f.6a, b (Arctic to California); Mesjatsev 1931:103 (Barents Sea); Johnson 1934:52 (Arctic Ocean to Georgia); Kuroda and Habe 1952:24 (Northern Japan); Eyerdam 1960:44 (Kodiak Island, Alaska); Troitskiy 1961:449 (Laptev Sea); Merklin et al. 1962:42, pl.8, f.1 (Chukotsk Peninsula); Richards 1962:66, pl.10, f.15, 16 (Arctic to Georgia); Filatova and Neiman 1963:1038 (Bering Sea); Allen 1965:983 (Northwestern Atlantic); Segerstrale 1965:195 (Baltic Sea); Golikov and Scarlato 1967:126 (Northern Japan); Petersen 1968:53 (Faroe Islands); Bernard 1970:89 (British Columbia); Scarlato 1974:104 (Bay of Peter the Great); Wacasey 1974:24 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Circumboreal in distribution, *M. balthica* is abundant in the North Sea, including England, Norway and Denmark. It is present in the waters of the Faroe Islands and north to Iceland, but has not been recorded from Greenland. On the Atlantic American coast it occurs from Labrador to South Carolina. It is present in the Bering and Okhotsk seas to Japan, and along the American coast to Monterey, California.

REMARKS: While this species has invaded the Arctic coasts adjacent to the Atlantic and Pacific oceans, it cannot be counted a true high Arctic member. This may, in part, be a reflection of its preference for low salinity near-brackish environments. Mokievskii (1960) lists this species from the Sea of Japan as *M. baltica solidula* (Pultney 1799). Coan (1971) gives a partial synonymy, including the Japanese *M. takahokoensis* Yamamoto and Habe 1959.

Family VENERIDAE Rafinesque, 1815

It is intriguing that such a large and cosmopolitan family should be so poorly represented in the Arctic, a situation first noted by Filatova (1962). Soot-Ryen (1932) listed four genera from the Arctic (*Liocyma*, *Turtonia*, *Saxidomus*, and *Paphia*), only the first is truly Arctic. *Turtonia* is a boreal genus, extending as far north as the west coast of Greenland, and the latter two generic identifications are certainly in error.

Genus *Liocyma* Dall 1870

Figure 84

Type species (original designation): *Venus fluctuosa* Gould 1841: Recent. North Atlantic.

DESCRIPTION: Shell ovate to trigonate, sometimes elongate. Surface with obscure concentric lirae, or large concentric ribs. Periostracum thin, polished, adherent. Interior porcelaneous. Shell margins smooth. Hinge well developed, three cardinal teeth in each valve. Ligament external. Adductor muscle scars subequal. Pallial line uniform. Pallial sinus small and rounded.

RANGE: Pleistocene to Recent. Recent distribution limited to north boreal Atlantic and Pacific Arctic. The genus is a shallow infaunal filter feeder, typically in sandy substrates in shallow water.

DEVELOPMENT: Thorsen (1936) has shown the ova of *L. fluctuosa* (Gould 1841) to be very large, indicating lecithotrophic

development.

REMARKS: This is the only venerid clam found in the high Arctic. In common with Arctic bivalves species it demonstrates wide morphometric variability. Following MacGinitie (1959) the current trend is to recognize a single species complex. However, after examination of all type material, I consider that two species are represented in the collection.

Liocyma fluctuosa (Gould 1841)

Figure 85

Venus fluctuosa Gould 1838:107 [nom. nud.]; Gould 1841:87, f.50.

Tapes fluctuosa (Gould), Deshayes 1853:176.

Liocyma fluctuosa (Gould), Dall 1874:249; Filatova 1948:441, pl.112, f.1; Scarlato 1955:193, pl.57, f.14; Fischer-Piette and Metivier 1971:74, pl.15, f.6, 7.

Gomphina (*Liocyma*) *fluctuosa* (Gould), Ockelmann 1958:123, pl.2, f.9.

Venus astartoides Middendorff (Beck MS) 1849:252, pl.20, f.5-13.

Liocyma beckii Dall 1870:257.

Liocyma scammoni Dall 1871:145, pl.14, f.9.

Liocyma schefferi Bartsch and Rehder 1939:111, pl.8, f.1a, b.

DESCRIPTION: Shell ovate to trigonal, compressed to inflated. Maximum length 33 mm, usually less than 15 mm. Surface with numerous small concentric ridges. Periostracum varnished, thin, grey to yellowish, strongly adherent. Umbones prominent, beaks frequently eroded. Interior porcelaneous, more

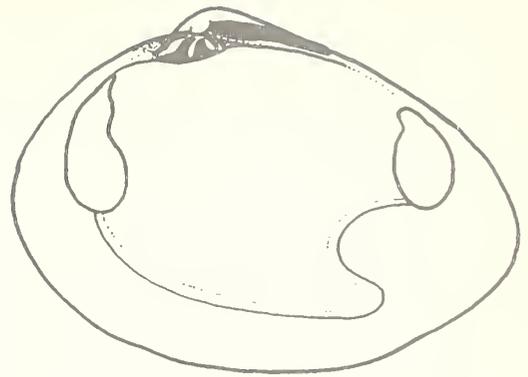
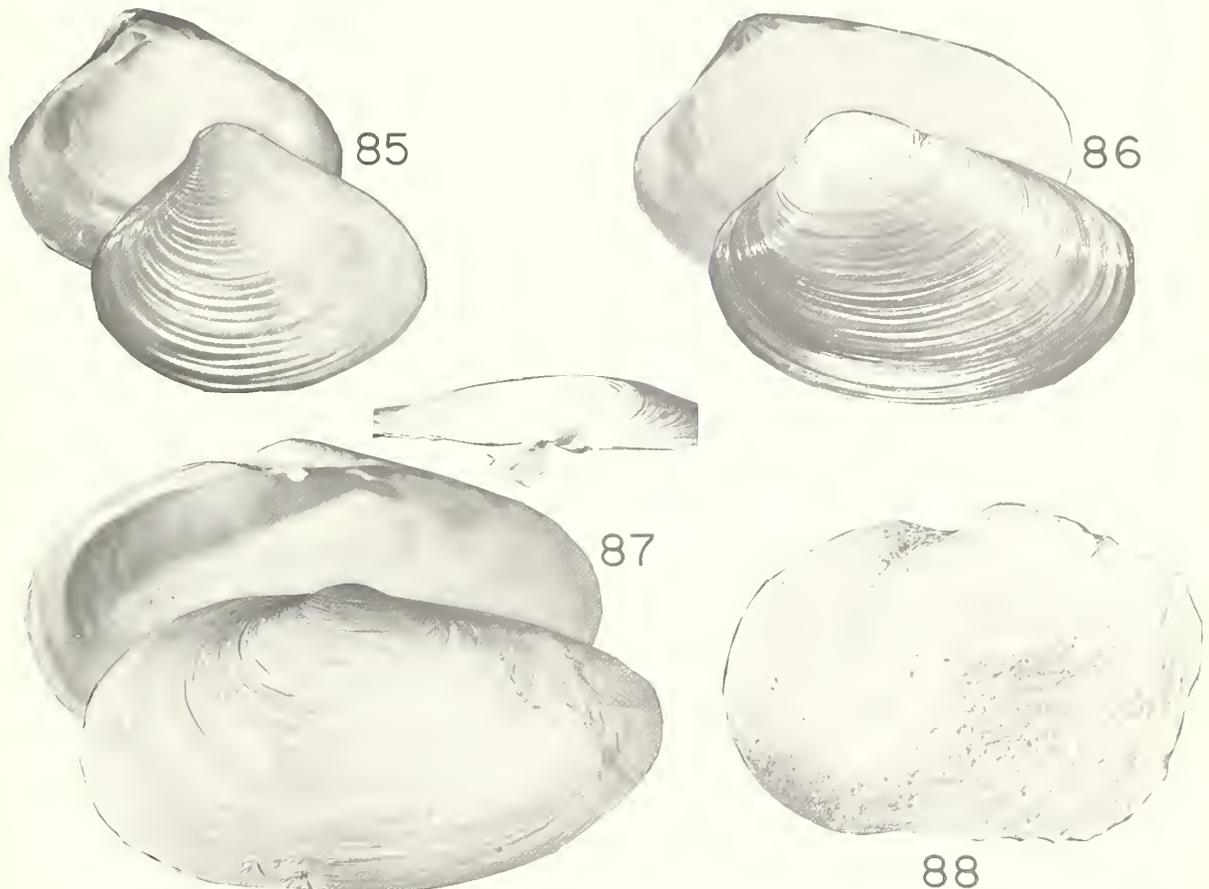


FIGURE 84. Interior of right valve of *Liocyma fluctuosa* (Gould).

rarely chalky. Shell margins smooth. Hinge not strong, three cardinal teeth in each valve, the central one bifid, others lamellar. Ligament external. Adductor muscle scars subequal. Pallial line irregular. Pallial sinus small, sharply angulate.

COMPARISONS: This is a highly variable species, but is easily separated from *L. viridis* Dall 1871 by the more ponderous dentition, deeper pallial sinus and thinner periostracum.



FIGURES 85-88. 85, *Liocyma fluctuosa* (Gould) length 10.6 mm; 86, *Liocyma viridis* Dall, length 28.8 mm; 87, *Mya* (*Mya*) *pseudoarenaria* Schlesch, length 41.7 mm; inset chondrophore of left hinge; 88, *Mya* (*Mya*) *truncata* Linné, fossil ?, length 31.6 mm.

COLLECTION: This species is represented by 154 specimens and numerous single valves collected from 34 stations between 10 and 101 m.

RECORDS: *Pliocene*—Wood 1874:144, pl.9, f.8 (Britain); Khomemko 1931:76, pl.15, f.3–5 (Kamchatka); Slodkevich 1938:147, pl.86, f.4, 5, 6, a, 7, 8 (Kamchatka); Ilyina 1963:78, pl.18, f.7, pl.26, f.10, 11a (Kamchatka); Petrov 1966:225, pl.18, f.6–16 (Chukotsk Peninsula). *Pleistocene*—Knipovitsch 1900:379 (Spitzbergen); Merklin et al. 1962:40, pl.7, f.1–4 (Chukotsk Peninsula); Allison 1973:20 (Aleutian Islands). *Recent*—Gould 1841:87, f.50 (Massachusetts); Crosse 1877:123 (Bering Sea); Leche 1878:14 (Novaya Zemlya); Leche 1883:440 (Kara Sea); Krause 1885:32 (Bering Sea); Stuxberg 1886:143 (Novaya Zemlya); Melvill and Standen 1900:5 (Franz Josef Land); Hägg 1904:49 (Greenland); Jensen 1905:309 (Greenland); Dautzenberg and Fischer 1910:20 (Novaya Zemlya); Odhner 1910:20 (Iceland); Odhner 1915:114 (Greenland); Grant and Gale 1931:336 (Arctic); Mesjatsev 1931:105 (Barents Sea); Johnson 1934:49 (Greenland to Nova Scotia); Soot-Ryen 1939:16, pl.1, f.8 (Franz Josef Land); Madsen 1949:67 (Iceland); Kuroda and Habe 1952:23 (Northern Japan); Filatova 1957b:55 (Eurasian Arctic); Ockelmann 1958:123, pl.2, f.9 (Greenland); Soot-Ryen 1958:23 (Greenland); MacGinitie 1959:177, pl.23, f.1–8 (Point Barrow, Alaska); Kotaka 1962:152, pl.35, f.14–17 (Okhotsk Sea); Hulsemann 1962:72 (Beaufort Sea); Kuznetsov 1963:83 (Kamchatka); McLaughlin 1963:27 (Bering Sea); Filatova and Barsanova 1964:20 (Bering Sea); Sparks and Pereyra 1966:834 (Chukchi Sea); Golikov and Scarlato 1967:110, f.92 (Sea of Japan); Ishikawa 1968:49, pl.3, f.3 (Northern Japan); Bernard 1970:89 (British Columbia); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal in distribution. This species is sporadically abundant across the North Atlantic from the Canadian Arctic Archipelago and Greenland to Iceland and Norway. On the American Atlantic seaboard it occurs throughout Hudson Bay and Labrador to Nova Scotia. The Pacific distribution includes the Bering and Okhotsk seas to Northern Japan and along the American coast as far south as Washington state. The species has been recorded along the Eurasian Arctic coast to Siberia and the Chukchi Sea.

REMARKS: MacGinitie considered all boreal and Arctic species proposed in the literature to be merely variants of *L. fluctuosa*. There is no doubt that a very variable group is involved, neither the height or spacing of the concentric ribs, nor the shell outline, form a basis for nomenclature, but I conclude that at least two species are involved, and have assigned the various junior synonyms to these, basing my opinion on hinge dentition structure, appearance of the periostracum, and prolongation of the shell posterior. Johnson (1934) listed *L. fluctuosa brunnea* Dall 1902 from the Gulf of St. Lawrence. La Rocque (1953) repeated the name and cited the Proceedings of the United States National Museum, volume 24, page 378. This reference is not correct, and Boss et al. (1968) do not include this species among those proposed by Dall. I have been unable to locate material in the USNM that may support a manuscript name, and do not believe it appears as a *nomen nudum* in Dall's writings. It may best be considered a *nomen nudum* of Johnson (1934).

Liocyma viridis Dall 1871

Figure 86

Liocyma viridis Dall 1871:146; Oldroyd 1925:159, pl.1, f.3; Fischer-Piette and Metivier 1971:76.

Liocyma aniwana Dall 1907:172; Fischer-Piette and Metivier 1971:76.

Liocyma subanivana Khomenko 1931:78, pl.5, f.6–8.

Liocyma hokkaidoensis Habe 1953:179, f.412–414.

DESCRIPTION: Shell thin, moderately inflated, posterior elongate, almost rostrate. Maximum length 25 mm. Surface with numerous sharp concentric ridges. Periostracum brilliantly var-

nished, color grey to greenish-yellow. Umbones not prominent, beaks eroded. Interior of shell with polished margin, but area between muscle scars and pallial line is chalky and pustulate. Shell margins smooth, usually with fringe of periostracum extending from shell exterior. Hinge weak, each valve with three diverging cardinal teeth, the central tooth bifid, others lamellar. Ligament external, seated on a small nymph. Adductor muscle scars subequal. Pallial line irregular. Pallial sinus very small, apex forming a right angle.

COMPARISONS: The species may only be confused with *L. fluctuosa* (Gould 1841), especially the attenuated variant, but the dentition in this species is nearly equal, while in *L. viridis* the central tooth is the largest, and the posterior cardinal tooth of the right valve is vestigial. Other distinguishing characters are the pustulate interior of the shell and the shallow pallial sinus, forming a more obtuse angle than that of *L. fluctuosa*.

COLLECTION: Five specimens and four valves were collected at two stations in 34 and 64 m.

RECORDS: *Recent*—Crosse 1877:123 (Bering Sea); Kuroda and Habe 1952:23 (Northern Japan); Eyerdam 1960:44 (Aleutian Islands).

DISTRIBUTION: The center of distribution is the Bering Sea, with sporadic occurrences along the Arctic Alaskan coast to Point Barrow and the western Beaufort Sea. The species has been collected in the Sea of Okhotsk, south to Hokkaido, Japan.

REMARKS: I consider *L. aniwana* Dall 1907 from Sakhalin Island to be identical to *L. subanivana* Khomenko 1931, from the Pleistocene of that island and that both prove to be synonyms of *L. viridis*. The Japanese representative was named *L. hokkaidoensis* by Habe 1952.

Family MYIDAE Lamarck 1809

Genus *Mya* Linné 1758

Figure 89

Type species (subsequent designation Children 1822): *Mya truncata* Linné 1758. *Recent*. North Atlantic.

DESCRIPTION: Shell ovate to elongate, chalky. Surface unsculptured, usually with irregular incremental lirae and growth checkmarks. Periostracum thin, adherent. Interior chalky to por-

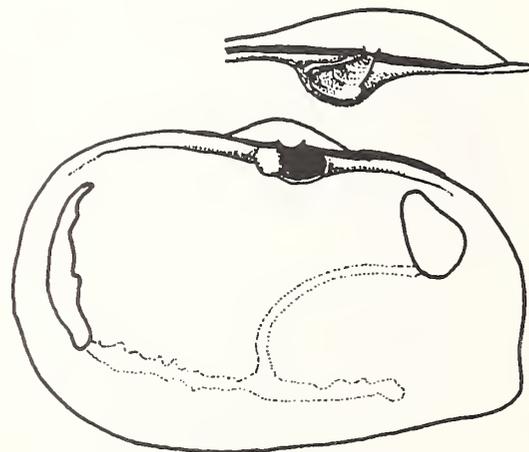


FIGURE 89. Interior of right valve and hinge of left valve of *Mya truncata* (Linné).

celaneous, shell margins smooth, valves closing with a posterior and anterior gape. Hinge edentulous, with a large projecting chondrophore in the left valve, projecting obliquely across a recessed ligamental cavity in the right valve. Posterior adductor muscle scar small, anterior scar elongate. Pallial line broad, rather irregular. Pallial sinus well developed.

RANGE: Oligocene to Recent. Recent distribution northern boreal and Arctic, in muddy and sandy substrates generally in less than 50 m. The long siphons enable the genus to be a deeply infaunal filter feeder.

DEVELOPMENT: Thorsen (1936) and others have shown that all species examined produce small eggs that undergo a prolonged planktonic development phase.

REMARKS: Although the genus is distributed in the Arctic, it is poorly represented in the present collections, both species collected were long dead, possibly fossil. This may be attributed to insufficient penetration of the substrate by the collecting apparatus to capture large deep burrowers. Wagner (1977) recorded *Mya arenaria* Linné 1758 from the eastern Beaufort Sea.

Subgenus *Mya* s. str.

Mya (Mya) pseudoarenaria Schlesch 1931

Figure 87

Mya intermedia Dall 1898:857 [in part; not *Mya intermedia* Sowerby 1814]; Oldroyd 1925:199, pl.15, f.5.

Mya truncata forma *ovata* Jensen 1900:139, f.3, 4 [not *Mya ovata* Donovan 1802]; Laursen 1966:406, f.2.

Mya pseudoarenaria Schlesch 1931:136, pl.13, f.10-12.

Mya (Mya) pseudoarenaria Schlesch, MacNeil 1965:37, pl.7, f.9-11, 13, 14, pl.9, f.4; Strauch 1972:141, pl.10, f.10.

DESCRIPTION: Shell ovate to elongate, inflated, maximum length 95 mm. Anterior end rounded, inflated, posterior produced, more compressed. Siphonal gape large, anterior gape small. Surface chalky, unornamented except for small irregular concentric striae and coarse growth checkmarks. Periostracum thin, dehiscent, folded and wrinkled and connected to the siphonal sheath on the posterior part of the shell. Interior chalky, sometimes polished in young specimens. Hinge edentulous with large projecting subtrigonal chondrophore in the left valve, and a sunken subumbonal pit-like chondrophore in the right valve. Ligament internal, inclined to the right so that it lies entirely within that valve. Anterior adductor muscle scar narrow and elongate, posterior scar smaller and subcircular. Pallial line wide and irregular. Pallial sinus large, anterior margin rounded, ventrally confluent with pallial line.

COMPARISONS: Externally, this species most closely resembles *M. arenaria* Linné 1758, but is separated by the nearly trigonal chondrophore. Further, *M. arenaria* does not occur in the Arctic. Internally, *M. pseudoarenaria* is close to *M. truncata* Linné 1758, but the pallial sinus is proportionately larger, and the chondrophore outline a right angled triangle, rather than the equilateral triangle of the latter species.

COLLECTION: One dead specimen and three valves were collected at one station in 64 m. The entire specimen was not articulated, but retained part of the ligament. These may represent fossil or transported material.

RECORDS: *Pliocene*—Merklin et al. 1962:48, pl.10, f.5-8 (Chukotsk Peninsula); Petrov 1966:237, pl.21, f.3-6, pl.22, f.1-9 (Chukotsk Peninsula). *Pleistocene*—Dall 1898:857 (Alaska); Jensen 1900:139, f.3, 4 (Greenland); Crickmay 1924:206 (British Columbia); Filatova 1948:442 (Arctic); MacNeil 1965:38 (Britain); Wagner 1970:43, pl.5, f.2a-c

(Eastern Canada). *Recent*—Odhner 1915:123 (Spitzbergen); Madsen 1949:76 (Iceland); Soot-Ryen 1951:3 (Norway); MacGinitie 1959:186, pl.19, f.7, pl.25, f.4 (Point Barrow, Alaska); McLaughlin 1963:28 (Bering Sea); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Probably panarctic. This species is found from the Canadian Arctic Archipelago to Greenland, Iceland, Spitzbergen and Norway. It has not been recorded from Hudson Bay or the Atlantic coast of America. It is present in the Arctic Alaskan coast, the Chukchi Sea and the Siberia Sea. It extends into Norton Sound in the northern Bering Sea.

REMARKS: The distinctness of the Arctic species was not recognized for a long time, the majority of authors referring it to *M. arenaria* or *M. truncata* and sometimes *M. japonica* Jay 1856; the situation is so confused that early bibliographic records are best discarded. Dall (1898) recognized the intermediate morphology of Arctic species and proposed *M. intermedia*, but the taxon may only be accepted in part as it included southern Bering Sea and Gulf of Alaska material. Furthermore, it is preoccupied by Sowerby 1814 for a British Eocene fossil. Jensen (1900) saw the close connection to *M. truncata* and proposed the form name *ovata* to denote the *M. arenaria*-like outline. The diagnosis is accurate but unfortunately the name is preoccupied by Donovan (1802), so Schlesch (1931) proposed a substitute name. Much remains to be done to untangle the systematic position of this taxon. It is possible that an earlier name will be recognized; for instance, the British *M. ovalis* Turton 1822 which MacGillivray (1843) considered to be related to *M. truncata*.

Mya (Mya) truncata Linné 1758

Figure 88

Mya truncata Linné 1758:670; Dillwyn 1817:42; Oldroyd 1925:197, pl.10, f.4; Filatova 1948:442, pl.112, f.4; Petrov 1966:238, pl.21, f.7, pl.23, f.1-9.

Mya (Mya) truncata (Linné), MacNeil 1965:38, pl.8, f.1-12, pl.9, f.1-3, 5-20; Strauch 1972:138, pl.10, f.5, 7, 8.

Mya praecisa Gould 1850:215.

Mya truncata uddevalensis Forbes 1846:407; MacGinitie 1959:184, pl.25, f.1-3.

DESCRIPTION: Shell with rounded anterior and truncate posterior with large siphonal gape. Length to 90 mm, generally less than 50 mm. Shell thin to ponderous, inflated, frequently distorted. Surface with irregular incremental striae and coarse growth checkmarks. Periostracum thin, grey-brown, dehiscent, thicker in posterior regions where it merges with the siphonal sheath. Umbones prominent, beaks opisthogyrate. Interior chalky, polished and porcelaneous in juvenile specimens. Hinge edentulous, with large projecting chondrophore in left valve, opposed to an inset subumbonal pit-like chondrophore in the right valve. Ligament internal. Anterior adductor muscle scar elongate, posterior scar nearly circular. Pallial line irregular, not continuous. Pallial sinus wide, not deep, ventral margin confluent with the pallial line.

COMPARISONS: This species is readily distinguished by the abruptly truncated posterior end, the large siphonal gape, and the nearly symmetrical triangular chondrophore in the left valve. *M. truncata* has the shortest pallial sinus of any living *Mya*, the pallial sinus scar joining the pallial line at an almost vertical inclination.

COLLECTION: Only two worn valves were present at one station in 64 m. No periostracum or trace of the ligament remain, so

it is likely this material is fossil.

RECORDS: *Miocene*—Arnold and Hannibal 1913:590, 596 (Oregon); Ilyina 1963:9 (Kamchatka); MacNeil 1965:38, pl.8, f.1–12, pl.9, f.1–3, 5–20 (California). *Pliocene*—Feilden 1877:438, 486 (Greenland); Schlesch 1924:15 (Iceland); Merklin et al. 1962:47, pl.10, f.3, (Chukotsk Peninsula); MacNeil 1965:38, pl.8, f.1–12, pl.9, f.1–3, 5–20 (Oregon); Zhidkova et al. 1968:133, pl.49, f.1 (Sakhalin Islands). *Pleistocene*—Grewinck 1850:171 (Alaska); Feilden 1877:438, 486 (European Arctic); Knipovitsch 1900:380 (Spitzbergen); Arnold and Hannibal 1913:590, 596 (British Columbia); Newcombe 1914:107 (British Columbia); Laurson 1950:86 (Greenland); Miller 1953:29 (Alaska); Fujie 1957:399, pl.3, f.1–4 (Japan); Merklin et al. 1962:47, pl.10, f.3 (Chukotsk Peninsula); Richards 1962:70, pl.13, f.1, 2 (Newfoundland to Massachusetts); MacNeil 1965:38, pl.8, f.1–12, pl.9, f.1–3, 5–20 (California); Hopkins et al. 1972:126 (St. Lawrence Island); Allison 1973:20 (Aleutian Islands). *Recent*—Montagu 1803:32 (Britain); Gould 1841:42 (Massachusetts); Møller 1842:21 (Greenland); Middendorff 1849:585, pl.14, f.13–15 (Arctic and Bering Sea); Middendorff 1851:266, pl.25, f.11–14 (Sea of Okhotsk); M. Sars 1859:61 (Arctic); Crosse 1877:126 (Bering Sea); Leche 1878:9 (Novaya Zemlya); M. Sars 1878:92 (Norway); Dunker 1882:176 (Northern Japan); Krause 1885:39 (Bering Sea); Stuxberg 1886:140 (Novaya Zemlya); Hägg 1904:55 (Greenland); Dautzenberg and Fischer 1910:21 (Novaya Zemlya); Grant and Gale 1931:414 (circumboreal); Mesjatsjev 1931:122 (Barents Sea); Johnson 1934:56 (Greenland); Soot-Ryen 1939:17 (Franz Josef Land); Gorbunov 1946a:46 (Arctic); Madsen 1949:76 (Iceland); Kuroda and Habe 1952:25 (Northern Japan); Filatova 1957b:56 (Arctic); Ockelmann 1958:144 (Greenland); MacGinitie 1959:184 (Point Barrow, Alaska); Ellis 1960:39 (Baffin Island); Richards 1962:70, pl.13, f.1, 2 (Arctic to Massachusetts); Kuznetsov 1963:108 (Kara Sea); Sparks and Pereyra 1966:834 (Chukchi Sea); Petersen 1968:36 (Faroe Islands); Bernard 1970:90 (British Columbia); Clarke 1974:11 (Baffin Bay); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Circumboreal and probably panarctic. This species is widely distributed throughout the Northern Pacific, the Chukchi Sea, the Siberian Sea, and along the Eurasian shallow continental shelf to Norway. It occurs as far south as England and the British Channel probably to the Iberian Peninsula. The species has been found at Novaya Zemlya, Iceland and Greenland and the Canadian Arctic Archipelago. Along the eastern coast of America it occurs south to Nantucket, Massachusetts, and on the Pacific coast to Puget Sound, Washington.

REMARKS: *M. truncata* is rather variable in outline, and is greatly influenced by substrate size and consistency. As the synonyms have been fully treated by MacNeil (1965), mention here is only made to *M. truncata uddevalensis* Forbes 1846, which is merely a frequently occurring abbreviated form. The species probably did not reach European seas until the Lower Pleistocene, and records of it from the English Coralline Crag (Pliocene) are doubtful. I have been unable to locate the specimen figured by Wood (1857) and could not identify with certainty *M. truncata* in the Crag collection of the British Museum (Natural History). I agree with MacNeil (1965:39) that Pliocene Crag specimens should be referred to *M. pseudoarenaria* Schlesch 1931.

Family HIATELLIDAE Gray 1824

No representatives of *Panomya* Gray 1857 were present in the collection, although MacGinitie (1959) recorded *P. arctica* (Lamarck 1818) and *P. ampla* Dall 1898 at Point Barrow. The former has a circumboreal distribution, but it is not a true high Arctic species, merely one of the Bering Sea elements carried into the southern Chukchi Sea by the Bering current.

KEY TO THE GENERA OF HIATELLIDAE

Beaks anterior; pallial sinus small but distinct *Hiatella*
Beaks posterior; no pallial sinus *Cyrtodaria*

Genus *Cyrtodaria* Reuss 1801

Figure 90

Type species (Subsequent designation Vokes and Cox 1961); *Mya siliqua* Spengler 1793. Recent. Arctic.

DESCRIPTION: Shell thick, elongate. Surface smooth with occasional growth checkmarks. Periostracum thick, dark brown to black, dehiscent, exposing the chalky shell. Shell interior usually chalky, sometimes porcelaneous in young specimens. Margins smooth, thick, with large posterior and anterior gapes. Hinge edentulous, with subumbonal thickening. Ligament external. Pallial line weakly to deeply impressed, entire. No pallial sinus.

RANGE: Pliocene to Recent. Recent distribution limited to North Atlantic and circumarctic including the Chukchi Sea, to Kuskodwim Bay, northern Bering Sea.

DEVELOPMENT: No information available.

REMARKS: The genus is limited to shallow boreal and Arctic waters and consists of only two species. Nesis (1965) reviewed the genus and thought its occurrence as characteristic of brackish water environments. Yonge (1971) published on the morphology and concluded species were adapted for horizontal burrowing through the substrate by anchoring the anterior end by dilation of the siphons and associated tissues, while forcing the wedge shaped anterior end forward and extending the large foot. The stomach is large and the intestine very long. The gills and palps suggest the taxon is a filter-feeder in regions of high turbidity. The periostracum is particularly thick and developed.

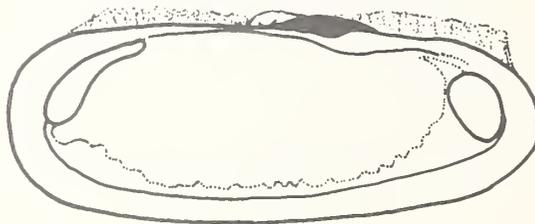


FIGURE 90. Interior of right valve of *Cyrtodaria siliqua* (Spengler).

Cyrtodaria kurriana Dunker 1862

Figures 92, 93, 94

Cyrtodaria kurriana Dunker 1862:38; Oldroyd 1925:208; Filatova 1948:444, pl.113, f.1; Strauch 1972:90, pl.9, f.13-16.

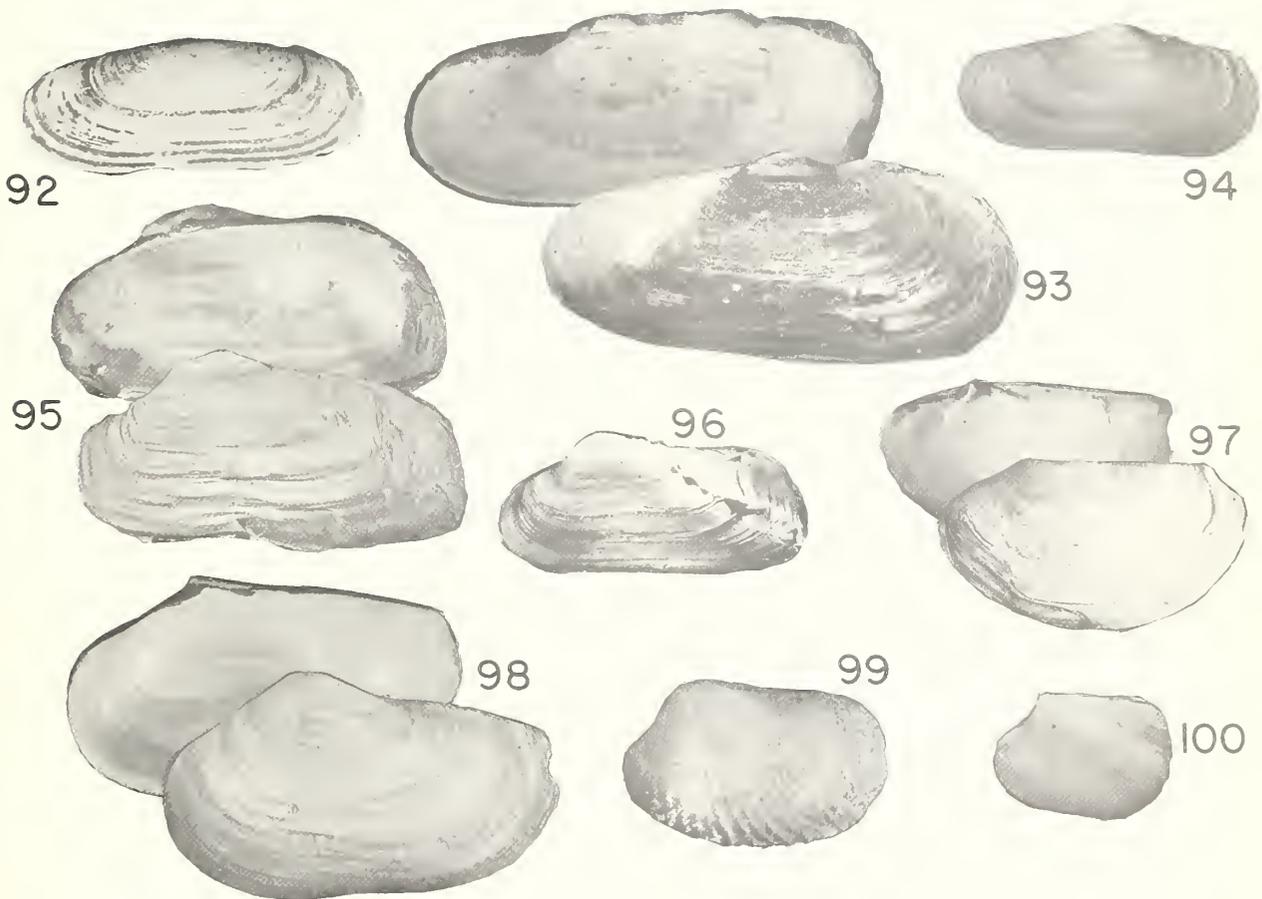
DESCRIPTION: Shell usually thick, very elongate. Maximum length 40 mm., generally less than 30 mm. Surface smooth, except for incremental striae and growth checkmarks. Periostracum thick, polished, brown to black, dehiscent to reveal the chalky shell. The periostracum is fused to the siphonal sheath, and bridges the dorsal shell margins. Umbones not prominent, beaks often eroded. Interior of shell chalky, sometimes polished in young specimens. Margins plain, meeting only ventrally with large posterior and anterior gapes. Adult hinge edentulous, but with subumbonal tuberosity. Ligament external, supported by a substantial nymph. Adductor muscle scars deeply impressed, anterior elongate, posterior nearly oval. Pallial line with irregular upper margin, widening near adductor muscles. No pallial sinus.

COMPARISONS: This species may be confused with the northeastern American *Cyrtodaria siliqua* (Spengler 1793) the only other representative of the genus, but is separable by its

smaller size and untwisted valves. The height-length ratio in *C. siliqua* is approximately 1:2, while in *C. kurriana* it is around 1:3. Worn valves may superficially resemble *Hiatella*, but the posterior position of the beaks and the continuous pallial line separate *Cyrtodaria*. A further useful distinguishing character is the ligament which is amphidetic (on either side of beaks) in *Cyrtodaria* and opisthodontic (posterior to beaks) in *Hiatella*.

COLLECTION: One decomposed valve from 270 m. The presence of fresh periostracum shows the specimen to have been recently living, but the friable and worn appearance is suggestive of transportation. The species was abundant in less than 2 m at Kaktovic Lagoon (70°4.9'N, 143°38.7'W), collected by Western Washington State College.

RECORDS: *Pleistocene*—Dall 1919:29A (Arctic); Merklin et al. 1962:45, pl.8, f.5 (Chukotsk Peninsula); Petrov 1966:234, pl.20, f.7, 10 (Chukotsk Peninsula); Petrov 1967:184 (Bering Sea); Hopkins et al. 1972:125 (St. Lawrence Island). *Recent*—Leche 1878:9 (Novaya Zemlya); Leche 1883:437 (Novaya Zemlya); Stuxberg 1886:139 (Novaya Zemlya); Hägg 1904:62 (Jan Mayen Land); Gorbunov 1946a:46 (Eurasian Arctic); Kuroda and Habe 1952:18 (Northern Japan); Ushakov 1952:61 (Chukchi Sea); Filatova 1957b:56 (Arctic); Ockelmann 1958:142, pl.2, f.14 (Greenland); Soot-Ryen 1958:26 (Greenland); Hulsemann 1962:68 (Beaufort Sea); Merklin et al. 1962:45, pl.8, f.5 (Chukotsk Peninsula); Wagner 1962:10 (Canadian Arctic); Clarke



FIGURES 92-100. 92, *Cyrtodaria kurriana* Dunker, fossil?, length 27.1 mm; 93, *C. kurriana*, length 19.0 mm; 94, *C. kurriana*, juvenile, length 12.4 mm; 95, *Hiatella (Hiatella) arctica* (Linné), length 27.8 mm; 96, *H. (H.) arctica*, juvenile, length 8.1 mm; 97, *Pandora (Pandorella) glacialis* Leach in Ross, length 21.0 mm; 98, *Lyonsia (Lyonsia) arenosa* (Møller), length 26.4 mm; 99, *L. (L.) arenosa*, juvenile, 7.2 mm; 100, *L. (L.) arenosa*, juvenile, length 2.1 mm.

1963:103 (Arctic); Wacasey 1974:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and high latitude North Atlantic, this species is most abundant in the Canadian Arctic Archipelago and Greenland and into Hudson Bay. It occurs in the Siberian and Chukchi Sea, and into the northern part of the Bering Sea.

REMARKS: Although not recorded by MacGinitie (1959), Baxter (pers. comm.) retrieved *Cyrtodaria* mixed with the *Hiatella* of the MacGinitie collection. *C. kurriana* was abundant in the stations worked by Hulsemann (1962), especially just east of Point Barrow. Nesis (1965) considered this species adapted to oligohaline conditions, so it should be well represented in the shallow Mackenzie estuary. The muscular foot and wedge-shaped anterior end are modifications for rapid and active burrowing, indicative of unstable shallow water habitat.

Genus *Hiatella* Bosc (Daudin MS) 1801

Figure 91

Type species (subsequent designation Winckworth 1932): *Mya arctica* Linné 1767. Recent. North Atlantic.

DESCRIPTION: Shell irregular, inflated. Surface with incremental striae. Periostracum brown, thin, dehiscent, frequently with attached sand particles. Interior polished, often nacreous. Margins plain, with large posterior gape. Hinge edentulous in the adult, but with ephemeral small cardinal in the right valve and two small teeth in the left valve of some juveniles. Ligament external, opisthodetic. Anterior adductor muscle scar elongate, posterior rounded, frequently deeply impressed. Pallial line in sections, Pallial sinus small, demarcated by large siphonal retractor muscle scars.



FIGURE 91. Interior of right valve of *Hiatella arctica* (Linné).

RANGE: Oligocene to Recent. Recent distribution cosmopolitan, especially in temperate zones, generally in shallow water in a variety of substrates, including boring into soft rock, or nestling in silicious sponge.

DEVELOPMENT: *H. arctica* (Linné) produces small eggs with prolonged planktonic development (Thorsen 1936). This appears common to all species of the genus (Bernard MS).

REMARKS: The genus includes some of the most widely distributed bivalve species. All representatives have remarkably plastic shells, which are profoundly influenced by substrate, and the taxonomy is not understood. There are at least three northern species, but high Arctic dwellers are best referred to *H. arctica* (Linné).

Subgenus *Hiatella* s. str. *Hiatella* (*Hiatella*) *arctica* (Linné 1767)

Figures 95, 96

Mya arctica Linné 1767:1113.

Saxicava arctica (Linné), M. Sars 1859:62; Oldroyd 1925:208, pl.9 f.6, pl.5, f.4; Filatova 1948:443.

Hiatella arctica (Linné), Lamarck 1819:30; Hanley 1843:150.

Didonta bicarinata Schumacher 1817:125, pl.6, f.2a, b.

Saxicava ungana Grewingk 1850:354, pl.6, f.1a-c; Dall 1904:117.

Saxicava orientalis Yokoyama 1920:106, pl.7, f.2, 3; Kuroda and Habe 1952:21; Yamamoto and Habe 1959:111, pl.12, f.16, 17.

Hiatella sakhalinensis Oyama, Mizuno and Sakamoto 1960:207, pl.63, f.1a-d.

DESCRIPTION: Shell elongated, rugose, frequently deformed. Moderately inflated with beaks towards the anterior end. Maximum length 75 mm, generally smaller. Surface chalky, with irregular incremental striae and large checkmarks. Periostracum thin, grey to light brown, dehiscent, wrinkled in posterior region. Juvenile specimens with two radial spinose ribs from umbones to posterior margin. In some rare individuals the ribs and spines may persist. Interior polished, frequently with central patch of brown or yellow. Hinge edentulous in adult, juveniles with two teeth in the left and one in the right valve. Ligament external, entirely posterior to the beaks. Adductor muscle scars deeply impressed, anterior elongate, posterior rounded. Anterior pedal retractor muscle scar large. Pallial line in several interrupted segments. Pallial sinus wide and shallow with two large pedal retractor muscle scars.

COMPARISONS: In spite of the extreme plasticity of outline and tendency to xenomorphic growth, the genus is easily recognized and all high Arctic representatives are referable to *H. arctica*. *H. pholadis* (Linné, 1767) occurs with this species in the North Atlantic and Bering Sea but has a more cylindrical outline and, according to Dodge (1952) is edentulous and spineless in the juvenile phase. It has not been reported from the Arctic Ocean.

COLLECTION: Sixty specimens together with numerous fragments and single valves were present at 13 stations between 27 and 159 m.

RECORDS: *Miocene*—Cossmann and Peyrot 1909:131, pl.3, f.20-27 (France); Sorgenfrei 1958:125, pl.20, f.66a-e (Denmark). *Pliocene*—Wood 1857:287, pl.29, f.4a, b (England); Tokunaga 1906:36, pl.2, f.21a, b (Japan); McNeil et al. 1943:75, pl.15, f.16 (Alaska); Hopkins and McNeil 1960:341 (Alaska); Merklin et al. 1962:44, pl.8, f.6, 7 (Chukotsk Peninsula); Petrov 1966:233, pl.20, f.5, 6 (Chukotsk Peninsula); Hertlein and Grant 1972:326, pl.56, f.15, 17, 18 (California); Zhidkova et al. 1968:129, pl.23, f.8, a (Sakhalin Islands); Zhidkova et al. 1972:141, pl.28, f.5 (Kurile Islands). *Pleistocene*—Arnold and Hannibal 1913:598 (Washington); Orcutt 1921:24 (Mexico); Johnstone 1923:50 (British Columbia); Hoots 1931:122 (California); Armstrong and Brown 1954:356 (British Columbia); Emerson 1956:339 (Mexico); Wagner 1959:5 (British Columbia); Merklin et al. 1962:44, pl.8, f.6, 7 (Chukotsk Peninsula); Richards 1962:71, pl.12, f.17-20 (Labrador to North Carolina); Zullo 1969:350 (Oregon); Hopkins et al. 1972:126 (St. Lawrence Island); Allison, 1973:20 (Aleutian Islands); Troitskiy 1974:265 (Siberia). *Recent*—Møller 1842:21 (Greenland); Carpenter 1857:16 (Mexico); Lischke 1869:134 (Northern Japan); Gould 1870:89 (Massachusetts); Jeffreys 1877:234 (Britain); G. Sars 1878:95, pl.20, f.8a-d (Greenland); Dunker 1882:175 (Japan); Melvill and Standen 1900:5 (Franz Josef Land); Baker 1902:42 (Mexico); Hägg 1904:58 (Greenland and Spitzbergen); Jensen 1905:357 (Greenland); Odhner 1915:129 (Greenland); Soot-Ryen 1925:6 (Spitzbergen); Yocum and Edge 1929:50 (Oregon); Massy 1930:276 (North Atlantic); Hatai and Nomura 1935:19 (Japan); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:73 (Iceland); Kuroda and Habe 1952:21 (Northern Japan); Scarlato 1955:196, pl.53, f.9 (Kara Sea); Filatova 1957b:56 (Arctic); Ockelmann 1958:135

(Greenland); Soot-Ryen 1958:27 (Greenland); MacGinitie 1959:190, pl.26, f.1-3 (Point Barrow, Alaska); Clarke 1960:12 (Canadian Arctic); Clarke 1961:7 (Gulf of St. Lawrence); Ellis 1960:39 (Baffin Island); Merklin et al. 1962:44, pl.8, f.6, 7 (Chukotsk Peninsula); Richards 1962:71, pl.12, f.17-20 (Arctic to West Indies); McLaughlin 1963:28 (Bering Sea); Filatova and Barsanova 1964:20 (Bering Sea); Sparks and Pereyra 1966:835 (Chukchi Sea); Petersen 1968:54 (Faroe Islands); Bernard 1970:70 (British Columbia); Kuroda et al. 1971:466, pl.102, f.11 (Japan); Clarke 1974:11 (Baffin Bay); Scarlato 1974:99 (Bay of Peter the Great); Scarlato and Ivanova 1974:304 (Kurile Islands); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. This species is probably the most cosmopolitan of continental shelf bivalves. It ranges through the North Atlantic, the Mediterranean and along the west coast of Africa to Gabon. In the Western Atlantic it occurs from Greenland to the Gulf of Mexico and probably Argentina. It is ubiquitous in the Bering Sea and Sea of Okhotsk and into the Sea of Japan. On the west American coast it is present from Alaska to Panama and probably to Patagonia.

REMARKS: Strauch (1968) considered this species to have a cosmopolitan distribution since the Early Tertiary. Material from the Pacific coast of South America is indistinguishable from Arctic and North Atlantic representatives; however, Olsson (1961) preferred to use *H. solida* (Sowerby 1834) for species from the Panamanian Province. I believe a single Eastern Pacific species is involved, including *Saxicava antarctica* Philippi 1845 and its numerous synonyms described from the Chiloe Archipelago, extending into the Magellanic Province and collected at the West Falkland Islands (Melville and Standen 1914). The wide distribution and plasticity of this species has resulted in a large synonymy, first consolidated by Hägg (1904). I consider the Miocene species *H. sakhalensis* Oyama, Mizuno and Sakamoto 1960 to be the earliest Pacific representative of *H. arctica*. *H. arctica* has not developed the boring habit of other members of the genus, but is frequently found in vacated burrows. The long siphons permit an infaunal habit, but this species is usually a byssally attached epifaunal nestler, often in crevices between rocks, or in siliceous sponges, or dead shells. Yonge (1971) described the functional morphology and drew attention to the hypertrophied pallial musculature, reflected by the wide and segmented pallial line. Strauch (1968) suggested that paleotemperatures could be estimated using fossil shell lengths, but Rowland and Hopkins (1971) found no such relationship for contemporary Pacific populations where shell length is chiefly governed by mode of life.

Family PANDORIDAE Rafinesque 1815 Genus *Pandora* Bruguière 1797

Figure 101

Type species (subsequent monotypy Lamarck 1799): *Solen inaequalis* Linné 1758. Recent. North Atlantic.

DESCRIPTION: Shell compressed with crescent-shaped outline. Left valve convex, frequently larger than the flattened right valve. Surface smooth, sometimes with incremental striae. Periostracum thin, grey, dehiscent. Interior polished, nacreous, margins plain. Hinge not developed, but with two or more diverging ridges bordering the resilifer. Resilium sometimes with a lithodesma.

RANGE: Oligocene to Recent. Recent distribution cosmopolitan in shallow water to 1000 m. The genus is epifaunal or shallowly infaunal, particularly in coarse and shifting sediments.

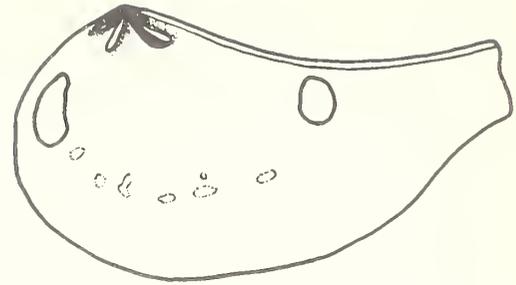


FIGURE 101. Interior of right valve of *Pandora inaequalis* (Linné).

DEVELOPMENT: All northeastern Pacific species produce large ova similar to *P. glacialis* Leach in Ross, described by Thorsen (1936) as surrounded by a thick gelatinous layer. The eggs probably adhere to the substrate near the parent and development is lecithotrophic but may undergo a short planktonic phase (Allen 1961).

REMARKS: *Pandora* has a short siphon and the frequent occurrence of epifauna on the flat right valve, supports the statement by Allen (1955) that *P. inaequalis* Linné is epifaunistic and lies on the cupped left valve. Stanley (1970) considered *P. gouldiana* (Dall) to be a shallow infaunal species with frequent periods on the substrate surface. *Pandora* s. str. although circumboreal, is not represented in the high Arctic, but the subgenus *Pandorella* Conrad (= *Kennerlia* Carpenter, 1864), characterized by radial striae or ribbing on the right valve and a lithodesma supporting the ligament, is widely distributed.

Subgenus *Pandorella* Conrad 1863

Type species (monotypy) *Pandora arenosa* Conrad 1834. Miocene. Eastern United States.

Pandora (Pandorella) glacialis Leach in Ross 1819

Figure 97

Pandora glacialis Leach in Ross 1819:174; Oldroyd 1925:89, pl.15, f.11, pl.42, f.3, 4.

Pandora (Kennerlia) glacialis (Leach), Filatova 1948:444, pl.13, f.4.
Calopodium (Kennerlia) glacialis (Leach), Soot-Ryen 1939:18.
Kennerlyia glacialis eutaenia Dall 1915:449.

DESCRIPTION: Shell very inequivalve, left valve convex, overlapping the smaller flat right valve, Posterior slightly rostrate. Maximum length 30 mm. Surface of left valve with irregular striae and growth marks. Right valve with fine indented radial lines. Periostracum thin, dehiscent, wrinkled in posterior ventral region. Umbones not prominent, beaks frequently eroded to expose nacreous shell. Interior nacreous, shell margins smooth. Hinge not developed, left valve edentulous, but with an oblique resilifer. Right valve edentulous. Left valve with peg-like anterior and lamellar posterior crura. Ligament internal with a small lithodesma. Pallial line represented by obscure isolated attachment scars. No pallial sinus.

COMPARISONS: This species is separated from boreal members of the genus by the radial lines of the right valve, which often appear on the inner side of the shell as slightly raised ribs.

In juveniles the left valve may also have two narrow radial ribs from umbones to posterior margin.

COLLECTION: One hundred sixteen specimens and 31 single valves were present at 11 stations between 10 and 270 m.

RECORDS: *Pliocene*—Waterfall 1929:78 (California); Petrov 1966:241, pl.23, f.10, 11 (Chukotsk Peninsula). *Pleistocene*—Bailey 1935:495 (California); Richards 1962:58, pl.6, f.1, 2 (Labrador to Maine). *Recent*—Leche 1878:11, pl.1, f.1a, b (Novaya Zemlya); Leche 1883:439 (Kara Sea); Krause 1885:38 (Bering Sea); Stuxberg 1886:141 (Novaya Zemlya); Melvill and Standen 1900:5 (Franz Josef Land); Jensen 1905:361 (Greenland); Odhner 1915:130 (Spitzbergen); Mesjatsev 1931:111 (Barents Sea); Soot-Ryen 1932:11 (Greenland); Grant and Gale 1931:262 (Arctic to Washington); Johnson 1934: (Arctic to Massachusetts); Gorbunov 1946a:46 (Eurasian Arctic); Filatova 1957b:57 (Arctic); Ockelmann 1958:152 (Greenland); Hulsemann 1962:68 (Beaufort Sea); Richards 1962:58, pl.6, f.1, 2 (Arctic to Massachusetts); Bernard 1970:90 (British Columbia); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. This species occurs sporadically through its range which includes the extreme North Atlantic, and along the American coast as far south as Massachusetts. It is present in the Bering Sea and Sea of Okhotsk and south to Northern Japan and the Kurile Islands. In the eastern Pacific it occurs south to Washington.

REMARKS: Shells closely resembling *Pandora* s. str. except for the radial striae on the right valve, and the presence of a lithodesma strengthening the ligament, were placed in a new subgenus, *Kennerlia* by Carpenter (1864). Vokes (1956) showed that an earlier name was *Pandorella* Conrad 1863, for which the type, *P. arenosa* Conrad (by monotypy), has a developed lithodesma. It may be concluded that the presence of this structure is the chief diagnostic character of *Pandorella*; it is therefore surprising that Keen in Moore (1969) states the lithodesma to be wanting. It must be surmised that this is a *lapsus calami*.

Family LYONSIIDAE Fischer 1887

Genus *Lyonsia* Turton 1822

Figure 102

Type species (monotypy): *Mya norvegica* Gmelin 1791. Recent. North Atlantic.

DESCRIPTION: Shell thin, brittle, elongate. Posterior produced and truncate with siphonal gape. Surface ornamented with radial threads and striae. Periostracum thin, adherent. Interior nacreous. Hinge edentulous, resilium situated in an elongate oblique resilifer. The ligament is supported by a wide, posteriorly bifid lithodesma. Adductor muscle scars obscure. Pallial line wide, barely impressed. No pallial sinus.

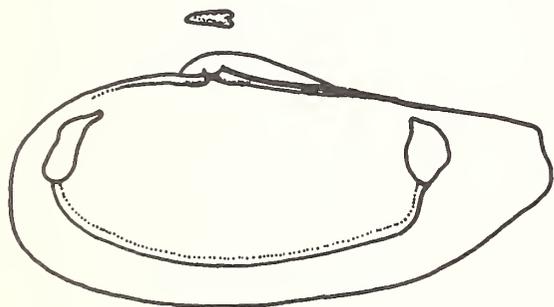


FIGURE 102. Interior of right valve and lithodesma of *Lyonsia norvegica* (Gmelin).

RANGE: Eocene (?) to Recent. Recent distribution northern circumboreal in shallow water, usually in sand or sandy mud substrata, or as byssally attached nestlers. A few species are present in warm waters.

DEVELOPMENT: According to Ockelmann (1958), *L. arenosa* (Møller) produces eggs with plentiful yolk that undergo lecithotrophic development with a curtailed, or absent, planktonic stage. *L. hyalina* Conrad 1831 has a similar development (Chanley and Castagna 1966).

REMARKS: Because of the shortness of the siphons, most species occur in the superficial infauna, anchored with several byssal threads, there is also a tendency for sand particles to be cemented to the periostracum, or for the shell to be covered with a coating of sediment mixed with mucus. Wagner (1977) recorded *Lyonsia schinkewitschi* Derjurgin and Gurjanova 1926 from the eastern Beaufort Sea. The original description was not very specific, so it may be considered a *nomen dubium*, and I believe it to be a morph of *L. norvegica* Gmelin 1791.

Subgenus *Lyonsia* s. str.

Lyonsia (Lyonsia) arenosa (Møller 1842)

Figures 98, 99, 100

Pandorina arenosa Møller 1842:20.

Lyonsia arenosa (Møller), Oldroyd 1925:92; Lamy 1928:250; Filatova 1948:444, pl.13, f.2.

Lyonsia (Pandorina) flabellata Gould 1861:23.

Lyonsia ventricosa Gould 1861:23.

Lyonsia arenosa sibirica Leche 1883:439, pl.32, f.3, 4.

DESCRIPTION: Shell thin, brittle, inflated. Anterior rounded, posterior end produced, truncated with narrow siphonal gape. Maximum length 50 mm, but usually less than 25 mm. Surface with irregular incremental striae and fine radial threads. Periostracum light brown to dark grey, adherent, often with attached sand grains and mucus-bound sediment. Interior nacreous, shell margins smooth. Hinge edentulous. Ligament internal, supported by a large, posteriorly bifid lithodesma. Adductor muscle scars not impressed. Pallial line wide, entire. Pallial sinus barely present.

COMPARISONS: This species may be confused with *L. norvegica* (Gmelin 1791), which is distributed through the European Atlantic and Mediterranean, and in the eastern Beaufort Sea according to Wagner (1977). It is distinguished by a thicker shell and coarser, less numerous, radial threads. The periostracum is thicker and concentrically wrinkled between the radial threads, but in *L. norvegica* the interstitial spaces are closely punctated.

COLLECTION: Twenty specimens and 14 separated valves occurred at 15 stations between 15–101 m.

RECORDS: *Pleistocene*—Laursen 1950:83 (Greenland); Richards 1962:57, pl.5, f.17 (Quebec to Maine); Petrov 1966:240, pl.23, f.12, 13 (Chukotsk Peninsula); Wagner 1970:44, pl.5, f.3a, b (Eastern Canada). *Recent*—Gould 1870:65 (Massachusetts); G. Sars 1878:81, pl.34, f.2a, b (Greenland); Leche 1878:11 (Novaya Zemlya); Stuxberg 1886:141 (Novaya Zemlya); Hägg 1904:62 (Greenland); Jensen 1905:359 (Greenland); Odhner 1915:131 (Spitzbergen); Grant and Gale 1931:264 (Arctic to Japan); Mesjatsev 1931:117 (Barents Sea); Johnson 1934:31 (Greenland to Massachusetts); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:80 (Iceland); Kuroda and Habe 1952:24 (Northern Japan); Filatova 1957b:56 (Arctic); Ockelmann 1958:149 (Greenland); Soot-Ryen 1958:16 (Greenland); Ellis 1960:39 (Baffin Island); Hulsemann 1962:64 (Beaufort Sea); Richards 1962:57, pl.5, f.17 (Greenland to Maine); McLaughlin 1963:26 (Bering Sea); Filatova and Barsanova 1964:31 (Bering Sea); Wacasey 1975:27 (Beaufort Sea); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: Panarctic and circumboreal. This species is represented in the shallow water off Northeastern America, Greenland and the Canadian Arctic Archipelago. It occurs sporadically at Spitzbergen and Novaya Zemlya, and eastwards to Siberia. It enters the Bering Sea, Sea of Okhotsk and northern Japan. The range south of Kodiak Island has not been confirmed.

REMARKS: The shell outline and number of radial striae are variable, as evidenced by the synonyms *L. (Pandorina) flabellata* Gould 1861, which is merely a thin-shelled inflated morph with more numerous striae; and *L. ventricosa* Gould 1861 from Hakodadi, Japan, which is the shorter, more rotund form. A greater difficulty is the confusion with the Atlantic *L. norvegica* (Gmelin). Middendorff (1849) considered the two species synonymous, a conclusion apparently accepted by Carpenter (1857). MacGinitie (1959) used the Gmelin name for a specimen and broken valve from Point Barrow. I have been unable to locate this material in the USNM as MacGinitie did not illustrate her specimen, but I feel confident in concluding that in fact it should be assigned to *L. arenosa*, as MacGinitie did not discuss the relationship of high Arctic to Atlantic representatives, nor give a reason for her nomenclature. A number of authors cited an Eastern Pacific range for *L. arenosa* as far south as northern Washington. I consider this to be in error, and have not seen specimens south of the northern part of the Gulf of Alaska.

Family PERIPLOMATIDAE Dall 1895
Genus *Periploma* Schumacher 1817

Figure 103

Type species (monotypy): *Periploma inaequalis* Schumacher 1817.
Recent. North Atlantic.

DESCRIPTION: Shell thin, ovate to quadrangular; right valve more convex than left valve. Surface smooth, frequently with minute pustules or concentric lirae. Periostracum very thin, dehiscent. Umbones prominent, beaks opisthogyrate, fissured. Interior smooth, subnacreous. Hinge edentulous, resilium in two chondrophores supported by an oblique rib running from beaks towards posterior margin of shell. Usually with lithodesma. Adductor muscle scars elongated, narrow. Pallial line feebly impressed; pallial sinus small and rounded.

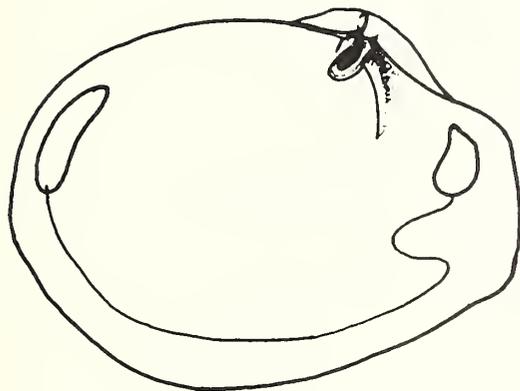


FIGURE 103. Interior of right valve of *Periploma inaequalis* Schumacher.

RANGE: Cretaceous to Recent. Recent distribution cosmopolitan, from the subtidal zone to 2500 m, mostly in warmer waters.

Contrib. Sci. Natur. Hist. Mus. Los Angeles County. 1979. 313:1-80.

DEVELOPMENT: I have been unable to locate any references to development in the literature.

REMARKS: The genus is unrepresented in OSU and Washington State College collections but a recently dead valve and some fragments were present at USGS location M6936 in the Beaufort Sea at 709 m.

Subgenus *Periploma* s. str.
Periploma (Periploma) aleutica
(Krause 1885)

Figure 104

Anatina ? aleutica Krause 1885:38, pl.3, f.7.

Periploma alaskana Williams 1940:37, f.1; Rosewater 1968:38.

DESCRIPTION: Shell thin, extremely fragile; ovate. Maximum length 30 mm. Surface smooth or with irregular incremental lirae. Posterior truncated, set off by shallow radial sulcus. Periostracum thin, with fine wrinkles on posterior and ventral shell margins. Beaks prominent, with apex divided by a vertical slit. Interior subnacreous. Hinge edentulous with prominent chondrophore supported by posteriorly directed buttress in each valve. The umbonal slit is prolonged ventrally as a furrow with inserted ligamental band. Lithodesma small. Adductor muscle scars unequal, pallial line obscure. Pallial sinus small.

COMPARISONS: The species bears a superficial resemblance to the Atlantic *P. papyraceum* (Say 1822), but is readily distinguished by the narrower, nearly vertical chondrophore.

COLLECTION: Two valves and several fragments collected by the United States Geological Survey at location M6936 (71°28.9'N, 151°40.9'W) in 709 m.

RECORDS: *Recent*—Williams 1940:37, f.1 (Chukchi Sea and Montagu Island, Alaska).

DISTRIBUTION: The species occurs in the Beaufort, Chukchi, and eastern Bering Sea and in the northern portion of the Gulf of Alaska. This is the initial record from the Beaufort Sea.

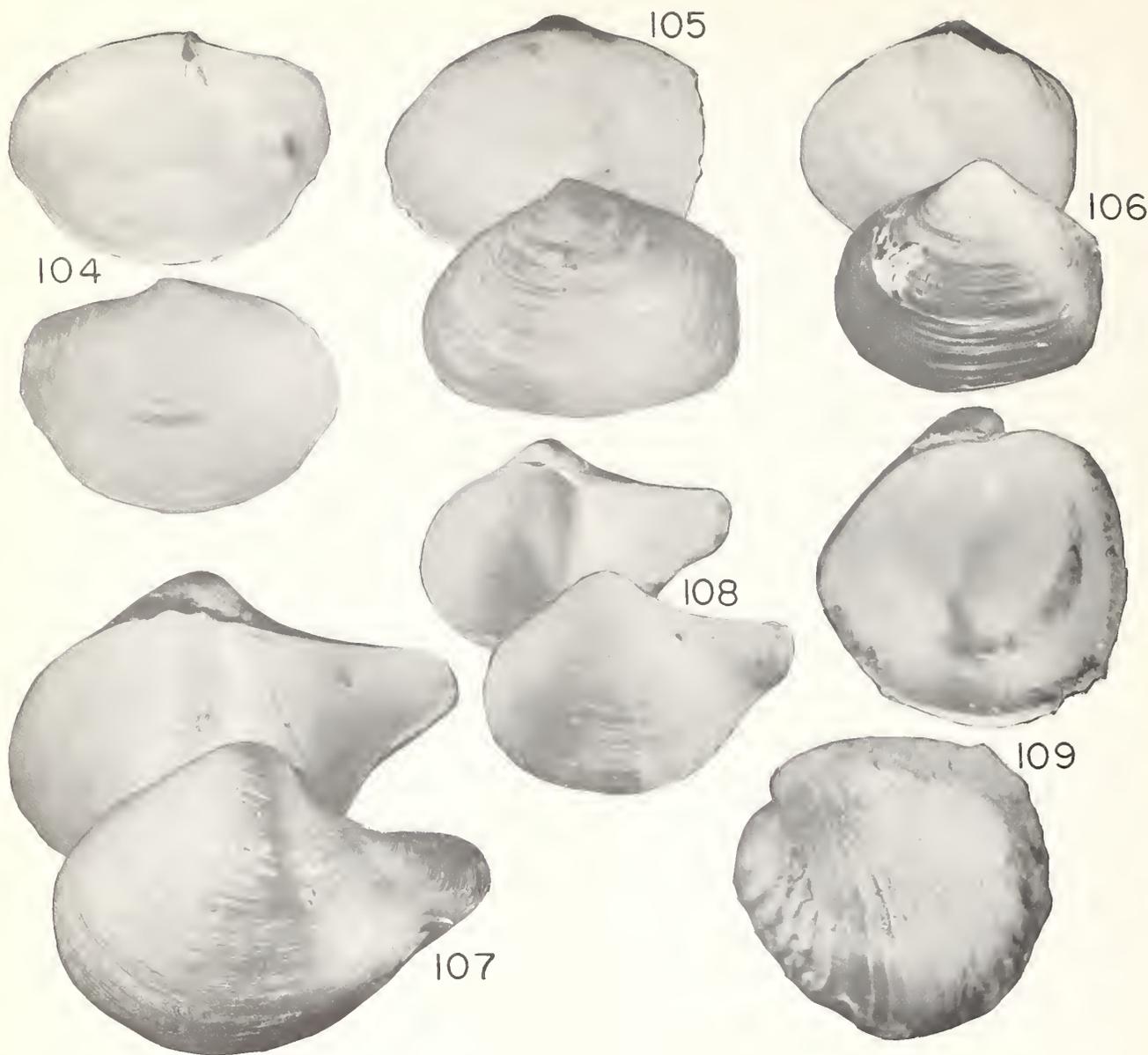
REMARKS: Krause's description of this species from the southern Bering Sea was overlooked by Williams (1940) who redescribed it from the Chukchi south to the Gulf of Alaska. This bivalve is probably descended from the Pacific discoidal *Periploma* and may be a comparatively recent migrant to the Arctic. In view of this, and the present distribution, it is puzzling that no representatives of the genus are found from British Columbia to southern Oregon, but in central and southern California a number of species occur. On the other hand, the genus is well represented in boreal Atlantic waters.

Family THRACIIDAE Stoliczka 1870
Genus *Thracia* Sowerby (Leach MS) 1823

Figure 110

Type species (subsequent designation Anton 1839): *Mya pubescens* Pulteney 1799. Recent. North Atlantic.

DESCRIPTION: Shell ovate, posteriorly produced and truncate. Surface with obscure concentric striae and many small granules. Umbones prominent, beak of right valve frequently abraded and perforated by opposite valve. Interior chalky. Hinge edentulous. Ligament partly external. Resilium attached to elongate narrow, nearly horizontal resilifer. A small lithodesma may be present.



FIGURES 104-109. 104, *Periploma (Periploma) aleutica* (Krause), length 36.8 mm; 105, *Thracia (Thracia) devexa* Sars, length 27.0 mm; 106, *Thracia (Thracia) myopsis* Møller, length 7.0 mm; 107, *Cuspidaria glacialis* (Sars), length 28.8 mm; 108, *Cuspidaria subtorta* (Sars), length 4.7 mm; 109, *Lyonsiella (Policordia) uschakovi* Gorbunov, length 4.0 mm.

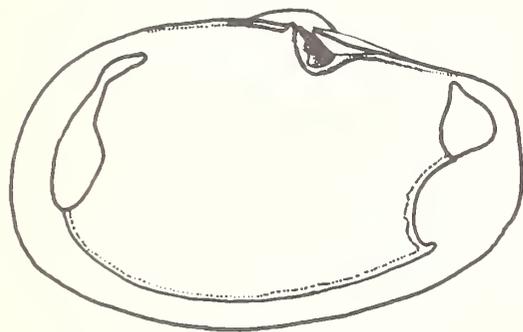


FIGURE 110. Interior of right valve of *Thracia pubescens* (Pultney).

RANGE: Jurassic to Recent. Recent distribution cosmopolitan from the low intertidal zone to 1000 m, usually in sandy substrates. The genus belongs to the deeply infaunal filter-feeding group of bivalves.

DEVELOPMENT: According to Thorson (1936), *T. devexa* G. Sars 1878 produces large yolk-rich eggs, so development is lecithotrophic with a reduced, or absent, planktonic stage.

REMARKS: Two species are in the present collection, but it is unlikely that further collecting will include *T. septentrionalis* Jeffreys 1872, of the North Atlantic and westward to Greenland and the Canadian Arctic Archipelago. *T. adamsi* MacGinitie 1959, from Point Barrow, was not collected. This interesting species, with a massively buttressed resilifer, was placed by MacGinitie in a new subgenus, *Lampeia*, but it is probably referable to *Asthenothaerus* Carpenter 1864 (Baxter pers. comm.)

Subgenus *Thracia* s. str.
Thracia (Thracia) devexa G. Sars 1878

Figure 105

Thracia truncata devexa G. Sars 1878:84, pl.6, f.11a, b.

DESCRIPTION: Shell ovate, anterior rounded, posterior broadly truncate. Maximum length 40 mm, usually less than 25 mm. Surface ornamented with irregular concentric striae and numerous fine granules. Periostracum yellow to grey, adherent. Umbones prominent, eroded in large specimens. Interior polished. Hinge edentulous, with central notch and two elongated tubercles in right valve. Resilifer small, oblique to nearly horizontal. Adductor muscle scars subequal, not impressed. Pallial line entire. Pallial sinus shallow and broad.

COMPARISONS: This species is readily distinguished from *T. myopsis* Møller by the more inflated umbones, shorter resilifer, and less numerous surface granulations.

COLLECTION: Eleven specimens and three single valves were present at nine stations between 28–101 m.

RECORDS: *Recent*—Jensen 1905:360 (Greenland); Odhner 1915:134 (Spitzbergen); Soot-Ryen 1941:23, pl.2, f.5, 6, pl.6, f.4, pl.9, f.5 (Norway); Ockelmann 1958:156, pl.3, f.5 (Greenland); Wagner 1977:2015 (Eastern Beaufort Sea).

DISTRIBUTION: A discontinuous panarctic species present in the Atlantic sector from Greenland to Northern Norway and Spitzbergen and Novaya Zemlya, then the Beaufort and Chukchi seas.

REMARKS: This is the second record for the species from the Beaufort Sea. I have also examined material from the Chukchi Sea collected by the United States Geological Survey. It is probable that a wider distribution will be established when confusion with the following species has been purged from the literature. It was originally proposed as a subspecies of *T. myopsis* Møller, which Sars thought was a junior synonym of *T. truncata* Brown 1827

Thracia (Thracia) myopsis Møller
(Beck MS) 1842

Figure 106

Thracia myopsis Møller (Beck MS) 1842:21; Filatova 1948:445, pl.13, f.6.

Thracia truncata typica G. Sars 1878:84, pl.6, f.10a, b.

DESCRIPTION: Shell ovate to elongate, anterior rounded, posterior truncated. Maximum length to 35 mm. Surface with concentric striae and irregular incremental lines. The entire shell is covered with coarse and densely packed granules giving a shagreened appearance. Periostracum ash brown to gray, adherent. Umbones not prominent, frequently eroded. Interior polished, sometimes iridescent in young specimens. Hinge edentulous, with central notch and obscure tubercles. Resilifer long and narrow. Adductor muscle scars subequal, not deeply impressed. Pallial line entire, barely visible. Pallial sinus shallow.

COMPARISONS: This species is readily distinguished from *T. devexa* G. Sars 1878 by the more closely spaced surface granulations, the less inflated umbones and the much longer resilifer.

COLLECTION: Twenty specimens were collected from 12 stations in 29–357 m.

RECORDS: *Recent*—Gould 1870:71 (Massachusetts); Verrill and Smith 1873:673, pl.27, f.196 (Massachusetts); Leche 1878:12 (Novaya

Zemlya); Stuxberg 1886:140 (Novaya Zemlya); Jensen 1905:360 (Greenland); Odhner 1915:132 (Spitzbergen); Mesjatev 1931:116 (Barents Sea); Johnson 1934:30 (Greenland to Massachusetts); Soot-Ryen 1939:18 (Franz Josef Land); Soot-Ryen 1941:22, pl.2, f.1–4, pl.6, f.3a, b, pl.8, f.4a–e (Norway); Gorbunov 1946a:46 (European Arctic); Filatova 1957b:57 (Eurasian Arctic); Ockelmann 1958:155, pl.3, f.4 (Greenland); Soot-Ryen 1958:17 (Greenland); MacGinitie 1959:162, pl.23, f.9, pl.24, f.4 (Point Barrow, Alaska); Ellis 1960:39 (Baffin Island); McLaughlin 1963:26 (Bering Sea); Petersen 1968:40 (Faroe Islands); Clarke 1974:11 (Baffin Bay); Wacasey 1975:27 (Beaufort Sea).

DISTRIBUTION: Probably panarctic and circumboreal in the Atlantic sector only. The species has been recorded in the Canadian Arctic Archipelago and along the American coast to Massachusetts. In the North Atlantic it occurs from Greenland to Norway, Spitzbergen, Novaya Zemlya, and south to the Faroe Islands and possibly Iceland. The species is rare in the Bering Sea and possibly extends into the Sea of Okhotsk.

REMARKS: MacGinitie (1959) synonymized this species in part with the Northeastern Pacific *T. curta* Conrad 1837, thus extending the range circumboreally. The latter is a larger, thicker shelled species with the posterior region set off by a radial sulcus, and is closely allied to the Atlantic *T. covradi* Couthouy 1838.

Family CUSPIDARIIDAE Dall 1886
Genus *Cuspidaria* Nardo 1840

Figure 111

Type species (monotypy): *Tellina cuspidata* Olivi 1792. *Recent. Mediterranean.*

DESCRIPTION: Shell globose with a narrow, tapering shell-covered siphonal sheath or rostrum. Surface unornamented, chalky, with occasional incremental lines. Interior polished. Hinge edentulous, sometimes with small peg-like tubercle in right valve. Resilifer small, spoon-shaped. Ligament supported by a lithodesma. Adductor muscle scars subequal, feebly impressed. Pallial line irregular. No pallial sinus.

RANGE: Cretaceous to Recent. Recent distribution cosmopolitan in cold and deep water. The genus is well represented in Arctic and abyssal to hadal environments. Shallow infaunal in friable substrates, where many species of the genus actively move around.

DEVELOPMENT: Eggs of all species examined (Ockelmann 1958; Knudsen 1970; Bernard 1974) are large and development is lecithotrophic with a reduced or absent planktonic stage.

REMARKS: The group is remarkably modified for macrophagy and feeding is entirely carnivorous, the gills are absent,

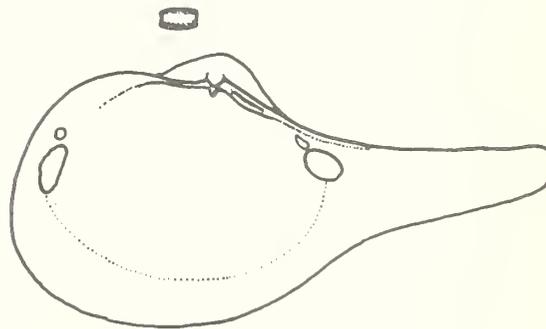


FIGURE 111. Interior of right valve and lithodesma of *Cuspidaria cuspidata* (Olivi).

the pallial cavity is divided by a muscular septum that functions as a powerful pump, drawing small crustaceans and other small benthic organisms into the inhalant opening. The alimentary system is invested with a muscle layer and the interior of the stomach is lined with a greatly extended gastric shield. No member of the closely related genus *Cardiomya* was collected although they are well established circumboreally at high latitudes (Scarlatto 1972).

Cuspidaria glacialis (G. Sars 1878)

Figure 107

Neaera glacialis G. Sars 1878:88, pl.6, f.8a-c; Smith 1885:35.
Cuspidaria glacialis (G. Sars), Verrill and Bush 1898:800; Oldroyd 1925:98, pl.19, f.3a; Knudsen 1970:155, pl.16, f.4, 5.

DESCRIPTION: Shell thin, globular with tube-like posterior rostrum. Surface unornamented except for fine incremental lirae. Periostracum thin, ash-grey, concentrically wrinkled on posterior part of shell. Interior polished or chalky, with numerous fine radial striae. Hinge weak, edentulous. Right valve with small tooth-like tubercle and posteriorly directed resilifer. Left valve with smaller resilifer. Adductor muscle scars subequal, scarcely visible. Pallial line irregular, weakly impressed. No pallial sinus.

COMPARISONS: This species is closely related to *C. arctica* G. Sars 1878; however, *C. arctica* displays a more globular shell and a shorter, more abrupt rostrum.

COLLECTION: Twenty-five specimens and 12 single valves were collected from 9 stations between 23-455 m.

RECORDS: *Recent*—Leche 1883:437 (Kara Sea); Jensen 1905:310 (Greenland); Odhner 1915:135 (Spitzbergen); Johnson 1934:33 (Quebec to Florida); Soot-Ryen 1939:18 (Franz Josef Land); Filatova 1957b:57 (Eurasian Arctic); Ockelmann 1958:164, pl.3, f.10 (Greenland); Clarke 1962:71 (Arctic); Bernard 1974:36, pl.13, f.3, 4 (Bering Sea); Clarke 1974:12 (Baffin Bay).

DISTRIBUTION: Panarctic and throughout the North Atlantic from Greenland to Norway, Spitzbergen, and Novaya Zemlya. The range includes the Canadian Arctic Archipelago south to Massachusetts. It is present in the Bering Sea and probably the Sea of Okhotsk to Northern Japan, but does not occur south of the Aleutian Islands.

REMARKS: Dall (1886) recorded this species in the Gulf of California but Bernard (1974) showed that Eastern Pacific, excluding the Bering Sea material should be assigned to *C. subglacialis* Dall 1913, which differs by the less inflated beaks, straighter rostrum, and the subtriangular tubercle in the right valve. Likewise, Atlantic records south of Massachusetts are probably referable to *C. media* Verrill and Bush 1889.

Cuspidaria subtorta (G. Sars 1878)

Figure 108

Neaera subtorta G. Sars 1878:87, pl.6, f.6a-c; Jeffreys 1877a:235; Smith, 1885:35.
Cuspidaria subtorta (G. Sars), Verrill and Bush 1898:806, pl.73, f.1, pl.74, f.4, 5.

DESCRIPTION: Shell thin, translucent, ovate, rostrum short, tapered, upturned and twisted to the left. Maximum length 10 mm. Surface unornamented, but with irregular concentric lirae and growth marks. Periostracum ash-grey, thin, adherent. Umbones inflated, beaks prominent. Interior polished. Hinge edentulous, right valve with obscure tubercle arising from posterior margin of the small resilifer. Ligament supported by a

lithodesma. Adductor muscle scars not visible. Pallial line obscure. No pallial sinus.

COMPARISONS: This species is readily distinguished by the short, tapered and twisted rostrum. It may be confused with *C. obesa* (Loven 1846), but that species is more globular and lacks the lateral ridge in the right valve.

COLLECTION: Four specimens were collected from two stations in 71 and 360 m.

RECORDS: *Recent*—Stuxberg 1886:140 (Novaya Zemlya); Odhner 1915:136 (Spitzbergen); Johnson 1934:33 (Nova Scotia); Gorbunov 1946a:46 (Eurasian Arctic); Madsen 1949:85 (Iceland); Filatova 1957b:57 (Arctic); Ockelmann 1958:161, pl.3, f.9 (Greenland); Soot-Ryen 1958:18 (Greenland); Clarke 1974:12 (Baffin Bay).

DISTRIBUTION: Probably panarctic. This species is abundant off Greenland and extends throughout the North Atlantic to Spitzbergen and Novaya Zemlya. It has been recorded off Iceland and Nova Scotia. It occurs in the Siberian Sea, but not in Chukchi or Bering Sea. It is absent from the Pacific.

REMARKS: This is the initial record from the Alaskan Arctic. Ockelmann (1958) comments on the similarity to *C. pellucida* (Stimpson 1853) from the western North Atlantic. Although *C. subtorta* rarely attains more than 4 mm in length and sports a wide, untwisted rostrum, it is likely that careful comparison will show it to be a synonym of *C. obesa* (Loven 1846).

Family VERTICORDIIDAE Stoliczka 1871 Genus *Lyonsiella* G. Sars (M. Sars MS) 1872

Figure 112

Type species (monotypy): *Pecchiolia abyssicola* G. Sars 1872. *Recent*. North Atlantic.

DESCRIPTION: Shell thin, fragile, inflated. Surface ornamented by radial lines or ribs, sometimes with minute granules. Periostracum thin, often with adherent sand particles. Interior nacreous, shell margins plain. Hinge edentulous, left valve with obscure thickening of shell margin below beak. A small resilifer

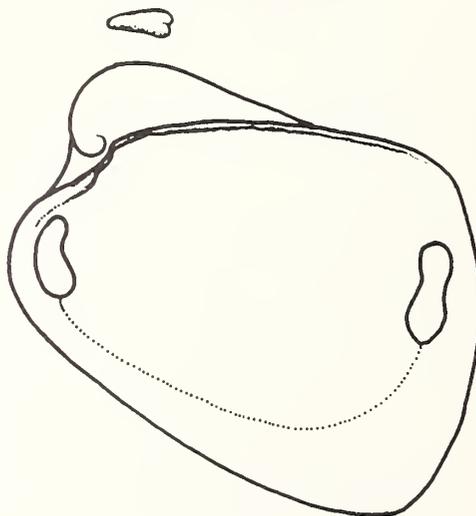


FIGURE 112. Interior of right valve and lithodesma of *Lyonsiella abyssicola* (Sars).

present in each valve. Ligament almost entirely internal, supported by large bifid lithodesma. Adductor muscle scars subequal, not impressed. Pallial line feebly impressed. No pallial sinus.

RANGE: Pliocene to Recent. Recent distribution cosmopolitan, typically in abyssal and hadal depths, generally in mixed to coarse sediments where the genus is nestling or shallowly infaunal.

DEVELOPMENT: The eggs of all species examined are large (Dall 1895; Knudsen 1970; Bernard 1974; Allen and Turner 1974), so development is lecithotrophic with a curtailed planktonic stage.

REMARKS: This genus is a member of a group of carnivorous bivalves, usually grouped with the Cuspidariidae into the superfamily Poromyacea, formerly the Order Septibranchia. I consider the phylogenies separate and any similarities the product of adaptive convergence during assumption of macrophagy and the progressive loss of the gill filter apparatus. I believe the verticordiids represent a terminal phase of a trend shown by typical anomalodesmacean genera such as *Lyonsia* and *Mytilimeria*, but are in no way transitional to the true septibranch genera of the poromyiids, *Cuspidaria* and *Cardiomya*, which demonstrate affinity to the Palaeotaxodonta. The siphons of Verticordiids are vestigial and there appears to be no burrow constructing ability as in the thyrasirids, so the group is restricted to the shallow infauna. The foot is well developed and the animal is capable of active movement over the substrate. There is a developed byssal apparatus, so at least some representatives may be epifaunal nestlers. Wagner (1977) recorded an unidentified member of the genus from the eastern Beaufort Sea.

Subgenus *Policordia* Dall,
Bartsch and Rehder 1939
Lyonsiella (*Policordia*) *uschakovi*
Gorbunov 1946

Figure 109

Lyonsiella uschakovi Gorbunov 1946:32, pl.1, f.4a-c.

DESCRIPTION: Shell suborbicular, inflated, translucent. Maximum length 6 mm. Surface with widely spaced thin radial lirae. Periostracum thin, ash-grey, with adherent particles and mucus-bound sediment. Umbones inflated, beaks prominent, area in front of beaks deeply sunken. Interior brilliantly nacreous. Hinge narrow, edentulous. Left valve with thickened posterior margin interlocking with right valve. There is an inconspicuous resilifer in each valve. Ligament almost entirely internal, supported by large cylindrical lithodesma. Adductor muscle scars not impressed. Pallial line weak, irregular. No pallial sinus.

COMPARISONS: This rotund little species is unlike any other north boreal *Lyonsiella*. It may be separated from *L. alaskana* Dall 1895 by the more globular outline and proportionately larger lithodesma. The other Arctic representative is *L. abyssicola* (G. Sars 1872) which is markedly trapezoidal in shape with the free edge of the valves sinuous, and the surface ornamented by numerous radial rows of short hexagonal spines.

COLLECTION: One broken specimen occurred at 71°19.3'N, 147°47.1'W in 2377 m.

RECORDS: *Recent*—Filatova 1957b:57 (Siberia); Clarke 1962:69 (Laurentian Basin); Clarke 1963:93, pl.2, f.3 (Laurentian Basin); Soot-Ryen 1966:21, pl.2, f.21 (Siberia).

DISTRIBUTION: Endemic in the Laurentian Basin and adjoining bathyal zones.

REMARKS: It is with some doubt that I identify this specimen with Gorbunov's species, which was collected off the New Siberian Islands (80°58'N, 142°50'E in 1475–1510 m, however Clarke (1960) has recorded the species from the northern Beaufort Sea (84°34'N, 146°24'W in 2210 m), and again (1963) from 77°42'N, 167°50'W in 711 m, firmly placing it in the Beaufort fauna. It appears to be one of the few endemic species, but doubtless others will be located when the deeper reaches of the Laurentian Basin are adequately collected.

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APPENDIX

LOCATIONS AND DEPOSITION OF ILLUSTRATED SPECIMENS

Figure	Geographical coordinates		Depth (M)	Station No.	Depository
2	70°19.3'N	147°47.1'W	2377	OSU SMG 890	LACM 71-415
3	70°19.8'N	146°26.5'W	34	OSU OTB 460	LACM 72-252
4	70°43.0'N	149°02.0'W	50	OSU OTB 419	LACM 71-363
5	71°19.6'N	147°48.2'W	2560	OSU SMG 891	LACM 71-416
8	71°12.0'N	149°15.0'W	64	OSU SMG 956	LACM 71-457
9	71°22.5'N	152°22.6'W	88	OSU SMG 1320	LACM 76-60
10	70°34.8'N	144°23.1'W	71	OSU OTB 450	LACM 72-243
11	71°31.0'N	156°02.2'W	110	OSU SMG 1272	LACM 76-58
12,13	70°10.2'N	144°33.0'W	27	OSU OTB 453	LACM 72-246
15	70°10.2'N	144°33.0'W	27	OSU OTB 453	LACM 72-246
16	71°08.2'N	152°57.5'W	26	OSU SMG 1360	LACM 76-61
17	70°37.6'N	148°32.0'W	29	OSU SMG 1295	LACM 76-59
18	71°45.1'N	150°35.0'W	2130	OSU SMG 1023	LACM 71-491
19	71°15.2'N	149°28.8'W	991	OSU SMG 948	LACM 71-452
20,21	70°34.8'N	144°23.1'W	71	OSU OTB 450	LACM 72-243
22	70°51.5'N	145°17.0'W	357	OSU OTB 457	LACM 72-250
23	71°05.7'N	148°41.0'W	55	OSU OTB 467	LACM 72-256
25	71°50.5'N	153°10.7'W	384	USGS PPB 42	USGS M6936
26	71°12.0'N	148°35.0'W	360	OSU OTB 418	LACM 71-362
27	70°41.6'N	145°23.8'W	79	OSU OTB 450	LACM 72-243
28	71°04.1'N	151°21.5'W	64	OSU SMG 972	LACM 71-464
30	70°56.1'N	147°50.6'W	47	OSU OTB 833	LACM 36528
31	71°05.7'N	148°11.0'W	55	OSU OTB 467	LACM 72-256
33	70°10.3'N	144°33.0'W	27	OSU OTB 453	LACM 72-246
34	71°05.7'N	148°11.0'W	55	OSU OTB 467	LACM 72-256
35	70°31.7'N	147°33.5'W	29	OSU OTB 463	LACM 72-254
36	70°10.2'N	144°33.0'W	27	OSU OTB 453	LACM 72-246
37	70°10.2'N	144°33.0'W	27	OSU OTB 453	LACM 72-246
42	70°43.0'N	149°06.0'W	31	OSU OTB 420	LACM 71-364
43,44	71°18.1'N	152°32.2'W	55	USGS PPB 55	USGS M6936
45	70°51.5'N	145°17.0'W	357	OSU OTB 453	LACM 72-246
49	71°01.0'N	148°22.7'W	48	OSU SMG 933	LACM 71-445
50	71°14.3'N	149°22.9'W	695	OSU SMG 950	LACM 71-454
51	71°22.0'N	150°38.0'W	997	OSU SMG 1022	LACM 71-490
52	71°14.3'N	149°22.9'W	695	OSU SMG 950	LACM 71-454
56	70°55.8'N	153°12.8'W	0.5	WWSC M12	LACM 36529
57	70°31.8'N	147°33.5'W	29	OSU OTB 463	LACM 72-254
58	71°14.1'N	149°21.7'W	603	OSU SMG 952	LACM 71-456
59	70°30.3'N	144°21.6'W	46	OSU OTB 451	LACM 72-244
63	70°50.0'N	147°21.6'W	47	OSU SMG 879	LACM 71-406
64	71°17.6'N	152°43.4'W	53	OSU SMG 1495	LACM 36530
65	70°43.1'N	143°42.8'W	464	OSU OTB 449	LACM 72-242
66	71°12.0'N	149°15.0'W	65	OSU SMG 954	LACM 71-457
67	71°10.0'N	149°18.9'W	51	OSU SMG 958	LACM 71-458
68	71°10.1'N	152°32.2'W	55	OSU SMG 1341	LACM 36531
69	71°12.0'N	152°49.0'W	30	OSU SMG 1502	LACM 36532
70	70°48.5'N	145°56.1'W	270	OSU SMG 855	LACM 71-402
71	71°12.0'N	148°36.0'W	80	OSU SMG 932	LACM 71-444
72	71°13.0'N	152°42.0'W	37	OSU SMG 1187	LACM 36533
75	71°04.1'N	151°21.5'W	64	OSU SMG 972	LACM 71-464
76,77	71°21.5'N	149°32.2'W	48	OSU SMG 946	LACM 71-450
79	70°43.0'N	149°00.0'W	23	OSU SMG 967	LACM 71-459
80	71°50.4'N	153°10.7'W	384	USGS PPB 78	USGS M6941
81	70°34.8'N	144°23.1'W	71	OSU OTB 450	LACM 72-243
82	70°31.7'N	147°33.5'W	29	OSU OTB 463	LACM 72-254
83	70°34.6'N	143°38.0'W	21	OSU SMG 839	LACM 71-399

85	70°14.7'N	143°23.6'W	28	OSU OTB 446	LACM 72-239
86	70°15.5'N	143°39.6'W	35	OSU SMG 821	LACM 36534
87	71°04.1'N	151°21.5'W	64	OSU SMG 972	LACM 71-464
88	71°04.1'N	151°22.2'W	21	OSU SMG 969	LACM 71-461
92	70°25.0'N	147°05.0'W	47	OSU SMG 872	LACM 71-405
93,94	70°04.9'N	143°38.7'W	2	WWSC CP 38	LACM 36535
95	70°10.2'N	144°33.0'W	27	OSU OTB 453	LACM 72-246
96	70°19.8'N	146°26.5'W	34	OSU OTB 460	LACM 72-252
97	70°19.8'N	146°26.5'W	34	OSU OTB 460	LACM 72-252
98	70°31.7'N	147°33.5'W	29	OSU OTB 463	LACM 72-254
99,100	71°19.0'N	152°38.5'W	55	OSU SMG 1159	LACM 36536
104	71°28.9'N	151°40.9'W	709	USGS PPB 42	USGS M6936
105	70°55.7'N	149°23.2'W	64	OSU SMG 998	LACM 71-482
106	71°05.7'N	148°41.0'W	55	OSU OTB 467	LACM 72-256
107	70°43.1'N	143°42.8'W	455	OSU OTB 449	LACM 72-242
108	70°34.8'N	144°23.1'W	71	OSU OTB 450	LACM 72-243
109	71°19.3'N	147°47.1'W	2377	OSU SMG 890	LACM 71-415

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Number 314

July 31, 1979

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

THE CATCH OF BOWHEAD WHALES (*BALAENA MYSTICETUS*)
BY ESKIMOS, WITH EMPHASIS ON THE WESTERN ARCTIC

By Floyd E. Durham



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Edward Ostermeyer
Editor

Number 314

July 31, 1979

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

THE CATCH OF BOWHEAD WHALES (*BALAENA MYSTICETUS*)
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By Floyd E. Durham



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THE CATCH OF BOWHEAD WHALES (*BALAENA MYSTICETUS*) BY ESKIMOS, WITH EMPHASIS ON THE WESTERN ARCTIC^{1, 2}

By FLOYD E. DURHAM³

ABSTRACT: The success of Eskimo spring whaling along the northwestern coast of Alaska depends on the opening of offshore leads in the sea ice, the presence of bowheads, and the number and ability of the hunters to kill, secure, and butcher these animals. Physical factors, such as wind, current, and temperature affect the formation of leads. The number and proximity of leads to shore, the frequency and manner of passing of bowheads, and the topography and duration of the ice platform are variable, but are most dependable at the promontories where the major whaling villages are located.

The time period and the actual number of years for which data are available (in parentheses), the number of whales killed, and the yearly average at the principal villages are: Barrow, 1852–1973 (52 yrs), 371 whales, 7/yr; Point Hope, 1879–1973 (60 yrs), 241 whales, 4/yr; and Wainright, 1922–1973 (32 yrs), 48 whales, 1.5/yr.

The total of the three villages is 660 whales with a combined average of 12.5/yr. Five of the several minor stations active from 1961 to 1973 took 22 whales, average of 2/yr, making a total average of known whales secured in Alaska 14.5/yr through 1973. Recent harvests (1974–1977) have been considerably higher than the stated average.

Bowhead whales (*Balaena mysticetus* Linnaeus 1758) of the western Arctic and the Eurasian coast migrate southward into the Bering Sea in winter. On their annual spring migration northward most of the bowheads swing eastward into the Beaufort Sea passing close to promontories along the northern Alaskan coast where Eskimo whaling villages (Fig. 1) have been active for perhaps 5000 years (Rice 1974).

Although several authors (Scammon 1874; Bailey and Hendee 1926; Brower, Farrelly and Anson 1942; Rainey 1940 and 1947; Sonnenfeld 1960; Maher and Wilimovsky 1963; Stefansson 1924; Johnson, et al. 1966; Lindsay 1968; Davidson 1972; Rice 1974; and Durham 1974) have described the hunting of bowhead whales by Eskimos, scant information is available on the number of whales taken.

Prior to the coming of commercial whalers, explorers, and missionaries to the Alaskan Arctic in the mid-19th century, the only evidence of bowhead catches were bone-strewn beaches of Eskimo shore whaling stations, such as the ancient one at Barter Island; whale bones in the ruins of old village houses, such as those at Point Barrow; and the jaw bones of whales in the cemetery fence at Point Hope. Because the Eskimos do not have a written language, only their legends and folklore reveal the feasting and starvings of those coastal people who relied mainly on bowheads for food, fuel, building materials, and tools. Relatively prosperous whaling cultures developed in some larger villages. With competition from commercial whalers, the Eskimo catch of whales and food supply derived from it decreased. Introduced diseases depleted the native population, resulting in fewer men to hunt the diminishing stock of whales.

A few of the commercial whalers, explorers, and scientists

made casual notes of bowheads taken. It was only after the Eskimos learned English that they started keeping written records of catches — beginning about 1890 at Point Hope and about 1928 at Barrow. Wainright people still rely on memory. During recent years the Naval Arctic Research Laboratory (NARL) at Barrow has recorded all whale kills along the north coast of Alaska, and several research institutions are keeping supplementary records. Several investigators (herein mentioned) have reported fragments of catch data for several Eskimo villages, but the only extensive record is that of Maher and Wilimovsky (1963) on Barrow whaling from 1928 to 1960. To these published sources I have added my data from 1961 to 1973 and numerous unpublished records, mostly from personal communications. In the few instances of conflicting data, I chose the source judged to be the most reliable.

Table 1 shows up to 1973 the known catch of bowheads by Eskimos from 1928 (46 yrs) for Barrow; from 1879 (60 yrs) for Point Hope; and from 1922 (32 yrs) for Wainright. Catch data

¹Sponsored in 1973 by the National Marine Fisheries Service and prior years by the Arctic Institute of North America with the financial support of the Office of Naval Research under contract N00014-70-A-0219-0001 (subcontract ONR-367).

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TABLE 1

Catches of bowhead whales at the Alaskan whaling villages of Barrow (including Point Barrow, Barrow Village, and Cape Smythe), Point Hope and Wainwright, 1852–1973. Data sources as follows (a blank indicates no data): *Barrow*, 1852–1853 from Simpson (1855); 1882–1885 from Murdoch (1885), (10 whales mentioned by Murdoch assigned to 1884); 1928–1960 from David Brower, reported in Sonnenfeld (1960), Maher and Wilimovsky (1963), and Bee and Hall (1956). *Point Hope*, 1879 from Bean (1887); 1890–1948 from Don C. Foote (personal communication); 1949–1960 from H. Kinneveauk (personal communication), and Johnson, *et al.* (1966). *Wainwright*, 1922 from Bailey and Hendee (1926); 1941, 1949–1950 from Maher and Wilimovsky (1963); 1961–62 from D.W. Rice (personal communication); remaining years from R. Aveoganna, W. Bodfish, W. Ekak, H. Killbear, and F. Milan (personal communication). All other data from author and NARL.

YEAR	BARROW			POINT HOPE	WAIN-RIGHT	YEAR	BARROW			POINT HOPE	WAIN-RIGHT
	SPRING	AUTUMN	TOTAL	TOTAL	TOTAL		SPRING	AUTUMN	TOTAL	TOTAL	TOTAL
1852			17			1937	9	0	9		
1853			7			1938	2	2	4		5
1879				5		1939	6	0	6		
1882			1			1940	0	0	0	5	
1883			1			1941	2	0	2	8	1
1884			10			1942	7	3	10		
1885			28			1943	6	0	6		1
1890				1		1944	0	0	0		2
1892				0		1945	3	0	3	3	6
1898				1		1946	4	5	9	2	1
1901				1		1947	2	2	4	5	1
1902				2		1948	5	0	5	0	
1903				0		1949	0	0	0	4	2
1904				0		1950	4	0	4	2	2
1907				0		1951	9	0	9	4	
1908				13		1952	0	0	0	2	2
1909				12		1953	17	0	17	4	
1911				3		1954	1	0	1	3	
1912				1		1955	15	0	15	1	1
1913				1		1956	1	1	2	2	0
1914				2		1957	0	0	0	3	0
1915				3		1958	0	0	0	2	0
1916				7		1959	0	0	0	1	0
1917				3		1960	15	0	15	4	0
1918				7		1961	2	2	4	2	1
1919				2		1962	0	3	3	6	1
1920				3		1963	2	1	3	3	2
1921				2		1964	1	10	11	1	1
1922				13	3	1965	3	1	4	2	0
1924				16		1966	3	4	7	4	1
1925				10		1967	0	3	3	1	0
1926				13	1	1968	9	0	9	3	2
1927				3		1969	10	0	10	3	4
1928	7	4	11			1970	15	0	15	8	0
1929	9	4	13			1971	11	2	13	5	2
1930	5	2	7			1972	15	4	19	14	2
1931	8	3	11	1		1973	15	2	17	5	3
1932	4	3	7			Totals	238	69	371	241	48
1933	0	5	5								
1934	1	3	4								
1935	6	0	6								
1936	4	0	4	4	1						

Grand total of three stations: 660

from 1961 (13 yrs) for five minor whaling stations in or near the Arctic are given in Table 2.

DISTRIBUTION AND DEPLETION

The bowhead, or Greenland whale, inhabits Arctic and occasionally sub-arctic waters. Of the three or possibly four principal stocks which flourished historically, that of the western Arctic (Chukchi and Bering Seas) has best survived commercial whaling of the species from the early 1600s to the early 1900s (Tomilin 1967). The commercial whale fishery is generally held responsible for the nearly worldwide extirpation of the bowhead by the end of the 19th century. Rice (1974) estimated the western Arctic

stock at 4000–5000 during the period from 1868 to 1884. The collapse of the baleen market and the end of commercial bowhead whaling occurred in 1909. Although all stocks show some recovery, the bowhead is still legally classified as an "endangered species" by the United States Endangered Species Act of 1973 and a "protected stock" by the International Whaling Commission.

During the summer months the western Arctic stock is principally in shallow waters of the northern Bering, Chukchi, and Beaufort Seas (Fig. 1), extending eastward as far as Banks Island (Rice 1974). However, Mansfield (1971) reports recent sightings of bowhead whales east of Banks Island in the Amundsen and Coronation Gulfs, and assigns these whales to the western Arctic

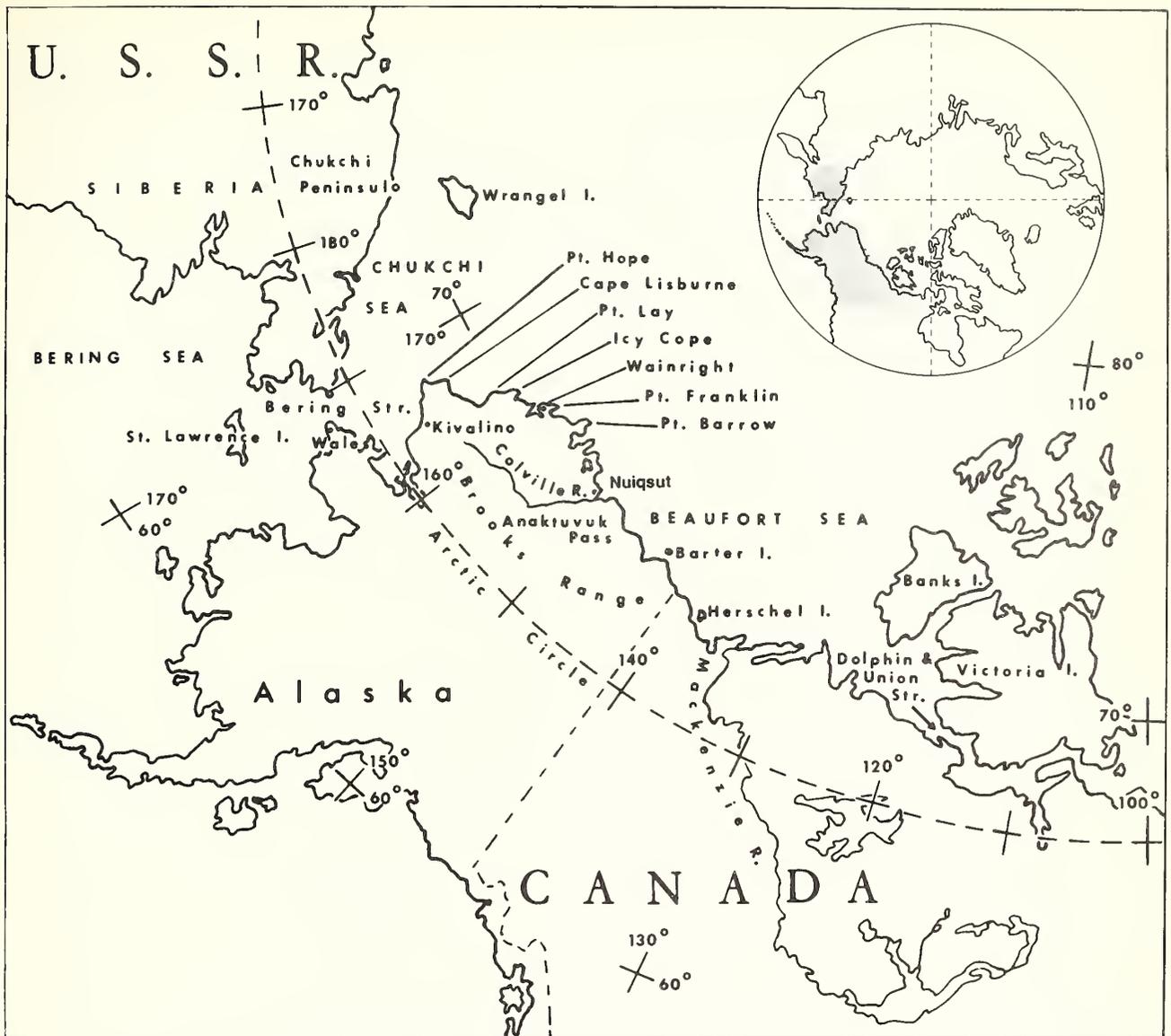


FIGURE 1. Principal Eskimo whaling villages in the western Arctic.

stock. Bowheads that occur in the Okhotsk and East Siberian Seas (Chukchi Peninsula) are thought to belong to this same stock (Tomilin 1967). However, Townsend (1935), based upon Scammon (1874), considered the Okhotsk bowhead as separate from the western Arctic stock, and Rice and Scheffer (1968) list it as a fourth stock. As the shore ice and pack ice form in autumn, the whales in the Arctic Ocean migrate southward through the Bering Strait.

PRINCIPAL VILLAGES

BARROW

Barrow is one of the largest (population about 2100) and oldest Eskimo whaling villages (Fig. 1). Bowheads appear there in mid-April. Spring whaling begins then and continues through

May. The whales return in the autumn ahead of the pack ice and are hunted from about mid-September to mid-October.

The oldest catch records are by Simpson (for years 1852–53), Murdoch (for 1882–85), and David Brower (for 1928–54) and were assembled by Sonnenfeld (1960). The annual catch of whales varied even more in the 19th century than in the 20th. The catch of 17 in 1852 indicated that the Barrow Eskimos, using only primitive whaling gear, were successful hunters even before the Yankee whalers arrived in 1854 (Table 1). Because of the reduced number of bowheads and competition from commercial whalers, the Eskimos took only a few whales during the 30 years following 1853 (Murdoch 1885). When the commercial fleet went beyond Barrow in the mid-1880s to better whaling grounds off the northwestern Canadian mainland and Banks Island, Eskimo whaling improved as indicated by the catch of 28 whales in 1885. The Cape Smythe whaling station was established at Barrow by Charles Brower in 1884 (Vanstone 1958). This enter-

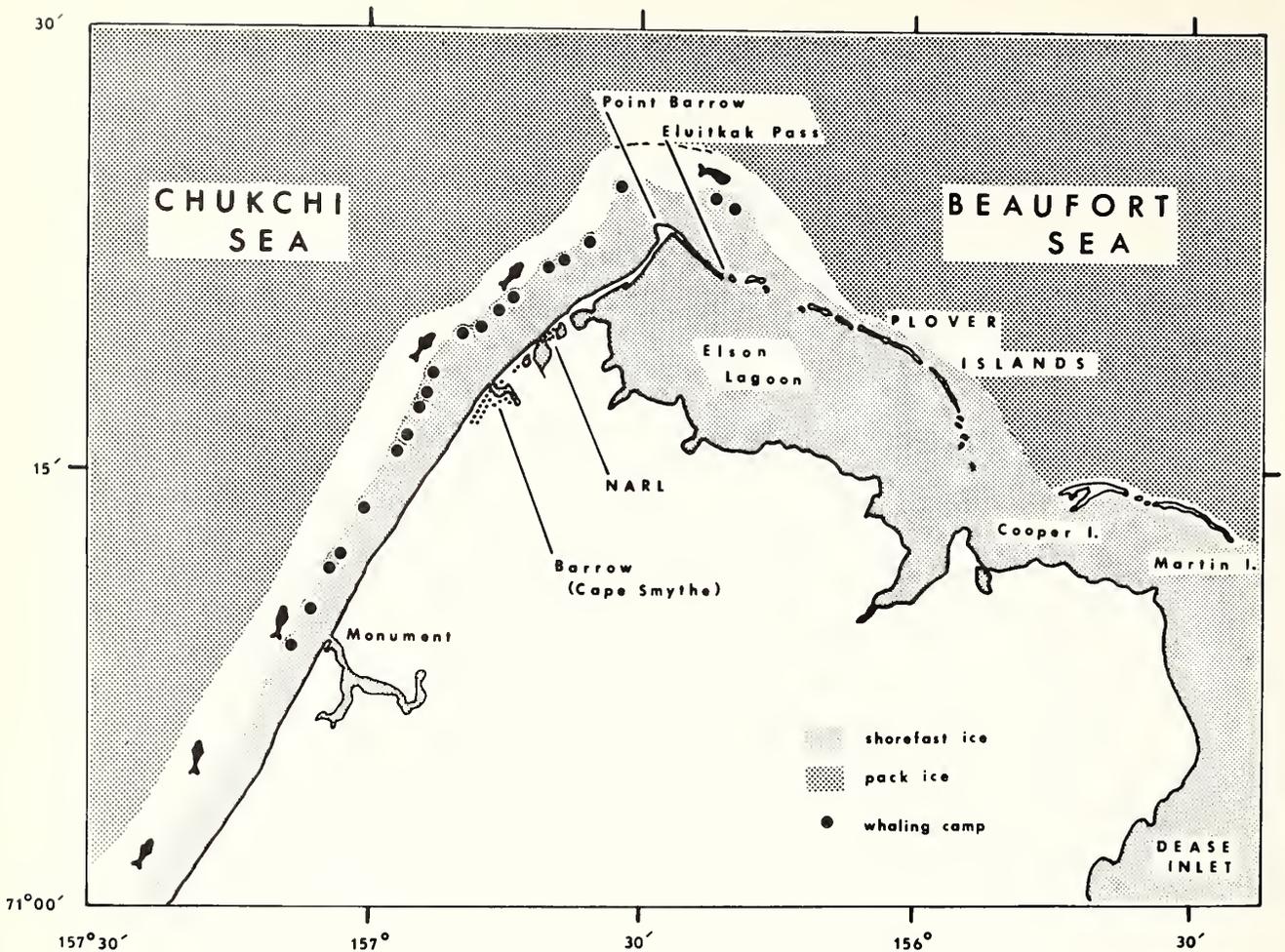


FIGURE 2. Typical ice conditions and bowhead whale migration route at Point Barrow, Alaska.

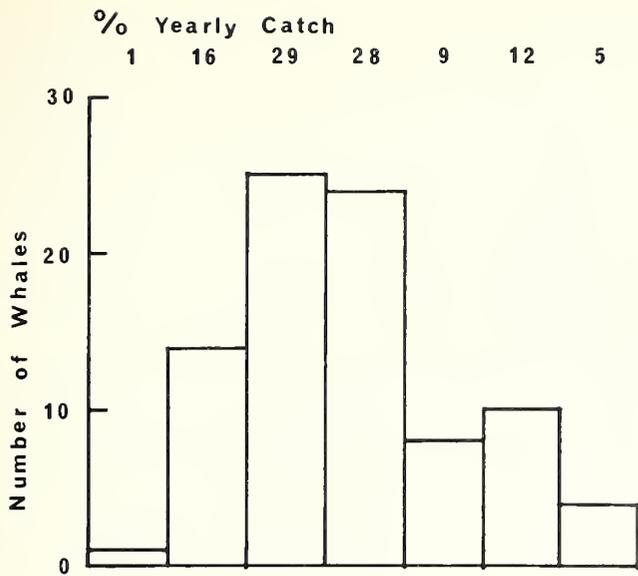
prise hastened the Eskimo's changing from the old style to early modern whaling, and has been described by authors previously cited.

More recent catch records (1928–1960) were summarized by Maher and Wilimovsky (1963). Thereafter, through 1973, I personally observed whaling at Barrow or obtained catch data from reliable sources. From 1852 to 1973 (data for 52 yrs) 371 bowheads (0–19 whales/yr, av 7) were taken. Seven years were lean (no whales taken) and 16 were feast years (ten or more whales at Barrow). Success in whaling varies from year to year and between spring and autumn seasons, particularly the latter. Whales were not taken in ten of the spring seasons and 24 of the autumn seasons. Ten or more whales (maximum 17) were taken in eight spring seasons, but ten whales were obtained in only one autumn season.

Bowheads are sometimes sighted by Eskimos off Barrow in early April, which agrees with the observations of Maher and Wilimovsky (1963), but are seldom hunted until mid-April. My data show that the earliest spring kill was 25 April 1969. However, the first kill usually occurs with remarkable regularity two weeks later. The records of NARL show that the first whale of the 1955 season was taken 6 May. The first bowhead I saw butchered was 6 May 1961. Records show that the first bowhead

obtained in the spring during the 13 years (1961–73) I was at Barrow, was taken from 4 to 6 May in 50 percent of the years. Of the 41 spring whales harvested during 1971–73, 11 (37 percent) were taken between 5 and 7 May. Fifty-two percent of the whales taken in the springs between 1961 and 1973 were harvested in the first two quarters of May, and 71 percent in the first three quarters (Fig. 3). Whales were taken in the last quarter in one-third of the years. The 1969 whaling season began unusually early (10 whales were taken in the last quarter of April) and continued unusually late (the last whale was taken 2 June, the first whale killed in June at Barrow for 15 years). September 21, 1965 was the earliest autumn catch from 1961–1973. During this period four whales were taken in the third quarter of September. The whalers are most successful in the first quarter of October when 11 (37 percent) of the 30 autumn bowheads were caught. Sixty percent of the autumn whales were taken in the first half of October. Whales were taken in the third quarter in only one-fifth of the years, the latest catch being 23 October in both 1966 and 1973. Autumn whaling is less rewarding than spring whaling. Often the best efforts of the whalers in autumn are entirely thwarted by the vastness of the hunting area, the frequency and severity of storms, or the encroachment of ice. The season ends about mid-October.

POINT HOPE



BARROW

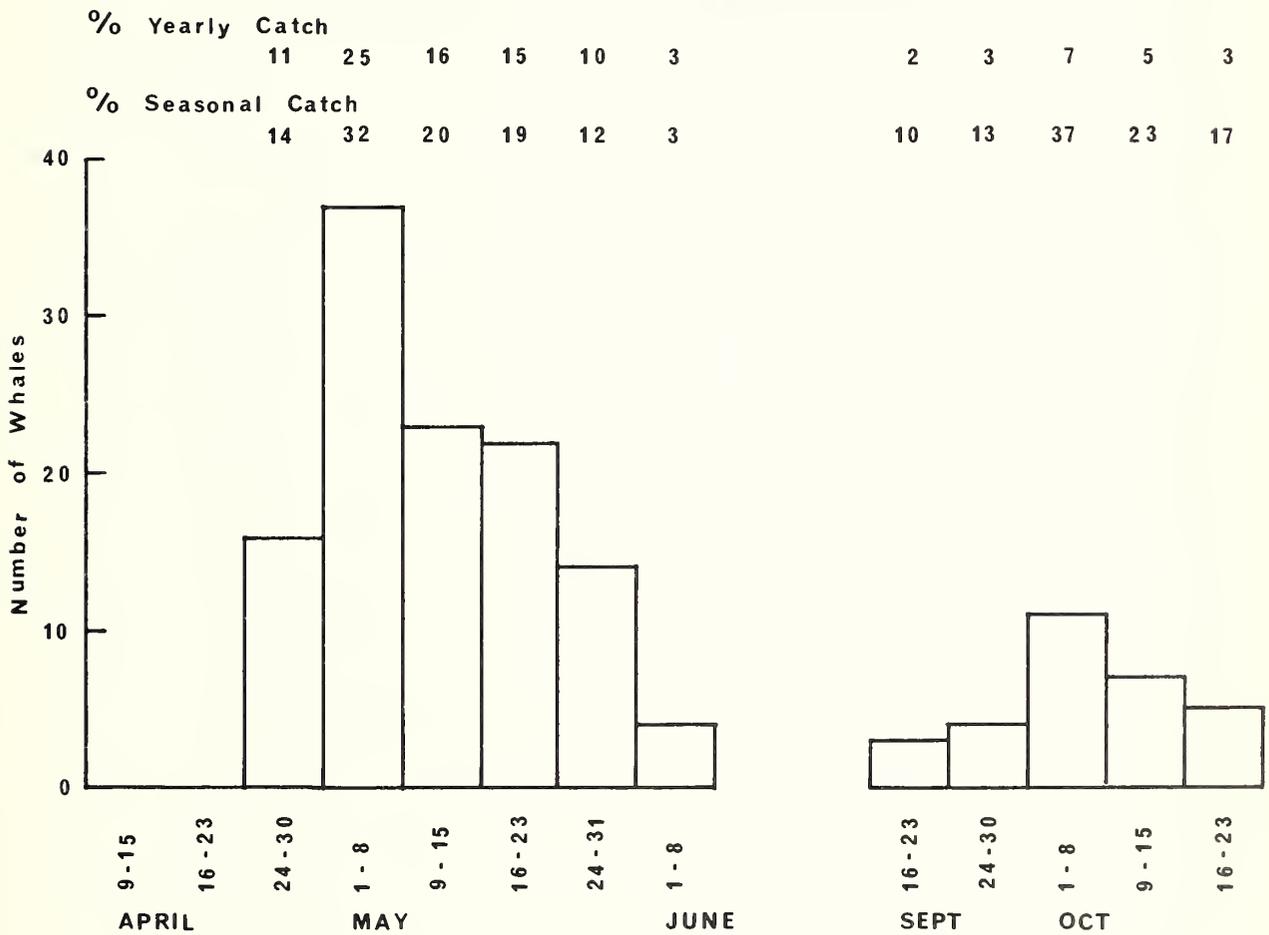


FIGURE 3. Histogram showing the actual and relative frequency of kills of bowhead whales of known dates by seasons and quarter months at Barrow (1928-1973) and Point Hope (1949-1973). Struck and lost whales are not included.

POINT HOPE

Point Hope, 560 km (350 mi) southwest of Barrow, is a village of about 500 Eskimos (Fig. 1). Although it has less than half as many whaling crews as Barrow, its catch of whales is more consistent. The first record for Point Hope is for 1879 and records are fairly consistent after 1890. The take of 241 whales in 60 years varied from zero to 16 per year (av 4). None were taken in five years, and ten or more were taken in seven years. A catch of five whales, constituting a feast year, occurred 16 times. Sixteen whales taken in 1924 is the largest recorded catch for the village (Table 1).

The lead near Point Hope opens in early April when bowheads are commonly seen, trails from the village to the lead are opened, and camps are set up on the ice. Foote (personal communication) gave 19 March as the earliest date when bowheads were sighted. However, in 1971 the first whale was seen 1 March (Herbert Kinneeveauk, personal communication via John Bockstoce).

During the last 25 years for which kill dates are available, 48 of the 86 bowheads (57 percent) were killed between 24 April and 8 May, 63 (73 percent) were killed between 16 April and 8 May (Fig. 3). The earliest and only catch prior to 16 April was 9 April 1954. Bowheads were taken 16–23 April in eight of 23 years. Because of adverse ice and wind in 1973, only a half dozen whales were sighted in April, and the first kill was not until 5 May. One whale was taken in the last quarter of May in each of four years. A single bowhead was taken 28 May 1967, the latest catch in 23 years. Whaling continues into June if ice conditions permit. Early records (1890–1948) of whales killed at Point Hope were casually kept. However, since 1949 written records have been faithfully kept by Herbert Kinneeveauk who supplied the information for 1949 to 1960. Thereafter, I kept in touch with the villagers.

Although Point Hope ranks second after Barrow (in whales taken), it is first in uniformity of catch, particularly from 1945 to 1969 (Table 1) when one to six whales were taken each year. Prior to 1945 the fluctuation in the catch of zero to sixteen whales may have been due to competition by commercial whalers, semicommercial whaling by the Eskimos, or faulty records.

WAINRIGHT

One hundred thirty-five km (85 mi) southwest of Barrow is Wainright, which ranks third in population (about 400 Eskimos) and in bowheads taken. Although there is a long spring season at this location, catches are sporadic, usually meager, and the arduous season often ends in failure. Although the village is not on a promontory, it is surprisingly successful at whaling. Bowheads have been reported off Wainright in March by seal hunters (Waldo Bodfish, personal communication), but hunting of whales usually starts in early May. Because of persistent shore-fast ice in late May and early June, many of the whales taken are large males and pregnant or lactating females which pass by late in the season (see Runs of Whales). The latest catch reported for any spring season is that of a 16 m (53 ft) male by Raymond Aguvluk on 20 June 1968. Bowheads are sometimes seen off Wainright in autumn, but never in sufficient numbers to justify hunting them. The village also lacks plank boats and heavy machinery for beaching and butchering whales in autumn. The 400 inhabitants of Wainright support about four whaling crews. Forty-three

whales (up to six per year) have been taken since 1936, interspersed with many lean years (Table 1). The most recent lean period was 1956–1960 when no whales were taken. My indications of whaling failures in the 1920s and 1930s may be misleading because the villagers concentrated their efforts at Icy Cape (see discussion of Icy Cape), averaging about one whale per year. The catch of six bowheads off Wainright in 1945 was a record. Three whales make a feast year for this small village.

SPRING MIGRATION AND THE RUNS OF WHALES

As the Yankee commercial fleet waited in the spring at St. Lawrence Island and Nome for a chance to enter the ice-choked Chukchi Sea, it was passed by bowheads on their way to the Arctic (Brower, Farrelly, and Anson 1942; Cook 1926; and Scammon 1874). This is the true beginning of the spring migration of the bowhead of the western Arctic, which occurred, and still does, with annual regularity. The inherent urge of the whale is timed with the breaking up of the ice pack. The whales use leads (channels of open water) as passageways through sea ice from the Bering Strait to their summer feeding grounds off the Mackenzie River and Banks Island, northern Canada. The lead opens with the first moderation of temperature and brisk easterly wind.

Normally a hunting lead 1.5 to 6.5 km (1 to 4.5 mi) offshore, from Will Rogers-Wiley Post Monument to beyond Point Barrow, is accessible to Barrow whalers so that some 20 to 25 hunting camps can be set up at strategic points along this 40 km (25 mi) stretch. Occasionally the leads are short and broken, or lie at nearly right angles to shore, as I observed in 1973. Rarely no shore lead opens as in 1968 when no shot was fired. In 1962 a continuous and reasonably stable lead, extending from Kotzebue Sound to Banks Island (Foote, personal communication), allowed the bowheads to pass Barrow 240 km (150 mi) offshore outside the hunting range of the Eskimos. Equally rare is a long and relatively stable lead that forms early near shore allowing whales to pass steadily for some three months, within easy reach of the hunters. Such may have been the case in 1882 and 1883 when Murdoch (1885) described the spring migration past Barrow as a "run." Maher and Wilimovsky (1963) agreed. However, on the basis of my observations, catch data, and the opinion of Eskimo whalers, I conclude that the spring migration normally consists of a series of runs with the peaks 7 to 15 days apart. A run is when many whales pass during a period of a few days. These runs are most evident at promontories such as Point Hope and Point Barrow, but they are also mentioned by John Burns (personal communication) at St. Lawrence Island where leads do not form.

Because of variations in temperature and currents, and in direction, velocity, and duration of wind, leads tend to open, close, and reopen, with shifting winds, to freeze over, and shift position throughout the season. These changes may be gradual, requiring days or weeks, or they may occur in moments with alarming speed and force sufficient to destroy a whaling camp, hunting equipment, and a secured whale, and to even threaten human life. Such changes in the lead affect the migration of the bowhead. Prolonged closing of a shore lead tends to confine the whales in "ponds" of open sea water (polynyas) or forces them to travel in leads so far from shore as to be beyond the sight and reach of the Eskimos. When the lead reopens the halted whales may pass through in considerable numbers, sometimes singly, in

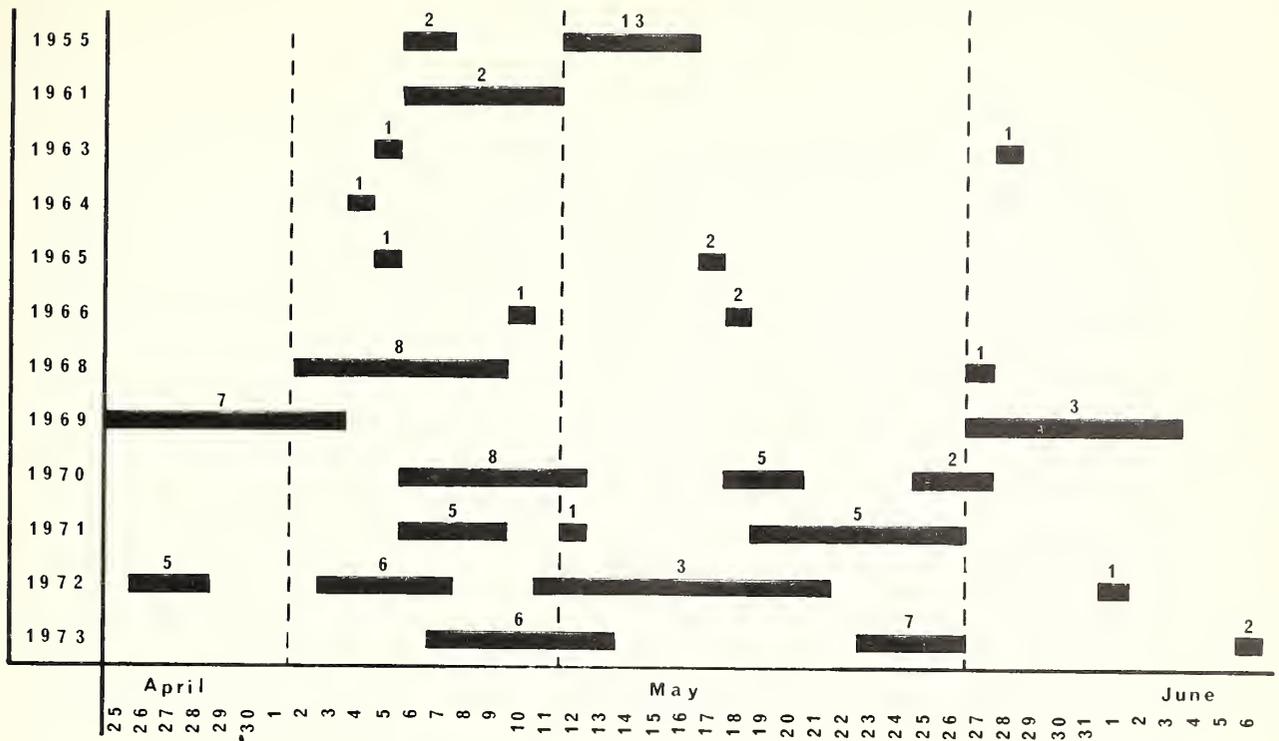


FIGURE 4. Successful hunting periods (indicated by horizontal black bars) and respective number of bowhead whales secured (numbers above horizontal bars) at Barrow during years for which date-of-kill data are available. The spacing of these periods of harvest suggest that most of the bowhead whales pass Barrow in a series of four runs (indicated by vertical, dashed lines).

twos and threes or in herds so large and compact that it is impossible to count them. For example, during a four day period (5–8 May) Sam Taalak (personal communication) observed a remarkably consistent pattern of one whale passing every ten minutes. Equally spectacular were the 500 whales that passed Wainwright (Nelson 1969), and the hundreds of whales seen daily at Point Hope in 1972 (Billy Weber, personal communication). Except for such unusual and long-remembered field observations by whalers and others, most of the evidence of runs is obtained from meager catch data which usually give only the number and dates of kills with no mention of size, sex, number of sightings, whales struck and lost, and the “days dead” of stinkers (dead whales found by hunters). On the basis of whales killed and recovered at Barrow, particularly during feast years, there appears to be four runs (Fig. 4). The data is best read horizontally by year. Breaks between runs are suggested by broken vertical lines. When few whales were taken (1961–1966) most of these were taken in the first three weeks of May (i.e. runs 2 and 3). It is only when the sampling is larger, and the killing span is longer, as in 1972, that the four runs are clearly shown from catch data. Although 1970, 1971, and 1973 also yielded large catches, the spans were short and only two or three runs at most are shown per season. This does not mean that bowheads did not pass and were not fired upon by hunters in the other runs. For example, the 1955 data illustrates this when adjusted to show dates of kills rather than dates of recoveries. That year the Barrow crews were on the lead 25 April for the first run but had no success. Two whales were taken 6–7 May in the second run. The third run, beginning 12 May when a whale was struck and lost, was very successful,

totaling 13 whales, and apparently extending to 23 May. However, the run actually ended 16 May after the 10th whale of the season had been killed and harvested and other whales had been struck but lost. The remaining 6 days (17–23 May) were expended in salvaging some muktuk and dog food from 5 stinkers, apparently all shot on or before 16 May. There was no need to hunt in June (fourth run) because the village was abundantly supplied with whale products.

It is apparent that the second run, about 2–11 May, is the most productive. However, if the lead develops and the whales appear in the last week of April, as was the case in 1969 and 1972, many whales may be taken during the first run. Disintegration of the sea ice the last half of May may allow great numbers of whales to pass and many to be killed as was the case in 1970, 1971, and 1973, although the whales of the third run are sometimes relatively inaccessible to hunters because the widening leads confine them less and less.

The segregation of age and sex groups in the first three runs is not sharp. The catch is primarily of immature whales (estimated to be one to three years old) 7.3 to 9 m (24 to 30 ft) long which are not wary and which tend to follow the flaw (edge of the shorefast ice) more closely than do the older whales. Although large whales are occasionally taken in the first run (e.g. an 18.3 m (60 ft) one on 24 April 1956) and in the second run (e.g. two 15.2 m (50 ft) whales on 5 and 7 May 1956), those 12 m (40 ft) and longer are not common until the second and third runs. Whales of all ages and both sexes pass in the fourth run, the last week of May and first week of June, but the run is characterized by the slow-moving cows with nursing calves. Large males may

also be present.

Usually the shore ice platform deteriorates by the end of May so that whaling becomes dangerous or impossible. Whaling is then casual and the take is small but occasionally late whaling (the fourth run) is successful at Barrow, as in 1969. It is often the best part of the season at Wainright.

It is thought that whales continue to pass Barrow during the rest of June but that the disintegrating sea ice keeps the Eskimos on shore and prevents their observing the migrating whales.

The speed of migration along the Alaskan coast in spring has already been suggested by the contrast in beginning, peak, and end of the spring whaling (Fig. 3). The same pattern of whaling as at Point Hope also occurs one to two weeks later at Barrow, suggesting that two weeks may be required for the whales to travel the 560 km (350 mi) from Point Hope to Barrow, that is, about 40 km (25 mi)/da or 1.6 km (one mi)/hr.

Improved airplane and radio communications allow a closer estimate of speed of migration. When a lead opens and whales pass Point Hope, whalers at Barrow are alerted and they prepare to intercept the whales ten days later (Pete Sovalik, personal communication). With ideal ice and weather conditions, the 10-day travel time indicates 56 km (35 mi)/da or 2.4 km (1.5 mi)/hr.

Tomilin (1967) gives speeds of 7.4 km (4.6 mi)/hr for a "relaxed bowhead" and 13 to 16 km (8 to 10 mi)/hr for a wounded whale. He also suggests that the migration may be interrupted for periods of sleep and by temporary confinement to polynyas (a small area of open water, or a pond, completely surrounded by sea ice).

RETURN MIGRATION AND AUTUMN WHALING

Anthropologists, explorers, whalers, scientists, and others have described ancient and current spring whaling by Eskimos, but little has been reported on autumn whaling. Actually most of the whales taken by commercial whalers in the western Arctic in the last half of the 19th century were taken in autumn. By the time the whaling ships worked their way from Bering Strait to Point Barrow, the whales were returning. Most of the commercial whalers operated from sailing or steam ships and harpooned the whales in the open sea. They used their open whale boats as drags for wearing down the whales. In certain areas off Alaska, these whales were and are accessible to the local Eskimos. They, too, made harpoon and line fast in the whale, but used floats of seal skin (currently of plastic), as in their spring hunting, to mark and tire the fleeing whale.

In summer the pack ice usually withdraws some 80 km (50 mi) making available the shallow seas where bowheads tend to feed in summer. Sometimes by early August the first whales start their return migration. They travel westward from Banks Island and the delta of the Mackenzie to Point Barrow. A few turn southwest to follow the coast, as illustrated by the three whales that were taken off Barrow in 1964, and the several I sighted off NARL in 1967. Formerly, when bowheads were more numerous, local folklore indicates that some autumn whaling occurred at Wainright and Point Hope. However, most of the whales avoid these coastal villages and travel westward across the Chukchi Sea. The whales then turn south and pass through the Bering Strait to winter in the Bering Sea where they frequent the southern edge of the ice, which usually extends across the Bering Sea

from southwestern Alaska to the Kamchatka Peninsula (Rice 1974). The southern extent of the winter pack ice varies from year to year; in less severe winters the whales may not need to escape through the Bering Strait (Nishiwaki 1967 and Scammon 1874).

Some autumn whaling occurs or has occurred at Barter Island and Cross Island; however, the Barrow area, from the Will Rogers-Wiley Post Monument to the Point and eastward along the Plover Islands, is the major place where autumn whaling is profitable. Point Barrow has a long whaling history, judging from the remains of the ancient Nuwuk village at the Point. It is to be noted that in Eskimo spring whaling the skulls are normally left on the ice after flensing or are returned to the sea in a ritual. Because of the numerous skulls I, and Bee and Hall (1956), found at the Point, I conclude that they are from whales taken in the local open sea in autumn which were towed to shore for butchering. It seems practical to me for the Eskimos to have used these skulls as abutments for sod houses rather than to move the massive, non-floating skulls back to sea to appease the spirits. The Nuwuk Eskimos also whaled in the spring (Murdoch 1885).

The Nuwuk village was abandoned, probably because of excessive shore erosion and the flooding of their drinking water pond with sea water. Living was also easier at Cape Smythe (the present Barrow village). Commuting between Barrow and the Point (16 km, 10 mi) for autumn whaling was not easy. There was seldom sufficient snow for dog sledding and the distance for paddling an umiak, particularly with a whale in tow, was excessive. It can be assumed that the major effort was thereafter focused on spring whaling at the lead which usually develops from the Monument to the Point. Nevertheless, autumn whaling has continued with varying degrees of success through historic time. Maher and Wilimovsky (1963) point out that the migration past Barrow starts in middle or late August and that 20 percent of the whales harvested from 1928 to 1960 were taken in autumn.

When power launches and outboard motors for umiaks were available, the Eskimos took renewed interest in autumn whaling. Distance to good whaling ground east of the Point was less of a problem. I observed that beginning about mid-September, the same few experienced crews, season after season pursued whales mostly in plank boats. Umiaks were also used, particularly for scouting prey and following wounded whales. Ten crews were about the maximum number for autumn whaling during the period of my observations. With the increased speed, power, and comfort accorded by the plank boats, the Eskimos extended their autumn hunting range off Barrow, particularly east of the Point. Although Cooper Island (Fig. 2) is one of the best hunting sites, aggressive hunters now go as far east as Tangent Point, or even to Cape Simpson, to be the first to meet the oncoming whales. The hunters sometimes encounter herds of 50 to 60 whales along the Plover Islands (Thomas Brower, personal communication). This area may be a rest stop for the whales and provide an opportunity for them to feed, judging from stomach contents. During autumn the whales are less wary than they are in spring. Unusual success was attained in 1964 when 10 whales, a record number for autumn whaling, were taken by 10 crews. Seven of the 10 whales were taken near Cooper Island. As the pack ice came in and young ice formed, the whales were confined closer to shore and were easier for hunters to reach and kill. Whaling at the Point ended 9 October, with the simultaneous butchering of three whales which were towed to the beach near NARL because Barrow was already blocked by young ice. By 16 October this ice

had thickened into a working platform off Barrow. Three whales were harvested in a lead in two days, in the manner of spring whaling.

Other autumn seasons have been failures, some costly. The severe storm of 3 October 1963 nearly inundated Barrow as the autumn season was getting under way. Many of the whaling boats, stored on the beach, were seriously damaged. Although only one whale had been taken, all efforts were turned to bracing the village for the approaching winter. In 1968 the pack ice went out 240 km (150 mi) and did not return until December, thus creating an expansive hunting area. One whale was taken, but so far from shore it could not be towed to the beach. In 1969 the ice never left shore all summer. In 1970 the pack ice came in early and remained on shore at Barrow preventing the launching of the plank boats. Two crews prepared to whale in umiaks at the Point. One crew set up camp on 30 September. On 6 October it returned to the village for a brief rest because the sea was rough, the fog thick, and no whales had been seen. The second crew never went out. The season ended 11 October because of the strong current of the Chukchi Sea and the formation of young ice. Thus the autumn failures in 1968 to 1970 (Table 1) can be attributed to abnormal, contrary ice conditions.

The advantages of autumn whaling are several. Although the catch shows an irregular harvest over the years, there is the possibility of taking half as many whales as in the spring. In plank boats or motor launches the whalers enjoy cabin comforts of warm meals, dry clothing and a sheltered place to sleep. Whaling can be done with minimum labor because the motorized umiak and whale boat transport men and supplies and tow dead whales to the village for butchering. On shore, tractors and trucks are available for beaching the whale and hauling whale products to storage areas. The ease of autumn whaling is in sharp contrast to the traversing of rough shore ice in spring to get the umiak launched in the lead, the man-handling of the dead whale with block and tackle, and the labor of hauling sled loads of meat back to the village. All this involves considerable time, manpower, whaling equipment, and the repairing and replacing of freight sleds and snowmobiles. With two harvest seasons per year, the average freshness of the consumed whale meat is increased.

The disadvantages of autumn whaling are its unpredictableness and hazards. Autumn weather in the hunting area is less stable. With vast expanses of Arctic Ocean, abrupt storms can imperil the small whaling boats. The relentless Chukchi current, particularly strong at this season, sweeps past Barrow and the Point like a river and can carry small, underpowered boats beyond the point of return. The planking of the best boat cannot hold up against the grinding action when the current carries ice floes. If the pack ice has withdrawn an unusually great distance, the hunting area is so vast that whales are not readily found, and in the search, the whalers may get lost, run out of fuel, or, if successful, be unable to tow their catch to shore. Whenever the pack is dangerously close to shore, the whalers, whether Eskimo or Yankee (Vanstone 1958), in rounding the Point, took the chance of the pack grounding on shore and blocking return. A half dozen men can beach an umiak and haul it out of reach of surf and ice, whereas plank boats require tractor power for beaching and launching. There are no harbors available. Plank boats are expensive and difficult to freight in. Maintaining one may be beyond the abilities of the owner.

SECONDARY BOWHEAD WHALING AREAS AND CATCH RECORDS SEA OF JAPAN

A young bowhead was accidentally taken by commercial Japanese whalers at Osaka Bay in the Sea of Japan in June 1969 (Nishiwaki and Kasuya 1970). The occurrence of a bowhead at this low latitude (33° 28' N), particularly in summer, is the southernmost record. Presumably the whale was a vagrant from the Bering-Chukchi Sea, Okhotsk Sea, or Sea of Japan. Whales in the latter two areas were nearly or completely extirpated many years ago. However, Rice and Scheffer (1968) reported sightings of bowheads in the Okhotsk Sea in 1966-68.

EAST SIBERIAN SEA

Siberian Eskimos north of Bering Strait took 19 bowheads in 1885 while the American fleet took 136 (Bodfish 1936). Stefansson (1924) noted that a good many bowheads were killed in the spring by Siberian Eskimos at Indian Point, Plover Bay, and East Cape (Mys Dezhneva). Residents of the Chukotskiy Peninsula took up to ten bowheads per year until recently (Tomilin 1967). According to A.V. Yablokov (personal communication) these Eskimos depend primarily on walrus and seals, although they may take a few, perhaps one to five, bowheads per year. Soviet scientists indicate that these people take almost no bowheads because they prefer gray whales (*Eschrichtius robustus*). Therefore the USSR government, using modern commercial whaling gear and vessel, took 125-194 gray whales per year during 1965-1973 purportedly for Eskimo subsistence (George Y. Harry, personal communication).

ST. LAWRENCE ISLAND

The Eskimos of St. Lawrence Island have traditionally taken only a few whales because the hunting of walrus and seals is more productive. However, a gray or "summer whale" is occasionally harvested, as in 1970 and 1972 (John Burns, personal communication). Spring whaling is also in the "open sea" because no lead forms for concentrating bowheads near shore. Strong currents and wind may retard towing a dead whale to shore. There are no sheltered beaches. The Eskimos had no heavy machinery to aid in beaching and butchering whales.

A 9.1 m (30 ft) bowhead was killed about 1966 (John Bockstoe, personal communication). Three bowheads were taken in 1967 (John Burns, personal communication). Thomas Poulter observed haphazard attempts to butcher an 18.3 m (60 ft) whale taken 1 May 1968 at Gambell. One bowhead was taken in 1971 and two in 1972 (John Burns, personal communication). The larger of the latter two was estimated at 13.5 m (45 ft) (Steven Burgess, personal communication).

Formerly the Islanders were more numerous and bowhead whaling was more productive, particularly at Southeast Cape and Southwest Cape, neither of which is now inhabited (John Burns, personal communication). By 1973 the snowmobile enabled whalers to reopen operations at Southwest Cape, and four small bowheads were taken during the first spring run in mid-April. Meanwhile, Gambell crews, working in local waters, took two small whales the same year. The Islander's success in the last

few years suggests that the combined take of the two villages, Gambell and Savoonga, may exceed that of Wainright, presently listed as the third ranking village (Table 2).

WALES

Wales is a small village of 120 Eskimos on the east shore of the Bering Strait. The pack ice normally blocks the Strait in winter. Yankee whaling ships, heading for the Arctic, occasionally took a bowhead near Wales as they encountered the southbound current laden with ice floes in April (Cook 1926). By May the currents run steadily to the northward and the sea mammals migrate into the Arctic (Bailey and Hendee 1926). Even in this turbulent hunting ground, Wales' Eskimos successfully hunted bowheads with stonetipped lances prior to the appearance of Yankee whalers about 1850, and they continued to be successful whalers after adopting steel harpoons and bomb guns (Bailey and Hendee 1926).

Chester Lampe, an Eskimo who lived in Wales as a boy, recalled six crews getting one or two whales a year about 1916 (personal communication). Winton Wayapuk, Sr. (personal communication), formerly a member of a whaling crew, recalled that bowheads up to 9 m (30 ft) were occasionally taken. Winton's brother-in-law, Arthur Navgeruk, probably took the last bowhead of that period in 1938. Nevertheless, the Eskimos unsuccessfully continued to hunt bowheads and gray whales using only rifles. The only whale meat available to them was an occasional stranded whale until 1969 when spring whaling was revived. The village acquired a darting gun and some simple whaling gear. A medium-sized bowhead was successfully taken and harvested 15 April 1970 by Silas Kaumanacheak and Mr. Christianson. This was Wales' first fresh whale since 1938.

TABLE 2

Recent catches of bowhead whales at secondary whaling sites in western and northern Alaska, 1961-1973. Data sources as follows (a blank indicates no data): *St. Lawrence Island*, from J. Burns, J. Bockstoce, S. Burgess, and T. Poulter (personal communications); *Kivalina*, from N. Hank (personal communication); *Cross Island*, from NARL. All other data from author.

STATIONS

YEAR	St. Lawrence Island		Wales	Kivalina	Cross Island	Barter Island	Total
	Island	Wales					
1961	0	0	0	0	0	0	0
1962	0	0	0	0	0	0	0
1963	0	0	0	0	0	0	0
1964	0	0	1	0	0	2	3
1965	0	0	0	0	0	0	0
1966	1	0	0	0	0	0	1
1967	3	0	0	0	0	0	3
1968	1	0	0	0	0	0	1
1969	0	0	0	0	0	0	0
1970	0	1	1	0	0	0	2
1971	1	0	1	0	0	0	2
1972	2	0	1	0	0	0	3
1973	6	0	0	0	1	0	7
TOTAL	14	1	1	4	1	2	22

KIVALINA

Kivalina is a small village 110 km (65 mi) south of Point Hope. Because a good whaling ground is not available there, some of the men join the crews at Point Hope each spring and thus, for their services, get a ton or more of whale meat for Kivalina. Murray Johnson helped revive whaling at Kivalina in 1960 by providing the village with whaling gear. No whale was taken until about 1964 (Table 2). Now there are four crews and an active whaling program. One whale was taken each year in 1970, 1971, and 1972 (Nicholas Hank, personal communication). Whales were not taken in 1973. A few of the Kivalina men continue to whale with Point Hope crews.

CAPE LISBURNE

Although Cape Lisburne, 60 km (35 mi) north of Point Hope, is an excellent promontory, it was apparently too windy for even the Yankee whalers to operate there. Bodfish (1936) made no mention of finding whales or Eskimos who had taken bowheads there. Max Brewer (personal communication) stated that bowheads pass 9-13 km (6-8 mi) offshore at the Cape. Takpuk (Agnassagga, personal communication) took a bowhead there in 1950. David Hickok (personal communication) reported a village site a few miles south of the Cape where Eskimos had killed several bowheads many years ago. Scott McVay (personal communication) saw several bowheads at close range in that vicinity in 1973.

POINT LAY

Although Point Lay is an excellent promontory 280 km (175 mi) southwest of Barrow, few whales are seen there. Max Brewer (personal communication) thinks that the ice is too broken in the spring for the Eskimos to venture offshore. However, Alva Shaglook took a small bowhead there in 1930, and Tony Joule, in 1940, killed one so large that it could not be removed from the sea and was only partly utilized (Samuel Agnassagga, personal communication).

ICY CAPE

Icy Cape is 75 km (45 mi) southwest of Wainright. Its history is primarily one of temporary Eskimo hunting camps and of Yankee ships trapped in the ice. After the commercial whalers left the Arctic, Samuel Kanayuuk began whaling in 1910 and by 1939 had taken five whales at Icy Cape. In 1940 he took his sixth with the aid of Peter Panik. Samuel Agnassagga's (personal communication) father and Upicksoun whaled successfully each session at Icy Cape from 1919 through 1922. As a boy, Samuel recalls seeing nearly all of the Wainright villagers in a chain of dog sleds going to the whaling leads off Icy Cape, reportedly 106 km (66 mi) by trail (Van Valin 1941) for spring whaling. Three whales were taken about 1924 by James Angushuk, Mark Kootook, and Adam Nikaktuak (Ned Nusunginya and Samuel Agnassagga, personal communication). Luke Akiuak was another whaler. Up to eleven crews operated at Icy Cape taking a maximum of five whales in a season. There was no autumn whaling. As an adult, Samuel Agnassagga worked on Fred Forsland's crew which took two whales in 1938 and one in 1939. At least 21 bowheads were taken between 1910 and 1940. Assuming that

one-fourth of the kills were forgotten, my estimated 28 whales represent a take of one whale per year. Thereafter whaling at Icy Cape worsened (Ralph Aveoganna, personal communication). Van Valin (1941) wrote that Tigalook took a whale 2 May at a lead 32 km (20 mi) offshore to save the sick and starving villagers, some of whom were then camped 24 km (15 mi) out on the ice. By 1940 it was no longer profitable for Wainright crews to whale there. Because drift wood for fuel was lacking and there was no school for the children, the local residents abandoned the site in favor of Point Lay.

NUNNIAUK

According to Pete Sovalik (personal communication) a small Eskimo village called Nunniauk once existed 30 km (18 mi) northeast of Wainright (probably at or near the map site of the now abandoned Atanik village). This village profited, at least until 1938, by whaling in autumn when young bowheads came near the beach. The sighting of bowheads in autumn off this beach in 1966 and 1967 was reported by Waldo Bodfish (via Frederick Milan, personal communication).

CROSS ISLAND

Cross Island is 250 km (160 mi) east-southeast of Barrow in the chain of Plover Islands. Traditionally it was an old whaling site for local Eskimos in the autumn, but was abandoned many years ago. However, Thomas Napageak took a bowhead there 27 September 1973, operating out of the recently established village of Nuiqsut on the Colville River.

BARTER ISLAND

Barter Island is 480 km (300 mi) east-southeast of Barrow. The beach was formerly strewn with whale bones from successful hunting by Eskimos using primitive weapons. The Eskimos also traded extensively with inland Athabascan Indians. Whaling declined with the advent of commercial whalers in the late 1800s and the Eskimos commercialized on the needs of the white men by exchanging native products for guns, food, and liquor. Barter Island was the principal supply station between Barrow and Herschel Island. Most of the 119 inhabitants lived in the village of Kaktovik on the adjacent mainland.

Whaling equipment at Barter Island is limited and recent catches have been small. In 1964 two whales were taken, one was found dead the last week in August by James Lampe, and the other was shot 21 September by Archie Brower. Numerous whales have been seen in autumn near shore, particularly in 1940 and 1966 (Ned Nusunginya, personal communication). There is no spring whaling.

CANADIAN ARCTIC

Formerly, Canadian Eskimos whaled extensively from Herschel Island east to Dolphin and Union Strait. However, these people have now lost their whaling techniques and it is unlikely that bowhead whaling will be resumed there (Don C. Foote, personal communication). Bowheads are occasionally seen in the Northwest Passage and in Hudson Bay (Vibe 1967). Only two have been taken in recent years in the Canadian Arctic (Mansfield 1971), one of which may be the one from Foxe Basin in

1965 (Bruemmer 1971). Preliminary reports on the present status of bowheads in northeastern and central Canadian waters is given by Mansfield (1971) and Sergeant and Hoek (1974).

GREENLAND

Bowheads were reportedly exterminated in Greenland waters by the end of the 19th century. However, they are regularly seen off Godhaven, and sometimes seen in Thule Harbor, Scoresby Sound, and Store Kildway (Vibe 1967). No bowhead has been taken in several decades because the Danish government currently prohibits Greenlanders from taking them.

EURASIA

Bowheads are sometimes sighted in the Barents Sea west of Novaya Zemlya (Jonsgård 1964). They are very rare between Barents Sea and the east Siberian seas (Tomilin 1967), and are taken only occasionally by Soviet Eskimos (Zemsky, via George Harry, personal communication).

SUMMARY

Most of the world's bowheads are in the western Arctic Ocean. The overfished stock of the early 20th century was protected from further commercial exploitation in 1931. Since then they have been hunted only by Eskimos, primarily those of Alaska and Siberia who live on the shores of the Chukchi Sea. From scanty records beginning in the 1850s the three major Alaskan villages, totaling less than 3000 Eskimos, have a known take of some 565 whales in a century (1852–1969) or about 6/yr. The annual take at minor Alaskan stations and in other countries has been of little significance. However, the accelerated Eskimo take of bowheads, starting at Barrow in 1969 caused a yearly average take of 26 whales for 1970–1973 for the three major villages.

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THREE NEW SPECIES OF THE PALAEOTROPICAL ARBOREAL
ANT GENUS *CATAULACUS*
(Hymenoptera: Formicidae)

By ROY R. SNELLING



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THREE NEW SPECIES OF THE PALAEOBOTROPICAL ARBOREAL¹ ANT GENUS *CATAULACUS* (Hymenoptera: Formicidae)

By Roy R. Snelling²

ABSTRACT: Three new species of ants in the genus *Cataulacus* are described and illustrated: *boltoni* (NIGERIA), *mckeyi* (CAMEROUN) and *pompom* (MALAYA). Each is compared with previously described, related, species.

The Old World arboreal ant genus *Cataulacus* was revised by Bolton (1974). Since then several undescribed species have been discovered. The first of these was sent to me by Mr. Doyle McKey who has conducted some studies on its ecology. Two additional species were sent by Bolton for inclusion in this paper.

The descriptions which follow are patterned closely after those developed by Bolton in his revision. One terminological difference should be noted: I prefer to use *mesosoma* rather than *alitrunk*. The latter is descriptively inappropriate in discussing the wingless thorax of worker ants. Although the *mesosoma* of higher Hymenoptera actually consists of the true *mesosoma* + the first abdominal segment (i.e., the propodeum) use of the broad term seems not to have generated any confusion. In the descriptions the abbreviation WL (Weber's Length) is used rather than AL (Alitrunk Length).

Special note must be made of the cephalic and mesosomal hairs. In the descriptions I have described the appearance of the hairs in terms similar to those used by Bolton. The terminology applies to these hairs as they appear under an ordinary dissecting microscope. When studied with a scanning electron microscope (SEM), the hairs are truly bizarre (Figs. 4, 5, 11, 21, 22, 23, 26). This seems the most rational manner of dealing with these hairs, for access to a SEM is by no means universal and to describe the hairs as they are would only confuse matters.

Cataulacus boltoni NEW SPECIES

Figures 1-8

DIAGNOSIS: *Worker*: Dorsal cephalic hairs clavate to subspatulate; propodeal rugae transverse; sides of pronotum not marginate.

DESCRIPTION: *Holotype Worker*. TL 2.74; HL 0.76; HW 0.72; CI 95; EL 0.38; OI 53; IOD 0.53; SL 0.37; SI 52; PW 0.50; WL 0.78; MTL 0.28.

Occipital crest absent; occipital margin raised, with low, blunt denticles, one on occipital corner and one mesad of it, several located behind eye. Preocular denticle small, separated from eye by a small gap. Pronotum not marginate laterally, humeral angle dentiform; side with minute denticle at about midlength and a

larger one at promesonotal junction. Mesonotum and propodeum not marginate, with a couple of widely spaced, minute denticles on each side; propodeal spines short and bluntly rounded apically. Promesonotal and mesometanotal grooves absent on dorsum. Sides of propodeum, in dorsal view, distinctly convergent posteriorly, those of mesonotum straight, more strongly convergent and separated from propodeum by a narrow V-shaped notch. First gastric tergum not marginate at sides.

Dorsum of head moderately shiny, finely rugoreticulate, the interspaces finely and densely reticulate-punctate, the punctures shallow. Mesosomal dorsum less shiny, with irregular close-set, longitudinally oriented rugulae, strongest at sides, those on posterior part of mesonotum and base of propodeum sharp, transverse; interspaces densely reticulate-punctate. Dorsal surface of petiole and postpetiole sharply longitudinally rugose. First gastric tergum finely and densely reticulate-punctate throughout, no longitudinal rugulae at base.

Hairs on clypeus and cephalic dorsum bizarre, stout and short to medium, clavate to subspatulate. Hairs on meso- and mesosoma numerous, stout and medium length on dorsum and sides, slender on venter.

TYPE MATERIAL: *Holotype worker*, NIGERIA: Gambari, 24 May 1975 (B. Taylor), in British Museum (Natural History).

ETYMOLOGY: This species is dedicated to Mr. Barry Bolton, who recognized the novelty of this species and sent it to me for inclusion in this paper.

DISCUSSION: This species is a member of the TENUIS GROUP of Bolton (1974) and is readily distinguished from other group members by the combination of bizarre cephalic hairs, transversely rugose propodeal base and nonmarginate mesosomal dorsum. In this last character it is most like *vorticus* Bolton, to

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FIGURES 1-8. *Cataulacus boltoni*: 1, frontal view of head; 2, oblique-lateral view of head; 3, lateral view of head and part of mesosoma; 4, bizarre setae mesad of inner eye margin; 5, bizarre setae at preocular tooth; 6, dorsal view of head and mesosoma; 7, lateral view of mesosoma; 8, dorsal view of gaster. Scale as indicated on individual figures.

which it runs in Bolton's key; *boltoni* differs from *vorticus* in the much stronger mesosomal sculpturation, the transversely rugulose propodeal base and the longer, stouter and more numerous setae of the first gastric tergum. The hairs of the cephalic dorsum are longer than in *vorticus*, especially on the vertex and occiput.

Cataulacus mckeyi NEW SPECIES

Figures 9–18

DIAGNOSIS: *Worker and female:* Head about as long as broad; cephalic and mesosomal dorsa with abundant erect, flattened hairs; first gastric tergum with very fine longitudinal rugulae in middle of disk and hairs arising from punctures conspicuously greater than their diameter. *Male:* see description and discussion.

DESCRIPTION: *Holotype worker.* TL 3.93; HL 0.91; HW 0.91; CI 100; EL 0.41; OI 45; IOD 0.74; SL 0.42; SI 46; PW 0.74; WL 1.06; MTL 0.44.

Occipital crest absent, vertex rounded into occiput. Occipital corner denticulate and with a small denticle on margin close to corner, denticles small; side of head denticulate behind eyes. Side of pronotum strongly marginate and denticulate. In dorsal view, mesonotum and propodeum abruptly narrower than pronotum, denticulate at sides; propodeum with a pair of broad dorsoventrally flattened spines. Thoracic dorsum without sutures. Subpetiolar process quadrate, with prominent anterior and posterior angles. Subpostpetiolar process short, simple, acute. First gastric tergum not laterally marginate.

Dorsum of head with a very fine, loose rugoreticulum; interspaces moderately shiny, finely, densely and weakly reticulate-punctate, punctures stronger on vertex. Mesosomal dorsum with a rugoreticulum, no coarser than that of head, with transverse meshes obsolescent, so that rugae are largely longitudinal; interspaces slightly shiny, strongly and densely reticulate-punctate. First gastric tergum moderately shiny, densely reticulate-punctate, with fine, irregular longitudinal rugulae resulting from fusion of margins of aligned punctures, without conspicuous longitudinal rugae. Piligerous punctures scattered, coarser than hairs arising from them.

Dorsal surfaces of head, body and appendages with numerous short, flattened (rarely weakly clavate on cephalic dorsum), simple hairs, longest on gaster; hairs of first tergal dorsum separated by less than their length.

Paratype workers. TL 3.58–4.04; HL 0.86–0.94; HW 0.87–0.94; CI 98–102; EL 0.38–0.44; OI 43–47; IOD 0.66–0.73; SL 0.38–0.42; SI 43–46; PW 0.65–0.77; WL 0.96–1.09; MTL 0.40–0.44 (18 measured).

Paratype females. TL 5.06–5.19; HL 0.95–0.97; HW 0.92–0.96; CI 97–99; EL 0.41–0.44; OI 44–47; IOD 0.73–0.76; SL 0.44–0.45; SI 45–49; PW 0.92–0.96; WL 1.37–1.45; MTL 0.45–0.47 (7 measured).

As workers, with usual modifications of mesosoma for flight. Denticulae of head behind eye and of pronotal margin reduced, sometimes absent. Mesoscutum strongly longitudinally rugate, with few or no cross meshes; rugation of propodeum coarser than that of mesoscutum. Metafemur often with conspicuous longitudinal rugae on posterior face.

Allotype male. TL 4.53; HL 0.81; HW 0.85; CI 105; EL 0.36; OI 42; IOD 0.70; SL 0.32; SI 38; PW 0.83; WL 1.44; MTL 0.55.

Occipital crest absent, occipital corner denticulate, the tooth broad and more or less sharply angulate mesad. Side of head behind eye not denticulate, though margin often irregular. Preocular denticle absent or present but small. Pronotal margin irregular but not denticulate. Anterior arms of notauli well developed and cross-ribbed, posterior arm absent or marked by a very weak depression. Propodeal spines short, stout. Subpetiolar and subpostpetiolar processes simple.

Dorsum of head densely reticulate-punctate with a few fine rugulae and a few weak rugulae close to and behind eyes, the cross-meshes reduced or absent. Pronotum densely reticulate-punctate, with a few irregular rugulae, especially at side. Mesoscutum densely reticulate-punctate, with fine longitudinal rugulae resulting from fusion of margins of aligned punctures. Scutellum similar but less shiny. Propodeal base densely reticulate-punctate and dull, with conspicuous fine longitudinal rugae. Dorsum of petiole densely reticulate-punctate and dull, with a few widely spaced fine rugae; dorsum of postpetiole densely reticulate-punctate and dull, sometimes with a few obscure rugulae at side. First gastric tergum moderately shiny and densely reticulate-punctate on basal one-fourth, punctures becoming increasingly faint caudad; with scattered coarse, setigerous punctures.

Simple, erect hairs present on all dorsal surfaces of head and body, some on head distinctly flattened.

Paratype males. TL 4.39–5.13; HL 0.78–0.86; HW 0.81–0.94; CI 103–109; EL 0.33–0.37; OI 40–43; IOD 0.66–0.77; SL 0.27–0.33; SI 33–37; PW 0.79–0.92; WL 1.44–1.60; MTL 0.47–0.56 (7 measured).

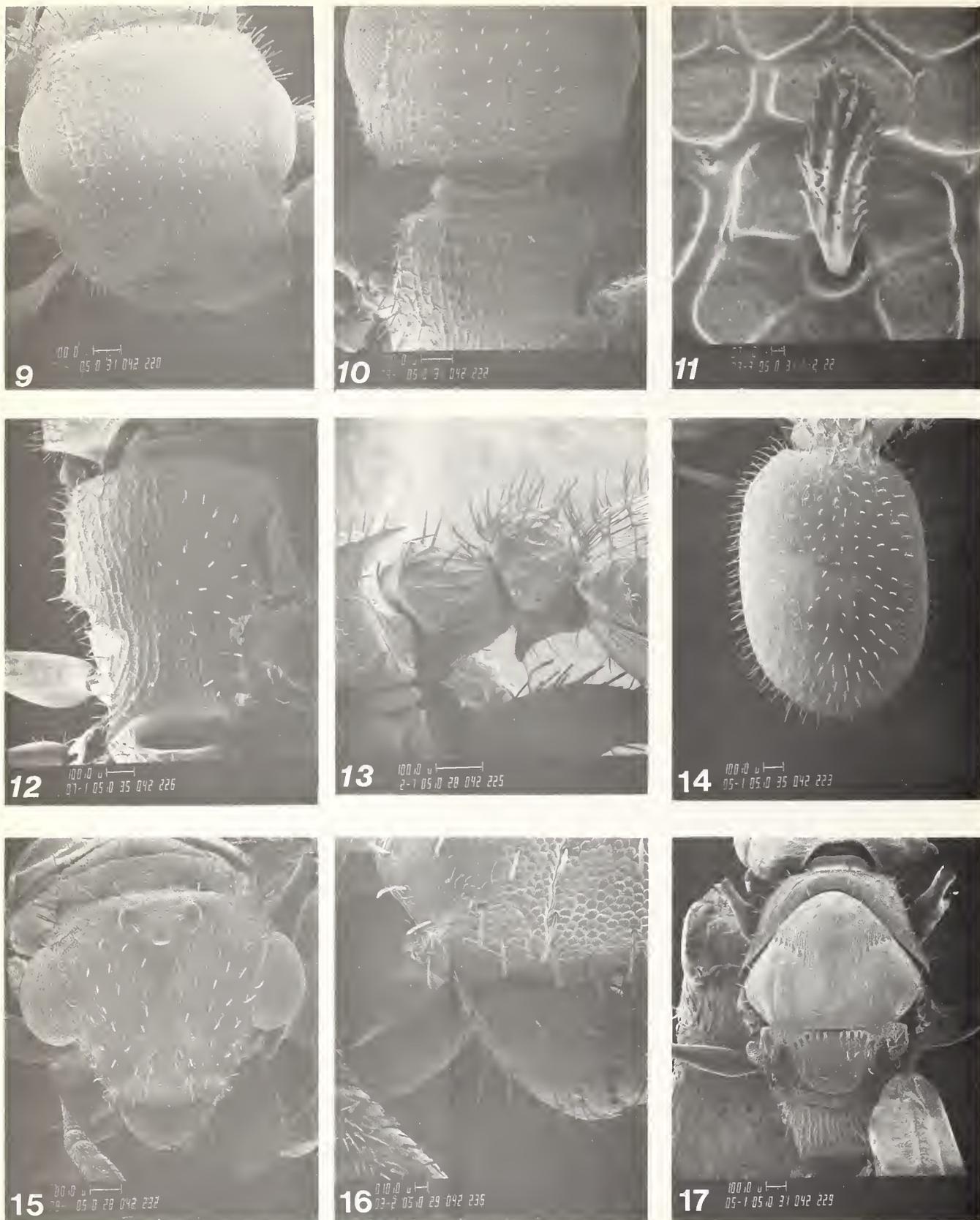
TYPE MATERIAL: *Holotype worker and allotype.* CAMEROUN: near Lac Tissongo, Douala-Edea Reserve (lat. 3°29' N, long. 9°50' E), about 5 km S of Sanaga River and about 15 km E of Mouanko, 18 July 1976 (D. McKey) in Natural History Museum of Los Angeles County. *Paratype females* (20), *workers* (135) and *males* (7) in BMNH, LACM, MCZ and collection of Mr. McKey.

ETYMOLOGY: This species is dedicated to its collector, Mr. Doyle McKey.

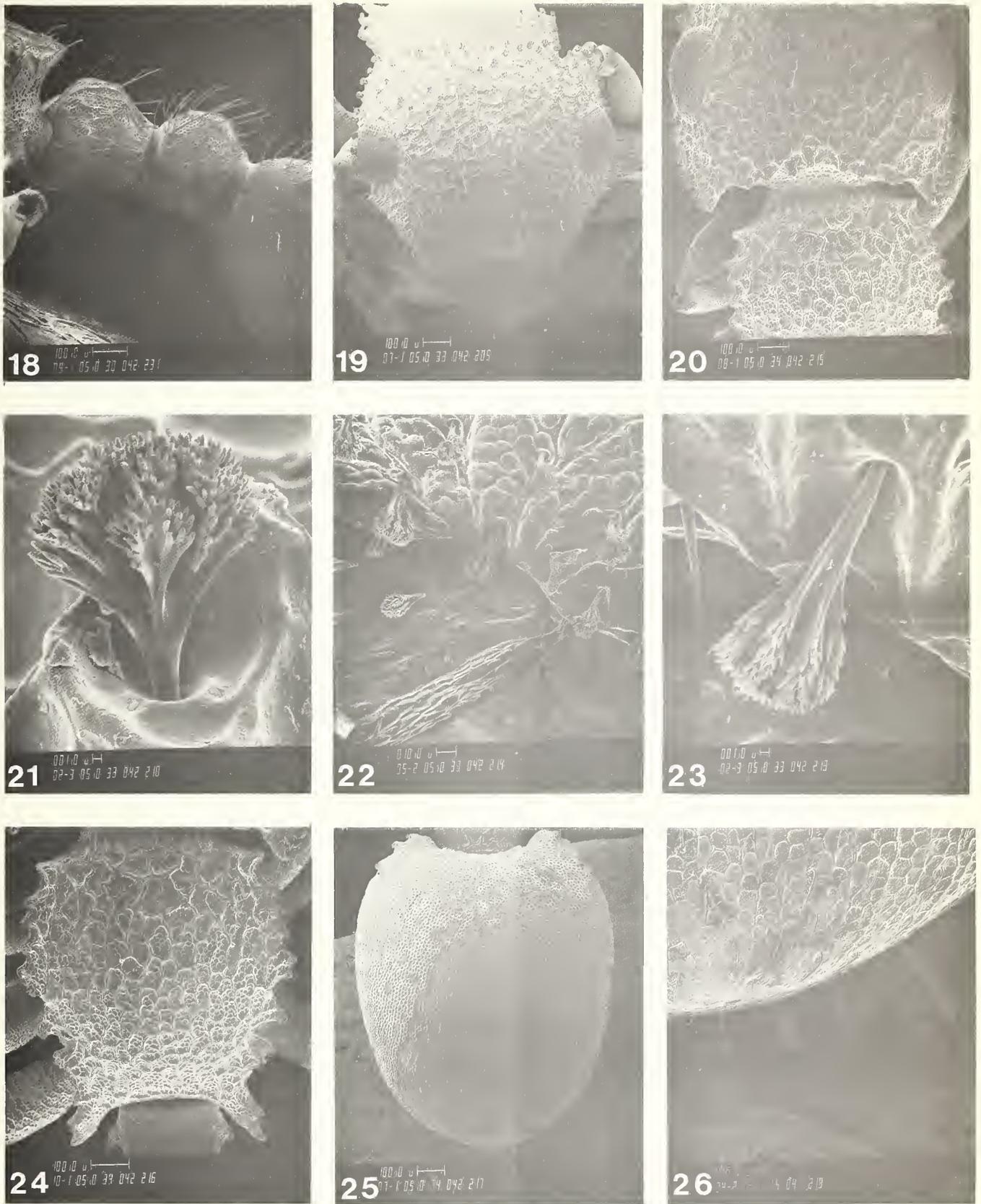
DISCUSSION: The worker of this species will run in Bolton's (1974) key to *pygmaeus* E. André and appears to be related to that species. The most obvious differences are the shorter and sparser pilosity, the more coarsely sculptured mesosomal dorsum and much finer piligerous punctures of the first gastric tergum of *pygmaeus*. The metafemur of *pygmaeus* has several conspicuous longitudinal rugae on the posterior surface; these usually are entirely lacking in *mckeyi*. According to Bolton the CI, OI and SI for *pygmaeus* are 94–97, 41–46 and 49–51, respectively, versus 98–102, 43–47 and 43–46, respectively, for *mckeyi*. The latter is also a smaller species, with a HW range of 0.87–0.94 versus 0.92–1.06 in *pygmaeus*.

The females of the two species are very similar, but *mckeyi*, with a HW range of 0.92–0.96 (1.08 in *pygmaeus*) is smaller. The CI, OI and SI of *pygmaeus*, as given by Bolton, are 92–95, 40–46 and 48–50, respectively. These are 98–102, 43–47 and 43–46, respectively, for *mckeyi*. Presumably there are differences in pilosity much like those between the workers of these species.

Bolton's description of the *pygmaeus* male does not suggest many differences between it and the male of *mckeyi*. According to Bolton, the side of the head, behind the eye, is denticulate (simple in *mckeyi*) and the pronotum is conspicuously rugoreticulate (very sparse rugulae laterad in *mckeyi*). Bolton does not



FIGURES 9–17. *Cataulacus mckeyi*. 9–14 of worker. 15–17 of male: 9, frontal view of head; 10, dorsal view of head and part of mesosoma; 11, bizarre setae on frons; 12, dorsal view of mesosoma; 13, lateral view of petiole; 14, dorsal view of gaster. 15, frontal view of head; 16, frontal view of lower part of face; 17, dorsal view of mesosoma. Scale as indicated on individual figures.



FIGURES 18–26. 18, *Cataulacus mckeyi*, male: lateral view of petiole. 19–26. *Cataulacus pompom*, worker: 19, frontal view of head; 20, dorsal view of head and part of mesosoma; 21, bizarre seta on frons; 22, bizarre setae near base of mandible; 23, bizarre seta near base of mandible; 24, dorsal view of mesosoma; 25, dorsal view of gaster; 26, apical area of first tergum. Scale as indicated on individual figures.

state that the punctures of the first gastric tergum become conspicuously weaker caudad as they do in *mckeyi* nor does he mention conspicuously coarse piligerous punctures. Until more males of members of the TENUIS GROUP become available, it is impossible to characterize that of *mckeyi* in a meaningful manner.

Cataulacus pompom NEW SPECIES

Figures 19–26

DIAGNOSIS: Cephalic and mesosomal sculpturation reduced; cephalic dorsum with abundant very short bizarre hairs (Figs. 24–26).

DESCRIPTION: *Holotype worker*. TL 3.46; HL 0.83; HW 0.94; CI 112; EL 0.32; OI 34; IOD 0.72; SL 0.45; SI 48; PW 0.69; WL 0.96; MTL 0.37.

Occipital crest complete, the median portion raised into a low, projecting ridge in full-face view; with well-separated weak denticles. Side of head denticulate behind eyes, occipital corner with a low, broad, triangular tooth. Sides of propodeum with a narrow, rectangular expansion, marked at each end by a blunt denticle and with another, smaller, denticle near middle. Sides of mesonotum roughly triangular in dorsal view, with a deep V-shaped notch separating them from propodeum. Propodeum behind this notch with a short free anterior face; side marginate, continuous with side of spine, margin with two or three minute denticles. First gastric tergum marginate on anterior one-fourth, margin with several weak, oblique denticles.

Dorsal surface of head finely rugoreticulate, interspaces finely and densely reticulate-punctate. Dorsal surface of mesosoma similar, but with longitudinal rugulae stronger. Dorsal surfaces of petiole and postpetiole very densely reticulate-punctate, with a few short, obscure longitudinal rugulae. First gastric tergum finely and very densely reticulate-punctate, with numerous short, fine obscure rugulae, the majority of which are more or less longitudinal.

Dorsal surface of head with numerous very short, bizarre hairs (Fig. 24), but with a few longer, subspatulate hairs along inner eye margin. Dorsal surface of mesosoma with short, bizarre hairs along margins and with two transversely arcuate rows across anterior part of pronotum. Petiole and postpetiole each with a few similar hairs; first gastric tergum with a short, bizarre hair on each marginal denticle. Dorsal surfaces of meso- and metafemora and external surface of mesotibia with 1–4 such hairs.

Paratype workers. TL 2.87–3.44; HL 0.74–0.85; HW

0.83–0.94; CI 110–114; EL 0.28–0.32; OI 33–35; IOD 0.65–0.71; SL 0.40–0.44; SI 47–49; PW 0.60–0.69; WL 0.81–0.97; MTL 0.33–0.40 (9 measured).

TYPE MATERIAL: *Holotype worker*, MALAYA: Selangor, Gombak, 2 Oct. 1973 (B. Bolton), from topmost twigs of felled forest tree, in British Museum (Natural History). *Paratype workers*, 9, same data as holotype, in British Museum (Natural History) and Los Angeles County Museum of Natural History.

ETYMOLOGY: The name proposed for this species is an arbitrary combination of letters and should be treated as a noun.

DISCUSSION: In Bolton's (1974) key to Indo-Australian and Oriental *Cataulacus* this species fails at couplet 13. It is, however, a member of the TAPROBANAE GROUP as evidenced by the reduced sculpturation, with the rugulae of the mesosomal dorsum principally longitudinal. The occipital crest is normal for the group, and is especially similar to that of such species as *praetextus* F. Smith and *reticulatus* F. Smith. It is immediately different from all TAPROBANAE GROUP species in the abundance of bizarre hairs on the cephalic and mesosomal dorsa. Hairs of this type appear to be of rare occurrence in the Indo-Australian-Oriental fauna although frequent in species of the Ethiopian Region. Somewhat similar, though less bizarre, hairs are seen in *simoni* Emery and, to a lesser degree, *granulatus* (Latreille). These are members of the GRANULATUS GROUP and differ from *pompom* in the nature of the cephalic and mesosomal sculpture.

ACKNOWLEDGMENTS

For making available the above-described new species, I extend my thanks to B. Bolton and D. McKey. The SEM photomicrographs which illustrate this paper have been made available through the generous assistance of Mr. Gerald E. Garner, Scanning Electron Analysis Laboratories, Inc., of Los Angeles, California.

LITERATURE CITED

- BOLTON, B. 1974. A revision of the Palaeotropical arboreal ant genus *Cataulacus* F. Smith (Hymenoptera: Formicidae). *Brit. Mus. (Nat. Hist.)*, Bull. 30:1–105.

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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

APHOMOMYRMEX AND A RELATED NEW GENUS OF
ARBOREAL AFRICAN ANTS
(Hymenoptera: Formicidae)

By Roy R. Snelling



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APHOMOMYRMEX AND A RELATED NEW GENUS OF ARBOREAL AFRICAN ANTS (Hymenoptera: Formicidae)¹

By Roy R. Snelling²

ABSTRACT: The African ant genus *Aphomomyrmex* is redescribed; it contains a single species, *A. afer*, with polymorphic workers; *A. murali* Forel is synonymized with *A. afer*. A related new genus, *Petalomyrmex*, is described and illustrated in all three castes. This ant is apparently an obligatory associate with the caesalpiniaceous tree *Leonardoxa africana*.

Aphomomyrmex was described by Emery (1895) for a single new species, *A. afer*, from Cameroon. A previously described Bornean ant, *Dimorphomyrmex andrei* Emery, tentatively placed in *Aphomomyrmex*, was removed to *Cladomyrma* by Wheeler (1920). *Pseudaphomomyrmex* was erected as a subgenus by Wheeler (1929) for the Philippine species *Aphomomyrmex emeryi* Ashmead. Later (1922) he raised *Pseudaphomomyrmex* to generic status. The ant is not well known and it seems best to leave it at this level for the present. Menozzi (1935) described *Neaphonus* as a Neotropical subgenus of *Aphomomyrmex*; this was treated as a junior synonym of *Myrmelachista* by Snelling and Hunt (1976).

Aphomomyrmex, then, is restricted to Africa as far as now known. In order that the related new genus, described below, may be adequately characterized, it is first necessary to re-examine *Aphomomyrmex*.

Aphomomyrmex Emery

Aphomomyrmex Emery 1899. Soc. Entomol. Belg. Ann. 4:493. Type species: *Aphomomyrmex afer* Emery 1899. Orig. design. Arnold 1920. S. Afr. Mus. Ann. 14:552-554; Wheeler 1922. Amer. Mus. Nat. Hist. Bull. 45:697; Emery 1925. *IN*, Wytzman, Gen. Insect. 183:44-45.

DIAGNOSIS: WORKER: Polymorphic; head rectangular; antenna nine-segmented, without distinct apical club; ocelli well below occipital margin. FEMALE: Antenna ten-segmented, without distinct apical club; head about one-third longer than wide, parallel-sided; frontal carinae separated by more than their length; atria of propodeal spiracle and metapleural gland large, nearly circular, latter without conspicuous guard hairs. MALE: Antenna ten-segmented, without distinct apical club; eye large, occupying most of side of head; ocelli large; frontal carinae obsolete; pygostyles present; mandible tridentate.

DESCRIPTION: WORKER: Polymorphic, HW of largest worker about twice that of smallest; head rectangular. Mandible with five or six teeth along apical margin; basal tooth indistinct

and greatly offset along basal margin. Maxillary palp five-segmented, labial palp three-segmented. Median lobe of clypeus broader than long, moderately convex longitudinally and transversely, basal margin below level of upper margin of antennal sockets; lateral margin confluent with antennal socket; apical margin of median lobe slightly projecting, subtruncate to weakly convex. Antennal scape not reaching occipital margin, broadened at apex, flagellum eight-segmented, only first and last segments longer than broad; gradually thickened apicad, without distinct club. Eye slightly higher than broad; placed slightly below middle of side of head; distance between eye and antennal socket slightly greater than distance between eye and head margin in frontal view. Ocelli present, distinct in large workers, minute in smallest workers, placed well below occipital margin in frontal view. Occipital margin broadly and weakly concave in largest workers, more narrowly and abruptly concave in smallest.

Mesosoma stout, about twice longer than wide, widest across pronotum; pronotum about twice wider than length along midline. Promesonotal suture distinct. Mesonotum, in dorsal view, wider than long; convex in profile and abruptly descending into metanotal depression. Metanotal spiracles slightly elevated; metapleural gland very large, atrium large, circular, not provided with guard hairs. Propodeum broader than long in dorsal view, sides gently convex; declivity flat in profile, about twice longer than basal face; spiracle large.

Profemur stout. Middle tarsal segments short, broader than long. Tarsal claws simple.

Node of petiole scaliform; spiracle minute, near base of scale.

Acidopore with conspicuous fringe of long, curled hairs.

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FEMALE: Head distinctly longer than wide, with straight, subparallel sides and straight occipital margin in frontal view. Eye large, lateral. Ocelli large. Antenna about as in worker, but flagellum nine-segmented. Mandible as in worker but basal tooth larger and set further basad.

Mesosoma normal for alate forms, somewhat flattened in profile; mesonotum flattened, about as broad as long. Scutellum flattened and on same plane as mesonotum. Metanotum and propodeum, in profile, strongly oblique, latter without distinct basal face.

Legs as in worker.

Forewing with a single submarginal cell; vein *m-cu* absent; fringe hairs present except along apical margin. Hindwing with *cu-a* far basad of *r-m*; 1A ending at *cu-a*; fringe hairs long, present along posterior margin.

Node of petiole low, thick; from above, about twice wider than long.

Gaster somewhat elongate, acidopore as in worker.

MALE: Head, across eyes, distinctly broader than long. Eye massive, occupying most of side of head, but distance between eyes greater than eye width in frontal view. Ocelli enlarged, ocellular distance less than maximum diameter of anterior ocellus. Mandible with three widely spaced teeth, apical tooth much broader and longer. Scape more slender than that of female, flagellum ten-segmented.

Mesosoma, from above, about one-third longer than wide; in profile, about one-third longer than high. Mesonotum wider than long. Scutellum, in profile, convex. Propodeum about as in female.

Legs slender. Wings as in female.

Node of petiole, in profile, bluntly triangular; from above, about as wide as long.

Gaster robust. Pygostyles present. Subgenital plate deeply excised. Paramere conspicuously longer than basal width, apex acute; ventral lobe of aedeagus nearly straight; edentate, basal angle dentiform.

DISCUSSION: Emery based this genus primarily upon the type species, *A. afer*. *Dinorphyrmex andrei*, tentatively placed here, was known only from females and its relationship to *Aphomyrmex* was uncertain. Wheeler (1920) removed *andrei* to *Cladomyrma*. A single cotype of *C. andrei* has been available. There are several obvious differences between the *Cladomyrma* female and that of *Aphomyrmex*. In *Cladomyrma* the head is quadrate, with the occiput arched well above the ocelli; the eyes are at the side of the head (rather than laterad on the frontal surface) and the lateral lobes of the clypeus extend below the margin of the median lobe. The mandible of *Cladomyrma* has four apical teeth; there is no tooth on the basal margin. The opening of the metapleural gland is partially closed. The petiolar spiracle is nearer the summit of the node than the base. It is impossible to reach a firm conclusion on the status of *Cladomyrma* with only a single female available, but it clearly cannot be included in *Aphomyrmex*.

In addition to the type species of *Aphomyrmex*, one other African form has been described, *A. muralti* Forel (1910) from Natal. I have examined the type of *A. muralti* and two other specimens from Cameroon which Forel believed conspecific with it. Also examined were four females and one worker of *A. afer*, all cotypes. Nontype material studied consists of one female, one worker and one male from Zaire, one female from Gabon and

one female from Cameroon. It is my opinion that these represent a single species.

Forel originally characterized *A. muralti* as being smaller, impunctate, shinier and less pubescent than *A. afer*. This is indeed true if the type of *A. muralti* is compared with two workers in the Forel collection which are conspicuously hairy and punctate and larger. It is not so clearly true if the type of *A. muralti* is compared with the worker cotype of *A. afer* in the Forel collection.

The two workers mentioned above are from "Cameroun (v. Muralt)." One label on the specimens identifies these as *A. afer* and, below that, another label identifies them as *A. muralti*. The two identification labels presumably indicate that Forel later believed his *A. afer* from Cameroon was indeed the same as his *A. muralti*. Since they are from Cameroon, they should be *A. afer* and they do differ from the *A. muralti* type in such a manner as to suggest that they are the source of the differences noted by Forel between the two species. The head widths of these two specimens are 0.83 and 0.84 mm. Both are conspicuously pubescent and with abundant fine, close punctures which are most noticeable on the head and the gastric terga. The type of *A. muralti* has a head width of 0.67 mm, the head and body are shiny, with only scattered punctures and very sparse pubescence. The cotype worker of *A. afer* has a head width of 0.81 mm. The head has numerous fine punctures, but the body is very sparsely punctate and the pubescence is scattered. Smallest is a single worker from Zaire, head width 0.47 mm. This specimen is virtually impunctate and apubescent, though the normal erect hairs are numerous and long.

It seems evident that there is a single, polymorphic species involved. The specimens available, few as they are, do present a continuum through the various morphs. As size increases, punctures become more abundant and more sharply defined. At the same time the appressed pubescence also increases. In my opinion, there are no essential differences between the type of *A. muralti* and the cotype of *A. afer*; those differences which do exist are correlated with size and are negated by other specimens available. Therefore, *A. muralti* = *A. afer* (new synonymy).

The available females (four cotypes plus three others noted above) are fairly uniform, except that one cotype has the punctures of the head and gaster very sparse, in sharp contrast to the dense fine punctation on these areas in the other cotypes. This is true also of one female from Zaire. I believe that this variation in the females supports my contention that *A. muralti* and *A. afer* are conspecific.

It is possible that the type of *A. muralti* is from Cameroon and not from Natal as stated by Forel. In the Forel collection are the two Cameroon workers collected by von Muralt. The type of *A. muralti* has the notation "Natal (v. Muralt)." but only on the identification label. That notation appears to have been made at a different time and with a different pen than the identification. It is not inconceivable that "Natal" is an error.

SPECIMENS EXAMINED: CAMEROON. 4 ♀♀, 1 ♂ (L. Conradt; BMNH, MNHG); 2 ♀♀ (v. Muralt; MNHG); 1 ♀, Nkoe-Mvone, 5 Sept. 1968 (Collingwood; BMNH). GABON. 1 ♀, Makokou, Oct. 1972 (I. Lieberburg; MCZ). ZAIRE. 1 ♀, 50 km S Tahela, 26 July 1957 (E.S. Ross & R.E. Leech; MCZ); 1 ♀, 1 ♂, 24 mi NE Lubefu, 12 Aug. 1957 (E.S. Ross & R.E. Leech; MCZ). SOUTH AFRICA. 1 ♀, "Natal" (v. Muralt; MNHG).

PETALOMYRMEX NEW GENUS

DIAGNOSIS: WORKER: Monomorphic; head cordate; antenna nine-segmented, without distinct apical club; ocelli near top of head. **FEMALE:** Antenna ten-segmented; head cordate, as broad as to broader than long; frontal carinae separated by more than their length; openings of propodeal spiracle and metapleural gland circular, latter with a few long guard hairs. **MALE:** Antenna ten-segmented; eye large, occupying most of side of head; ocelli normal; frontal carinae obsolete; pygostyles absent; mandible six-toothed.

DESCRIPTION: WORKER: Monomorphic. Head cordate in frontal view. Apical margin of mandible oblique, with six distinct teeth, basal somewhat offset. Maxillary and labial palpi three-segmented. Median lobe of clypeus broader than long, entire apical margin of clypeus continuously gently convex; basal margin at about midpoint of antennal sockets, lateral margin confluent with antennal sockets. Antennal scape reaching occipital margin; flagellum eight-segmented, without distinct club, only first and last segments longer than broad. Eye oval, at about middle of side of head; distance between eye and antennal socket much greater than distance between eye and margin of head in frontal view. Ocelli small but distinct, placed little below occipital margin. Occipital lobes distinct.

Mesosoma much as in *Aphomyrmex*, but metanotum, in profile, distinctly convex and with spiracle minute, dorsal; opening of metapleural gland with a few long guard hairs.

Legs as in *Aphomyrmex*.

Petiole about as in *Aphomyrmex*, but spiracle about one-third of distance from base to summit of scale.

Head and body without appressed pubescence but with conspicuous erect hairs of varied length on all areas, including appendages.

FEMALE: Head about as in worker but occipital margin broadly concave so that head is not truly cordate. Mandible eight-toothed. Eye large, lateral, slightly below middle of side of head. Ocelli slightly enlarged, near occipital margin. Flagellum nine-segmented.

Mesosoma conspicuously flattened. Mesonotum flat, broader than long. Scutellum, metanotum and propodeum, in profile, continuously oblique.

Wings as in *Aphomyrmex*.

Node of petiole low and thick in profile, with spiracle near summit; from above about twice wider than long; summit, from behind, much wider than base, broadly concave.

Gaster somewhat elongate.

Pilosity as in worker.

MALE: Head, across eyes, distinctly wider than long. Eye massive, occupying most of side of head, interocular distance twice eye width in frontal view. Ocelli large, ocellular distance about twice maximum diameter of anterior ocellus. Mandible four-toothed, preapical tooth often minute. Maxillary palp four-segmented, labial palp three-segmented.

Mesosoma similar to that of female, but proportionately a little broader. Legs slender. Wings as in female.

Petiole about as described for *Aphomyrmex*; spiracle near summit of node.

Gaster robust. Pygostyles absent. Subgenital plate deeply excised. Paramere much longer than basal width, apex narrowly rounded. Ventral lobe of aedeagus weakly convex along lower margin, margin irregular but not dentate, basal angle rounded.

Body and appendages with numerous suberect to erect hairs of varied length.

TYPE SPECIES: *Petalomyrmex phylax*, new species.

ETYMOLOGY: *Petalos* (Gr., flattened) + *myrmex* (Gr., ant).

DISCUSSION: This new genus appears to be closely allied to *Aphomyrmex*. The strongly cordate head of the worker will separate *Petalomyrmex* from *Aphomyrmex* and related genera. *Petalomyrmex* workers and females differ from those of *Aphomyrmex* by the reduced palpal segmentation and the worker caste is monomorphic rather than polymorphic. The strong dorso-ventral flattening of the mesosoma of the *Petalomyrmex* female and male is unusual and distinctive; it is reminiscent of the bizarre females of the Neotropical subgenus *Myrmostenus* of *Camponotus* and of certain species of *Myrmelachista*.

Petalomyrmex phylax NEW SPECIES

Figures 1–7

DIAGNOSIS: Same as for genus in all castes.

DESCRIPTION: HOLOTYPE WORKER: HL 0.55 mm; HW 0.56 mm; CI 102; SL 0.38 mm; SI 68; EL 0.13 mm; OI 23; PW 0.36 mm; WL 0.68 mm; TL 2.36 mm.

Head broadest near upper margin of eyes, strongly cordate in frontal view, width at mandibular base 0.61 x HW. Eye flattened, in frontal view not interrupting lateral head margin; OMD 1.4 x EL. Scape stout, not attaining occipital corner; flagellum gradually swollen, flagellomeres 2–5 broader than long, 6–7 about as long as broad, 8 almost twice longer than broad.

Mesosoma robust, PW 0.53 x WL. Pronotum, from above, about 1.75 wider than long; posterior margin concave. Mesonotum not fused to pronotum, a little wider than long; weakly convex in profile, sloping from pronotal margin to metanotum; mesometanotal suture impressed dorsally, absent on pleura. Metanotum, from above, short, broader posteriorly, sides slightly raised; metanotal-propodeal suture impressed dorsally and on upper third of side; metanotal spiracle absent. Propodeum, from above, broadened posteriorly; spiracular atrium fully visible, large; in profile, basal face convex and rounded into oblique, much longer posterior face, spiracle a little below juncture of faces.

Scale of petiole thick in profile, margins nearly parallel below level of spiracle, sharply convergent above to acute apex; spiracle at about midpoint; in posterior view, margins parallel below spiracle, convergent above, crest narrow and broadly emarginate; from above, about twice wider than long.

Gaster rather broad, a little longer than mesosoma in dorsal view.

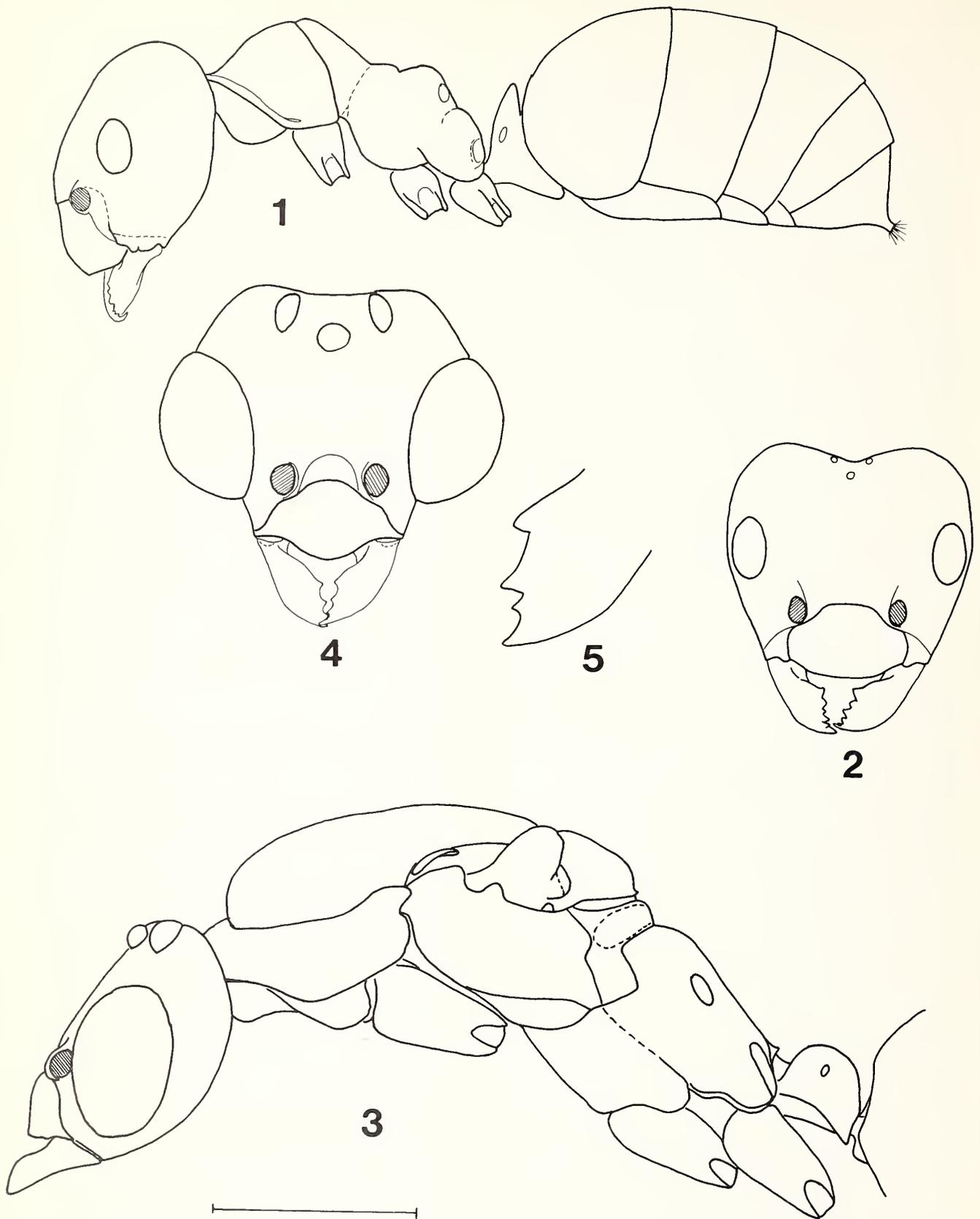
Integument smooth and shiny, without conspicuous coarse punctures except on clypeus and mandible.

Body and appendages with abundant erect hairs of very varied length, longest hairs on occiput and mesosomal dorsum exceeding EL. No obvious appressed pubescence.

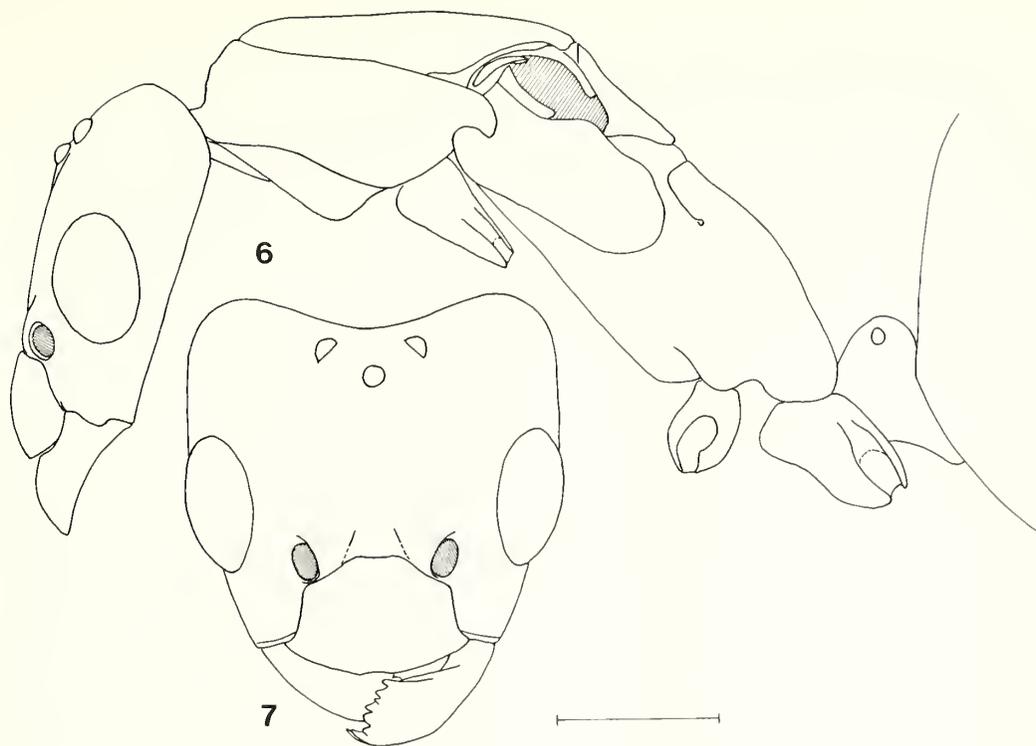
Reddish yellow, occiput and gaster brownish; mandibular teeth dark reddish.

PARATYPES: HL 0.47–0.55 mm; HW 0.49–0.59 mm; CI 100–109; SL 0.33–0.38 mm; SI 64–72; EL 0.12–0.14 mm; OI 23–28; PW 0.31–0.37 mm; WL 0.59–0.71 mm; TL 1.78–2.46 mm (54 measured).

PARATYPE FEMALES: HL 0.90–1.08 mm; HW 0.90–1.08 mm; CI 99–107; SL 0.31–0.37 mm; SI 56–60; EL 0.58–0.62 mm; OI 32–36; PW 1.03–1.23 mm; WL 1.81–2.10 mm; Wing length 4.6–6.0 mm (10 measured).



FIGURES 1-5. *Petalomyrmex phylax*. 1, Worker, profile. 2, Worker head, frontal view. 3, Male, head and mesosoma, profile. 4, Male, head, frontal view. 5, Male, apex of mandible, enlarged. Scale line = 0.5 mm.



FIGURES 6-7. *Petalomyrmex phylax*, Female. 6, head and mesosoma, profile. 7, head, frontal view. Scale line = 0.5 mm.

Head shape similar to that of worker, but eyes more bulging and interrupting side margin of head in frontal view; occipital margin, in frontal view, broadly concave; ocelli slightly below occipital margin, interocellar distance about twice diameter of anterior ocellus, ocellocular distance almost four times diameter of anterior ocellus. Head, in profile, strongly flattened, about 2.7 x longer than thick. OMD 0.55-0.68 times EL.

Mesosoma greatly flattened, angled about 45° at anterior margin of scutellum; thickness at metanotum about 0.36 x length from anterior margin of tegula to apex of metasternal lobe. Propodeal spiracle on posterior face, atrium large, circular.

Scale of petiole, in profile, low, thick, spiracle near summit; crest broadly, shallowly concave in posterior view; from above, about twice wider than long.

Gaster about as long as combined head and mesosoma, elongate-ovoid, three basal terga almost parallel-sided in dorsal view.

Pilosity about as described for worker, but hairs more abundant on cephalic dorsum and with conspicuous long hairs on gena (short, sparse hairs on gena of worker).

Color as in worker. Wings medium brown, veins and stigma dark brown.

ALLOTYPE MALE: HL 0.62 mm; HW 0.65 mm; CI 106; SL 0.44 mm; SI 66; EL 0.32 mm; OI 52; PW 0.85 mm; WL 1.45 mm; Wing length 4.2 mm.

Head somewhat flattened, eye large and strongly bulging in frontal view, OMD 0.2 x EL. Head margins strongly convergent above eye level, abruptly rounded onto nearly flat occiput. Interocellar distance and ocellocular distance about twice diameter of anterior ocellus.

Mesosoma flattened and angled about as in female, thickness at metanotum about 0.47 x length from anterior margin of tegula to apex of metasternal lobe.

Integument smooth and shiny, without conspicuous punctures.

Pilosity about as in female and worker, but cephalic hairs relatively a little shorter.

Color yellowish; occipital area and margins of gastric terga brownish. Wing light brownish, stigma medium brown, veins yellowish brown.

PARATYPE MALES: HL 0.59 mm; HW 0.62 mm; CI 104; SL 0.45 mm; SI 73; EL 0.32 mm; OI 54; PW 0.83-0.85 mm; SL 1.29-1.39 mm; Wing length 4.2 mm (2 measured).

TYPE MATERIAL: *Holotype worker*, *allotype male*, 394 worker, 19 female, 4 male paratypes: CAMEROON: near Lac Tissongo, Douala-Edea Reserve (lat. 3°29'N, long. 9°50'E), about 5 km S of Sanaga River, about 15 km E of Mouanko, 15 July 1976 (D. McKey). Holotype, allotype and most paratypes in LACM; paratypes also in BMNH, MHNG, MCZ and collections of D. McKey and G.C. & J. Wheeler.

ETYMOLOGY: *phylax* (Gr., guardian), appropriate to this ant which protects leaves of the host plant, *Leonardoxa africana*.

DISCUSSION: Some aspects of the behavior and ecology of this ant are discussed by McKey, ms. Colonies are apparently polycalic and are situated within the internodes of the host plant. The worker ants patrol young leaves of the *Leonardoxa* plants and protect them from herbivores. Older leaves are not patrolled but are protected by chemicals within the leaves. Sustenance for the ants is derived largely from specialized food bodies on the plant.

One of the female specimens has a malformed head. The left

occipital corner is shaped about as it is in males, while the right approximates the condition of the female caste, but the occipital lobe is a little less pronounced. The right eye is 0.31 mm long and the left is 0.27 mm long; the right OMD is 0.58 x EL, the left OMD is 0.95 x EL. That for the right side is thus within the range for the female, but on the left the OMD/EL ratio is very different from that of either sex. Since the antennae and mandibles are typical of females, the specimen is apparently teratological rather than an intersex.

ACKNOWLEDGMENTS

Special thanks go to Mr. Doyle McKey for allowing me to study and describe this unusual ant. Important comparative material of related genera was sent by: C. Besuchet, Geneva Natural History Museum (MHNG); B. Bolton, British Museum (Natural History) (BMNH); E.O. Wilson, Museum of Comparative Zoology (MCZ).

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CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

REPRODUCTIVE PERFORMANCE OF THE EASTERN BROWN PELICAN,
PELECANUS OCCIDENTALIS

By Ralph W. Schreiber



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REPRODUCTIVE PERFORMANCE OF THE EASTERN BROWN PELICAN, *PELECANUS OCCIDENTALIS*

By Ralph W. Schreiber²

ABSTRACT: Data collected during eight breeding seasons, 1969—1976, on the reproductive biology of the Brown Pelicans (*Pelecanus occidentalis*) nesting on Tarpon Key, Pinellas County, west coast of Florida are presented. Human disturbance bias is discussed in relation to clutch size, hatching success, and fledging success, and data are presented showing that visits by scientific investigators can influence the results obtained. Seasonal differences in reproductive parameters are considered and late nests are shown to be less successful than earlier attempts. Year to year fluctuations in productivity characterize this colony, and by comparison to the published literature, are shown to be usual for this species. Data on production calculated by five different monitoring methods are compared. The prospect of deriving a precise figure for reproductive performance is discussed and a recruitment standard, based on extensive field data, of 0.9–1.0 young per breeding pair is suggested for this species.

INTRODUCTION

The goal of breeding biology studies of birds should be to precisely determine the reproductive parameters necessary for accurate prediction of the status of the wild population. J.J. Hickey (1955) sagely pointed out that "bird populations have a field reality and a paper existence." Startlingly few students have heeded Hickey's intended warning in the intervening years to pay strict attention to the methodologies involved in carrying out studies of avian reproductive biology. However, Ricklefs (1973) thoroughly reviewed this subject and noted that "the data required to construct a life table are straightforward in their meaning and interrelationships, but their estimation is almost always difficult." He further noted that some parameters, "particularly clutch size and nesting success are relatively easy to obtain." R.J. Robel (1973) noted that "... life tables are constructed by people not directly involved in the collection of the field data, who may therefore incorporate some major biases in their preparation ... the mere appearance of data in a life table is impressive and data contained in them are often accepted without close scrutiny of how, where, and when they were collected." Woolfenden and Rohwer (1969) and Ricklefs (1969) discussed calculation methods and Mayfield (1975) noted that calculations of reproductive success contain "not only hard facts but elements of judgment, none of this difficulty is apparent in published tables or figures, which convey an air of indisputable finality."

Unfortunately, all of these biases in scientific study have occurred relevant to the reproductive biology of the Brown Pelican (*Pelecanus occidentalis*) during the past decade of intense interest in the species. In this paper I present data gathered on clutch size, hatching success, and fledging success during a study of this species from 1969 through 1976 in Florida. I further relate

some of my difficulties in deriving these "relatively simple" figures. I hope to elucidate the problems involved in calculating reproductive success from extensive field data and the difficulties in obtaining a precise figure that can be used in a modeling equation.

I stress that for comparative purposes, we must pay strict attention to the methodologies used in obtaining data to calculate productivity, especially as regards investigator bias on the results. Only through long term studies done in a consistent manner can accurate, useful data be obtained.

METHODS

From January 1969 through August 1976 I studied the Brown Pelican population of Tampa Bay, specifically Boca Ciega Bay in Pinellas County, centering on Tarpon Key, Pinellas National Wildlife Refuge (27° 40'N, 82° 40'W), on the Gulf of Mexico coast of mid-peninsula Florida. During the nesting seasons (roughly January through September) of these eight consecutive

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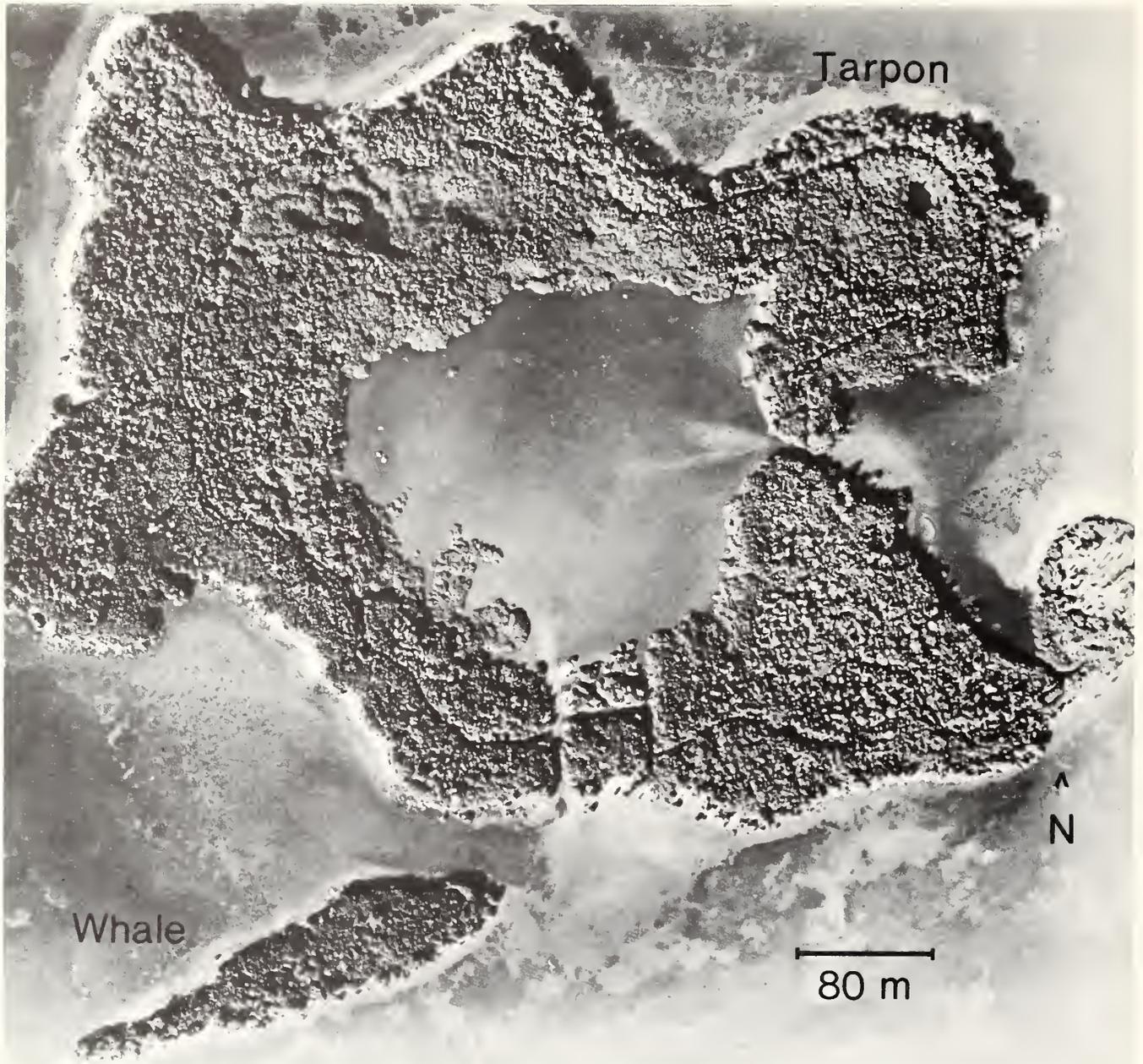


FIGURE 1. Tarpon and Whale Keys, Pinellas National Wildlife Refuge, Boca Ciega Bay, Pinellas County, Florida (27°40'N, 82° 40'W).

years I visited Tarpon and Whale Keys essentially weekly and occasionally three to five times per week. Only on five occasions did more than ten days, but never more than 18 days, separate visits, and then only once each session.

These Keys (Fig. 1) provided a good situation for studying various aspects of the biology of Brown Pelicans. The pelicans nest in Black Mangrove (*Avicennia germinans*), the majority along the edges of the central lagoon, and are quite undisturbed by humans. The total colony naturally divided into eight units, each of which could be studied discretely without disturbing other units.

In one of these units I measured growth and development of nestlings (Schreiber 1976a); at another I carried out behavior observations (Schreiber 1977); and each year nestlings were

banded in the whole colony (Schreiber 1976b). As noted in Schreiber and Risebrough (1972) two other units were checked in 1969 and 1970, one visited weekly and one more frequently. In subsequent years (1971–1976) the weekly visit schedule was continued on the former unit. In addition, on each visit to the colony, all adults, nests, subadults, immatures (by plumages, Palmer 1962; Schreiber *unpublished data*), nestlings, and later fledglings were counted in all units from a consistent location in the center of the lagoon. Data on timing of the nesting season and population structure will be presented in detail elsewhere (Schreiber *in preparation*) but I use the seasonal data on nests, eggs, and young to calculate reproductive success here.

I began visits to units on the week following the first sighting of a nest structure on which an adult was sitting. I marked each

nest with a numbered plastic streamer hanging below the nest. I used a small mirror attached on a 2.5 m aluminum pole to check contents of nests which were too high for me to reach. Nest contents were recorded directly onto nest record cards. Visits were made on the high tide, to facilitate access across the lagoon by boat, unless the high tide occurred between 11.00 and 16.00 hours during late May through August. At those times, to avoid excessive heat stress to both the pelicans and myself, I visited the colony prior to 11.00. I use the following definitions: NEST, a structure with adults, eggs, or young present; NESTLING, a young bird prior to making its first sustained flight (at 10 to 12 weeks of age) which takes it away from its nest permanently. (Nestlings may move some distance from their nests but usually return to the site to be fed by their parents, and frequently the nests are destroyed by the nestlings within five to seven weeks of age. I prefer to call these birds nestlings, rather than young or pulli, even though they may not actually be in a nest); FLEDGLING, a nestling which has permanently flown from its nest but which has not yet departed from the immediate vicinity of the colony; SUCCESSFUL NEST, one from which one or more nestling has fledged; PRODUCTIVITY, the number of fledglings per total nesting attempts in the colony, or sample of the colony.

RESULTS AND DISCUSSION

EFFECTS OF HUMAN DISTURBANCE

Since I am concerned about the effects of human disturbance on measurement of reproductive success, and especially in this case that of the "scientific" investigator, in 1969 and 1970 I compared productivity figures for two units in the colony, one disturbed once weekly and one more frequently. I believe it valid to assume that the adult pelicans in the two units of the colony used for this "experiment" were uniform in age and breeding experience.

The data in Table 1 confirm that in this species disturbance can bias the results, especially with increased number of visits to a colony. Not only were fewer eggs laid in more frequently disturbed nests, but hatching success (Schreiber and Risebrough 1972) and productivity were also reduced ($P < 0.01$, t test). Interestingly, the percentage of eggs hatched that produced fledged young and fledglings per successful nest were not affected, indicating that the effects of human disturbance are more pronounced during the pre-egg and incubation periods.

To examine further whether lower reproduction is a matter of the type of human disturbance or of the number of visits, I compared reproductive success between two units of the colony. One was the same unit visited weekly in 1969 through 1976 and the other was the unit used to measure growth and development of nestlings from 1969–1972 (Schreiber 1976a). I checked nests in one unit (60 nests) for presence and number of eggs and young which required about 15–30 minutes. I measured all eggs and nestlings in another unit (26 nests) which required up to an hour and a half. During the incubation period I handled most eggs in the latter unit at least twice and each nestling was handled on each weekly visit. In 1972, no significant differences existed between the units in any of the parameters measured (Table 2). Similar results were obtained in 1969–1971. In fact, for the nests near which I spent more time, a tendency existed to hatch more

eggs, more nests were successful, and fledgling success was higher.

DISCUSSION OF HUMAN DISTURBANCE FACTORS

Few studies have directly examined the effects of human disturbance relative to productivity parameters in birds. A recent increased awareness of the investigator bias is occurring (Gottfried and Thompson 1978; and especially Ellison and Cleary 1978). Skutch (1966) noted that any human activity at nests "increased to an inassessible degree the incidence of predation" in Central American land bird species. Fyfe and Olendorff (1976) briefly but thoroughly discussed the problems involved and offered solutions to scientific and amateur disturbance at raptor nests specifically. Their information undoubtedly holds for most avian species. Studies of Bald Eagles (*Haliaeetus leucocephalus*) showed that the timing and kinds of human activities reduce the occupation and productivity of nests of that species (Newman, et al. 1977). Burger and Hahn (1977) examined crow predation on Black-crowned Night Herons (*Nycticorax nycticorax*) but they say nothing about human disturbance facilitating the predation although that is implied since the authors disturbed the heron nests to check their contents. Werschkul, et al. (1976) found a lower fledging rate in a Great Blue Heron (*Ardea herodias*) colony near logging operations in Oregon than in colonies further away.

Robert and Ralph (1975) conducted a detailed controlled study on the effects of human disturbance in a colony of Western Gulls (*Larus occidentalis*) and demonstrated that frequent human visits reduced productivity by increasing loss of eggs. Also, hatching failure was directly proportional to the amount of disturbance, as Western Gulls destroy eggs in neighboring unattended nests. However, chicks survived better in more frequently disturbed nests, apparently because less frequent human visitation resulted in a more intensely "frightened" chick which ran further from its territory and thus encountered a greater risk of being killed. Overall mortality was higher in disturbed than undisturbed areas. These studies indicate that predation is the most usual cause of decreased production that accompanies human disturbance.

However, in a purely experimental approach to predation effects on reproduction in an "old field habitat" situation, Gottfried and Thompson (1978) found that visits to nests by investigators did not affect success or failure. Schreiber, et al. (*in preparation*) found in one colony of Laughing Gulls (*Larus atricilla*) that human visits had no effect on productivity. Gillett, et al. (1975) found human visits decreased mortality of young by only 3–5 percent, primarily in the young chick stage, and did not affect hatching success in the Glaucous-winged Gull (*Larus glaucescens*). Willis (1973) found that survival rates at visited and unvisited nests were similar in the Bi-colored Antbird (*Gymnophis bicolor*). Nisbet and Drury (1972) found that daily visits to tern colonies (*Sterna hirundo* and *S. dougallii*) apparently caused some desertions of nests early in incubation. They did not detect significant differences in productivity related to frequency of visits.

The above data indicate that species differences do exist in response to human intrusion. However, in all the pelecaniformes that have been examined specifically for the problem, human visits to colonies have caused severe problems and Nesbit (1978) believes that "human disturbance by biologists is one of the

TABLE 1

Reproductive success of the Brown Pelican in relation to frequency of human disturbance. Tarpon Key, Pinellas County, Florida 1969 and 1970. Does not include nests in which re-laying occurred or "nests" that did not receive eggs.

	1969		1970	
	Visited weekly	Visited frequently	Visited weekly	Visited frequently
Number of nests	13	63	25	37
Number of eggs laid	37	142	64	77
Clutch size	2.85	2.25**	2.56	2.08**
Number of eggs that hatched	31	80	45	22
Eggs hatched per nest	2.38	1.27**	1.80	0.59**
Hatching success	84%	56%	70%	29%
Number of young that fledged	22	53	26	13
Percentage of eggs laid from which young fledged	59%	37%	41%	17%
Percentage of eggs hatched from which young fledged	71%	66%	58%	59%
Number of successful nests (fledged one or more young)	13	44	21	10
Percentage of successful nests	100%	70%	84%	27%
Fledglings per successful nests	1.7	1.2	1.2	1.3
Productivity (fledglings per total nests)	1.7	0.8	1.0	0.4

** = highly significant difference at 0.01 level, t statistic.

major threats to seabirds." Kury and Gochfeld (1975) reported greatest loss early in the nesting season in gull and cormorant colonies. Johnson and Sloan (1976) summarized the published literature on the intolerance of White Pelicans (*Pelecanus erythrorhynchos*) to human disturbance during the nesting season and noted that gull predation and physical stress on the young were the major causes of mortality. Vestjens (1977) noted the extreme susceptibility of *P. conspicillatus* in Australia. Brown and Urban (1969) and Schreiber (*in preparation*) noted that *P. onocrotalus* in Ethiopia and South West Africa are also extremely sensitive to even the slightest human presence, and especially during the courtship and egg stage of the nesting cycle. Nelson (1966) found that egg loss was proportional to the amount of human disturbance in the Gannet (*Sula bassana*) on Bass Rock, Scotland, and noted that many earlier studies had not taken into account the artifacts introduced into productivity figures by human disturbance. He recently reiterates and emphasizes this point (Nelson 1978). Snow (1960) noted that Ravens (*Corvus corax*), Herring and Great Black-backed Gulls (*Larus argentatus* and *marinus*) took eggs of the Shag (*Phalacrocorax aristotelis*) after she disturbed some adults. They were slow in returning to their nests and she stated that "normally the eggs would not be open to predation, never being left uncovered unless the bird is put off by human activity." Ellison and Cleary (1978) found that frequent visits caused nest abandonment, allowed gull predation, discouraged late nesters from settling in disturbed colonies, and delayed clutch commencement in Double-crested Cormorants (*Phalacrocorax auritus*).

Anderson and Keith (1979) and Keith (1978) have thoroughly reviewed the effects of human disturbance, including investigator bias, in marine bird colonies in west Mexico. They showed that human visits, both by "scientists" and "tourists," significantly decreased productivity in Brown Pelican colonies. They demonstrated dramatic effects of this disturbance on Heermann's Gulls (*Larus heermanni*) and populations of Brown Pelicans, especially on Isla San Martín (see also Jehl 1973). These effects were manifested primarily through predation of eggs by Western Gulls. Abandonment of nests (eggs and small young) by adult pelicans for even a brief period of time resulted in predation of contents of unattended nests. They found total abandonment if colonies were visited early in the nesting season, with a 50 to 100 percent decrease in productivity between "disturbed" and control colonies.

However, Blus and his coworkers (Blus, et al. 1974, and references therein) have published a series of overlapping papers documenting the effects of DDE on egg shell thickness and have purported to relate such effects to the reproductive success of Brown Pelicans in South Carolina since 1969. Most of that work entailed collecting eggs for organochlorine residue analysis but some field studies were also carried out. Blus, et al (cited) have suggested that depressed productivity has occurred in those colonies. However, their papers do not indicate how the figures for productivity were derived other than from annual counts of nests and young and no mention is made of the possibility of human disturbance affecting production. They do state that in 1971 the nesting colony was visited on seven occasions and in 1972 it was

TABLE 2

Comparison of reproductive parameters in colony units with different quality of disturbance, 1972. Does not include nests in which re-laying occurred or "nests" that did not receive eggs.

	Nests checked only	Nestlings measured
Number of nests	60	26
Number of eggs laid	156	68
Clutch Size	2.6	2.6
Number of eggs that hatched	103	49
Eggs hatched per total nests	1.7	1.9
Number of nests in which eggs hatched	49	24
Hatching success	66%	72%
Number of young that fledged	69	40
Percentage of eggs laid from which young fledged	44%	59%
Percentage of eggs hatched from which young fledged	67%	82%
Number of successful nests (fledged one or more young)	44	23
Percentage of successful nests	73%	88%
Fledglings per successful nest	1.6	1.7
Productivity (fledglings per total nests)	1.2	1.5

visited on 16 occasions. In Blus and Keahey (1978) they note that in 1975 "visits . . . were limited to ONE OR TWO (emphasis mine) one-hour periods each week from April through mid-August" and, lacking evidence to the contrary, presumably a similar irregular schedule of visits was used in earlier years.

In the study reported here, during a controlled experiment in this colony in 1969 and 1970, human disturbance significantly decreased clutch size, hatching success, and total fledging success; but the number of eggs that hatched that fledged a young and fledglings per successful nest were not affected. The duration of each visit and the handling of eggs and nestlings were not significant factors affecting reproductive success. The total number of visits was the determining factor, more visits producing lowered reproductive success. Prolonged stays in the colony could have disastrous effects during hot, sunny weather since the eggs and small young are highly susceptible to elevated temperatures (Bartholomew and Dawson 1954; Schreiber *unpublished data*).

These data indicate that only colonies which have been visited with a consistent visitation pattern may/should be used to compare productivity within years and between years. Thus, while general comparisons between or within colonies by a different or the same workers may be possible, unless similar patterns of nest checking have been utilized, precise comparisons should not be made (Nelson 1966, 1978; Robert and Ralph 1975). This is especially true since significant differences in natural productivity exist between years even in one colony and human disturbance probably compounds these natural fluctuations.

BROWN PELICAN BEHAVIORAL REACTIONS TO HUMAN DISTURBANCE

During my weekly nest-checking in 1972–1976, Elizabeth Anne Schreiber observed the reaction of adult Brown Pelicans in the colony. This information revealed that they become habituated to human intrusion, if it was carried out in a routine manner and pattern. Following is a generalized description of the pelican's reaction to human disturbance in the colony. On the first few seasonal disturbances the adults simultaneously flew from nests or perches while I was approaching at 40–60 m away, although they individually had stood up, assumed an alert posture, and wing-flapped (Schreiber 1977) when I was still 50–80 m away. This early take-off seemed to involve considerable "panic." Most adults circled back and forth over the nest sites during these disturbances but a few landed on the lagoon 30–50 m from the colony unit. If I left the unit and waved my arms or shouted loudly to flush the adults off the water, they flew and circled over the nests and most landed again on their nests within three to five minutes. If not flushed from the water, as much as 15 minutes ensued before all adults returned to their nests, or potential nest sites. Early in the season, adults occupying the colony without a nest structure often abandoned the area when disturbed. This was evident as adults flew out of the colony entirely and did not return during the hour or so after disturbance. By the fourth or fifth weekly visit to the colony the adults stood up and wing-flapped as I approached but few flew from their nests until I was 15–30 m from the nests. Some did not fly until I was in the

mangrove and actually underneath the nests. Most of the adults flew directly to and landed on the water but a few continued to circle over the colony throughout my presence there. By the fifth or sixth weekly visit they did not fly from nests until I was essentially in the colony and then they either circled or sat on the water. When flushed from the water they all returned directly to their nests, usually within two minutes. The return to the nest always entailed one or two passes over the nest sites, but the number of these passes decreased from several early in the season, probably as the birds learned the precise location of their nests or became habituated to the disturbance. Early departure from nests upon approach was a good sign that additional birds had moved into the colony and had commenced nesting activities. These early flushers were usually not yet associated with nest structures or nests containing eggs.

This general pattern of reaction to my disturbance took place each year. It was our impression in 1975 and especially 1976 that birds reacted less to my disturbance early in the year than in previous years. The presence of banded birds, as many as six to eight in this unit in 1976, indicated that they probably had been banded as nestlings in this colony in previous years. Brown Pelicans readily learn to beg for fish at boats and fish piers in Florida and it seems likely that they also learn to accommodate to some extent to disturbances in the nesting colony when activities are undertaken in a regular and consistent manner. This same pattern can be seen in the behavior of birds in a colony situation near considerable human activity (i.e. Port Orange, Florida) compared to one which routinely received little disturbance or amount of human activity.

Different levels of disturbance were caused by walking across the lagoon and by approaching the colony in a boat, either rowing or motoring. The upright human figure considerably increased the flight distance (Hediger 1950), especially early in the season. Additionally, a direct approach toward the birds caused a higher level of disturbance than an indirect approach. I have observed fishermen moving within 5 m, but parallel to, the edge of the mangrove colony without causing any birds to take flight, although the birds always assumed the alert standing posture while the fishermen were near. If nests were disturbed on an infrequent or occasional basis, the birds did not seem to habituate, but always departed nests in a "panic."

Comparison of these data with the reaction of the pelicans nesting on the ground in California and Mexico (Anderson and Keith 1979; Keith 1978; Schreiber unpublished data) and in South Carolina (Schreiber unpublished data) clearly indicates that mangrove-bush nesting birds are far less susceptible to disturbance. Apparently, the substrate is an important mitigator to the panic reaction. Young on the ground wander, walk, or in "panic," run away from nests much more readily than young in bushes. In Mexico almost all adult pelicans fly from nests, either casually if they have seen the observer for some time, or in panic if suddenly surprised (Keith personal communication). In mangrove, young birds up to four to six weeks old tend to remain in their nests but older nestlings will either attempt to defend the nest (or themselves) or will attempt to run or take-off, often falling to the ground below the nests. In the mangrove, most young are unable to climb back to their nests if displaced more than a few meters laterally.

I have observed an adult feeding a pre-fledgling away from its nest on only three occasions and if the young do not return to their nests they undoubtedly will starve. It thus seems that strong

selection exists for young in bushes to remain in their nests, while in ground colonies pods do form and young birds wander considerably.

I have the definite impression that flight distance (Hediger 1950) in Mexico and California pelicans is much greater than in Florida. Perhaps this resulted from the close proximity of the Florida colonies to man's activities and the lower level of predatory type behavior there than in the western colonies. Predation in colonies, originally by mammalian predators and snakes, undoubtedly caused all pelicans to nest on islands, thus avoiding the high predation rates that would occur on mainland nesting colonies. I have noted two colonies on mangrove islands that have been destroyed and abandoned in Florida after raccoons (*Procyon lotor*) gained access to those islands (Schreiber, unpublished data).

Human disturbance in the pelican colonies in Florida allows Fish Crow (*Corvus ossifragus*) predation (Schreiber and Risebrough 1972). I know from observations that no predation occurred in the Tarpon Key colony behavior study units unless adults were flushed from their nests (Schreiber 1977). Also, in three years of this study, and many two to three-week periods during other years, I know that no predation occurred in these study units. The crow problem noted as severe in 1969 and 1970 (Schreiber and Risebrough 1972) was much reduced or nonexistent in later years due to the removal of some crows from the population early in the nesting season. Thus, losses of eggs and small young must occur from other causes such as: adults abandoning nests, either permanently or for so long that incubation temperatures were allowed to fluctuate and the developing embryo died; breakage of eggs or displacement from nests when adults fly from the nests; adults shaking eggs so violently when taking-off that embryological development ceases.

If visits to a colony are necessary, as in many cases they are (see below), nests should be approached slowly and in full view of the birds to prevent undue disturbance effects. When approached in this manner the birds can stand up and remove their feet from the eggs before take-off, rather than flushing from an incubating position with their totipalmate toes wrapped around the clutch. Nests should not be visited during the heat of the day. When the investigator leaves the colony, adults sitting on the water should be flushed so they will return to their nests more quickly than if left sitting on the water to go back "in their own time." Early season visits to colonies should be avoided since they appear to cause greater disturbance than visits made after incubation is well along.

Further study of egg loss and nestling mortality for this and all marine bird species is clearly indicated.

SEASONAL FLUCTUATIONS IN REPRODUCTIVE SUCCESS

In the previous section I demonstrated that only colonies visited on a consistent schedule can be used to compare reproductive success. In this section I discuss the seasonal data on reproductive success in the unit of the colony visited weekly each year 1969-1976. These seasonal data then form the basis for annual comparisons. These annual differences will also be obvious in Tables 3-11, with details presented in Appendices 1-8.

In order to compare seasonal parameters of early, middle, and late nests for all years I combined data for each season by two

week or one month periods, depending on the span of laying (vertical divisions in Tables 3–10). These data do not include any nests in which re-laying may have occurred or "nests" that were constructed but never received eggs. The same unit in the north-west portion of the colony was used for checking reproductive success during 1970 through 1976; in 1969 an isolated unit about 50 m to the north away from the lagoon was used. The 328 clutches in this sample from eight years were thus broken down into 104 early, 189 middle, and 35 late initiations. The number of nests in the unit varied considerably between years and the small sample sizes for any one part of a year did not allow complete statistical comparisons. Still, general seasonal trends were apparent.

CLUTCH SIZE (Table 3): Was smaller later in the season and especially so if laying continued beyond mid to late April (see especially 1971, 1972, 1974, and 1976). Clutch size early in the season was nearly as high as in those nests started during the middle of the season. Mean clutch size was 2.5 and 2.6 for the early and middle periods but 2.2 for the late period. The latter is highly significantly different from the earlier periods ($P < 0.01$, t test). This general pattern of lower clutch size holds for all years except 1969 (with a small sample) when an increase in clutch size occurred through the year, and in 1971 and 1972 which had higher clutch sizes in mid-season. Major annual differences in the seasonal pattern of clutch size are not obvious.

HATCHING SUCCESS (Table 4): A distinct, but not statistically significant, decrease in hatching success occurs between early and mid-laying periods (84% and 70%), but a highly significant difference ($P < 0.01$, t test) exists between both the early and mid-season and the late period (43%); 1973 differs from this general pattern in that the eggs laid in early May (10 clutches) were more successful in hatching than were earlier clutches that year.

The percentage of nests in which one or more eggs hatched (Table 5) are essentially similar between periods (81%, 82%, and 77% of nests). The latest nest I recorded in all eight years (a nest started in late June 1973) did successfully hatch one egg. However, in four of the six years in which laying extended longer than two months, late nests were usually unsuccessful at completing incubation. The differences of the three unusual years (1973, 1974, and 1976) will be discussed more fully below, but I note here that the usual seasonal pattern of egg success shown above does not occur in the two years in which total nesting success was lowest, 1974 and 1976.

FLEDGING SUCCESS: Has been variously defined in the literature so I present my data on this parameter in several methods. Seasonal differences existed in the percentage of eggs laid that actually produced a fledged young (Table 6), with middle eggs producing slightly more than early eggs (41% vs. 33%), and both more than late eggs (28%). Statistically significant differences occurred only between the middle and late nests ($P < 0.05$, t test). However, a different pattern of seasonal differences existed in the percentage of eggs which hatched that produced a fledged young (Table 7), with late eggs producing more young than both early and middle period eggs (64% vs. 39% and 59%). Sixty-five percent of early nests were successful (Table 8), 69% of middle nests were successful, while only 43% of late nests were successful. No statistical differences existed between early and middle nests, but late nests were highly significantly less successful than both early and middle ones ($P < 0.01$, t test).

Comparing the number of young fledged per nest in nests that

TABLE 3

Clutch size by date of clutch initiation, presented as the mean for two week periods and number of clutches in ().

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
1969	2.8	—	—	—	2.8 (4)	2.9 (7)	3.0 (2)	—	—	—	—
1970	2.5	—	—	3.0 (4)	2.6 (5)	2.4 (11)	2.4 (5)	—	—	—	—
1971	2.5	—	—	2.0 (2)	2.9 (8)	2.5 (19)	2.6 (8)	1.5 (2)	—	—	—
1972	2.6	2.4 (5)	2.6 (7)	2.8 (23)	2.7 (35)	2.2 (12)	1.8 (4)	—	—	—	—
1973	2.6	—	—	—	2.6 (7)	2.5 (2)	2.5 (2)	2.6 (10)	3.0 (1)	—	2.0 (1)
1974	2.7	—	3.0 (11)	2.8 (18)	2.8 (20)	2.2 (10)	2.0 (1)	1.0 (1)	—	—	—
1975	2.6	3.0 (9)	2.6 (19)	2.9 (8)	—	2.5 (8)	2.2 (4)	2.2 (4)	—	—	—
1976	2.6	—	3.0 (3)	2.8 (13)	2.5 (4)	2.6 (6)	2.0 (2)	2.0 (1)	—	—	—
Means		EARLY = 2.5		MIDDLE = 2.6		LATE = 2.2					

TABLE 4

Hatching success (eggs hatched per eggs laid) by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	89	—	—	—	73	95	67	—	—	—	—
1970	70	—	—	67	77	67	75	—	—	—	—
1971	62	—	—	75	74	58	62	0	—	—	—
1972	68	66	61	83	68	52	0	—	—	—	—
1973	53	—	—	—	22	40	40	85	0	—	50
1974	78	—	91	88	73	59	0	0	—	—	—
1975	83	96	96	83	—	75	33	44	—	—	—
1976	64	—	100	62	50	64	0	100	—	—	—
Means		EARLY = 84%		MIDDLE = 70%		LATE = 43%					

were successful (Table 9), early nests fledged 1.3 young per nest, middle period nests fledged 1.6 young, and late nests fledged 1.5 young per nest. No statistical differences exist between any of these three nest periods.

Comparing the number of young fledged per all nests in the study area (Table 10), early nests fledged 0.8 young per nest, middle period nests fledged 1.1 young, and late nests fledged only 0.6 young per nest. No statistical differences exist between early and middle period nests, or early and late period nests, but the late nests fledged statistically fewer young than the middle period nests ($P < 0.02$, t test).

SUMMARY: To summarize the general patterns of seasonal

TABLE 5

Percentage of nests in which one or more eggs hatched by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	100	—	—	—	100	100	100	—	—	—	—
1970	76	—	—	100	100	91	100	—	—	—	—
1971	74	—	—	100	100	68	75	0	—	—	—
1972	85	80	100	100	91	58	0	—	—	—	—
1973	61	—	—	—	28	50	50	90	0	—	100
1974	85	—	100	100	85	60	0	0	—	—	—
1975	94	100	100	100	—	100	50	75	—	—	—
1976	76	—	66	38	50	33	0	100	—	—	—
Means		EARLY = 81%		MIDDLE = 82%		LATE = 77%					

TABLE 8

Percentage of successful nests, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	100	—	—	—	100	100	100	—	—	—	—
1970	84	—	—	100	80	82	80	—	—	—	—
1971	69	—	—	100	100	63	62	0	—	—	—
1972	78	80	86	83	88	58	0	—	—	—	—
1973	56	—	—	—	28	50	50	80	0	—	100
1974	33	—	64	44	15	20	0	0	—	—	—
1975	83	88	84	100	—	100	25	50	—	—	—
1976	34	—	67	31	50	33	0	0	—	—	—
Means		EARLY = 65%		MIDDLE = 69%		LATE = 43%					

TABLE 6

Percentage of eggs laid from which a young fledged, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	59	—	—	—	45	70	50	—	—	—	—
1970	41	—	—	50	38	41	33	—	—	—	—
1971	47	—	—	50	65	42	48	0	—	—	—
1972	49	50	44	51	55	37	0	—	—	—	—
1973	27	—	—	—	11	20	20	42	0	—	50
1974	12	—	21	16	5	9	0	0	—	—	—
1975	49	41	51	70	—	55	22	22	—	—	—
1976	14	—	22	14	20	14	0	0	—	—	—
Means		EARLY = 33%		MIDDLE = 41%		LATE = 28%					

TABLE 9

Fledging success measured as young fledged per successful nest, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
1969	1.7	—	—	—	1.2	2.0	1.5	—	—	—	—
1970	1.2	—	—	1.5	1.2	1.2	1.0	—	—	—	—
1971	1.7	—	—	1.0	1.9	1.7	2.0	0	—	—	—
1972	1.6	1.5	1.3	1.7	1.7	1.4	0	—	—	—	—
1973	1.2	—	—	—	1.0	1.0	1.0	1.4	0	—	1.0
1974	1.0	—	1.0	1.0	1.0	1.0	0	0	—	—	—
1975	1.6	1.4	1.6	2.0	—	1.4	2.0	1.0	—	—	—
1976	1.1	—	1.0	1.2	1.0	1.0	0	0	—	—	—
Means		EARLY = 1.3		MIDDLE = 1.6		LATE = 1.5					

TABLE 7

Percentage of eggs hatched from which a young fledged, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	67	—	—	—	63	74	75	—	—	—	—
1970	58	—	—	75	50	61	44	—	—	—	—
1971	77	—	—	67	88	71	77	0	—	—	—
1972	72	75	73	61	80	71	0	—	—	—	—
1973	52	—	—	—	50	50	50	50	0	—	100
1974	16	—	23	18	7	15	0	0	—	—	—
1975	59	42	53	84	—	73	66	50	—	—	—
1976	23	—	22	22	40	22	0	0	—	—	—
Means		EARLY = 39%		MIDDLE = 59%		LATE = 64%					

TABLE 10

Fledging success measured as young fledged per total nests, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
1969	1.7	—	—	—	1.2	2.0	1.5	—	—	—	—
1970	1.0	—	—	1.5	1.0	1.0	0.8	—	—	—	—
1971	1.2	—	—	1.0	1.9	1.0	1.2	0	—	—	—
1972	1.3	1.2	1.1	1.4	1.5	0.8	0	—	0	—	1.0
1973	0.7	—	—	—	0.3	0.5	0.5	1.1	0	—	1.0
1974	0.3	—	0.6	0.4	0.2	0.2	0	0	—	—	—
1975	1.3	1.2	1.3	2.0	—	1.4	0.5	0.5	—	—	—
1976	0.4	—	0.7	0.4	0.5	0.3	0	0	—	—	—
Means		EARLY = 0.8		MIDDLE = 1.1		LATE = 0.6					

TABLE 11

Summary of seasonal parameters of reproductive success in the Brown Pelican.

	Early nests	Middle nests	Late Nests
Number of nests	104	189	35
Number of eggs laid	265	497	78
Clutch size	2.5	2.6	2.2
Number of eggs that hatched	223	351	34
Number of nests in which eggs hatched	84	155	27
Hatching success	84%	70%	43%
Number of young that fledged	88	208	22
Percentage of eggs laid that produced a fledged young	33%	41%	28%
Percentage of eggs hatched that produced a fledged young	39%	59%	64%
Number of successful nests	68	131	15
Percentage of successful nests	65%	69%	43%
Fledglings per successful nest	1.3	1.6	1.5
Productivity (fledglings per total nests)	0.8	1.1	0.6

fluctuations in clutch size, hatching success, and fledgling success for all eight years (Table 11 and Fig. 2); with the exception of the percentage of eggs hatched that produced a fledged young, all parameters are highest in the middle or early portions of the nesting season. Clutch size was essentially similar between early and middle nests but was lower in late nests. Hatching success was highest early in the season and then declined through the year, being much lower in the late nests. The percentage of eggs that produced a young varied between those laid and hatched. Of those laid, most produce a young in the middle period, with late nests being less successful than early nests. However, of the eggs that hatched, the late nests were the most successful with the early eggs being least successful. The middle period had the highest percentage of successful nests, but only somewhat more so than the early nests, with late nests being statistically less successful. Fledglings produced per successful nest was similar between late and middle period nests with early nests producing fewer but not significantly so. However, in fledglings per total nests, early and middle period nests were most successful with the late nests significantly less so.

DISCUSSION OF SEASONAL PATTERNS IN REPRODUCTIVE SUCCESS

Perrins (1970), reviewed the available avian literature and indicated that young hatched earliest in the season have the greatest chance of surviving to breed. He discussed the selective factors involved in this seasonal phenomenon. In recent years many studies have clearly demonstrated seasonal changes in clutch size and reproductive success, especially in gulls and terns (Laridae). The Herring Gull (*Larus argentatus*) has received the most attention and showed a decline in nest success through the season

(Parsons, et al. 1976; for summary) although early and late layers produced fewer fledged young than those nesting at the peak of the season (Parsons 1975). Haycock and Threlfall (1975) showed decreasing clutch size through the season in the Herring Gull, except in late nests when replacement clutches were involved. They did not measure seasonal nesting success and only presented a figure for total nesting success. Morris, et al. (1976) reported higher hatching success in early than middle or late nests of Common Terns (*Sterna hirundo*). They also did not report seasonal reproductive success but did find that fledging success was not related to clutch size. Coulson and his students demonstrated these seasonal effects are related to the age of individual Kittiwakes (*Rissa tridactyla*), with older or experienced birds nesting early or at the peak of the nesting season (Coulson 1966; Coulson 1978; Coulson, et al. 1969; Parsons 1976) with age and previous experience perhaps overriding any seasonal effect.

Nelson (1966) found in the Gannet (*Sula bassana*) that experienced breeders nested earlier than inexperienced individuals but that no difference existed between nesting success rate throughout the whole laying period. He related this to an abundant, reliable food supply near Bass Rock, Scotland. Snow (1960) showed that the Shag (*Phalacrocorax aristotelis*) on Lundy, Great Britain, exhibited a slight decrease in clutch size through the season with a well marked decrease in breeding success as the season advanced. She related this decrease to later nesting by younger birds and also to reduced availability of food at the end of the season. Keith (1978) found differences between early and late cohorts of Brown Pelicans in Baja California with later breeders less successful than the early birds. He indicated that food became scarce in August and the late nesters lost their young through starvation. Knopf (1975) found a significant decrease in young fledged with later nest establishment, and a decrease in

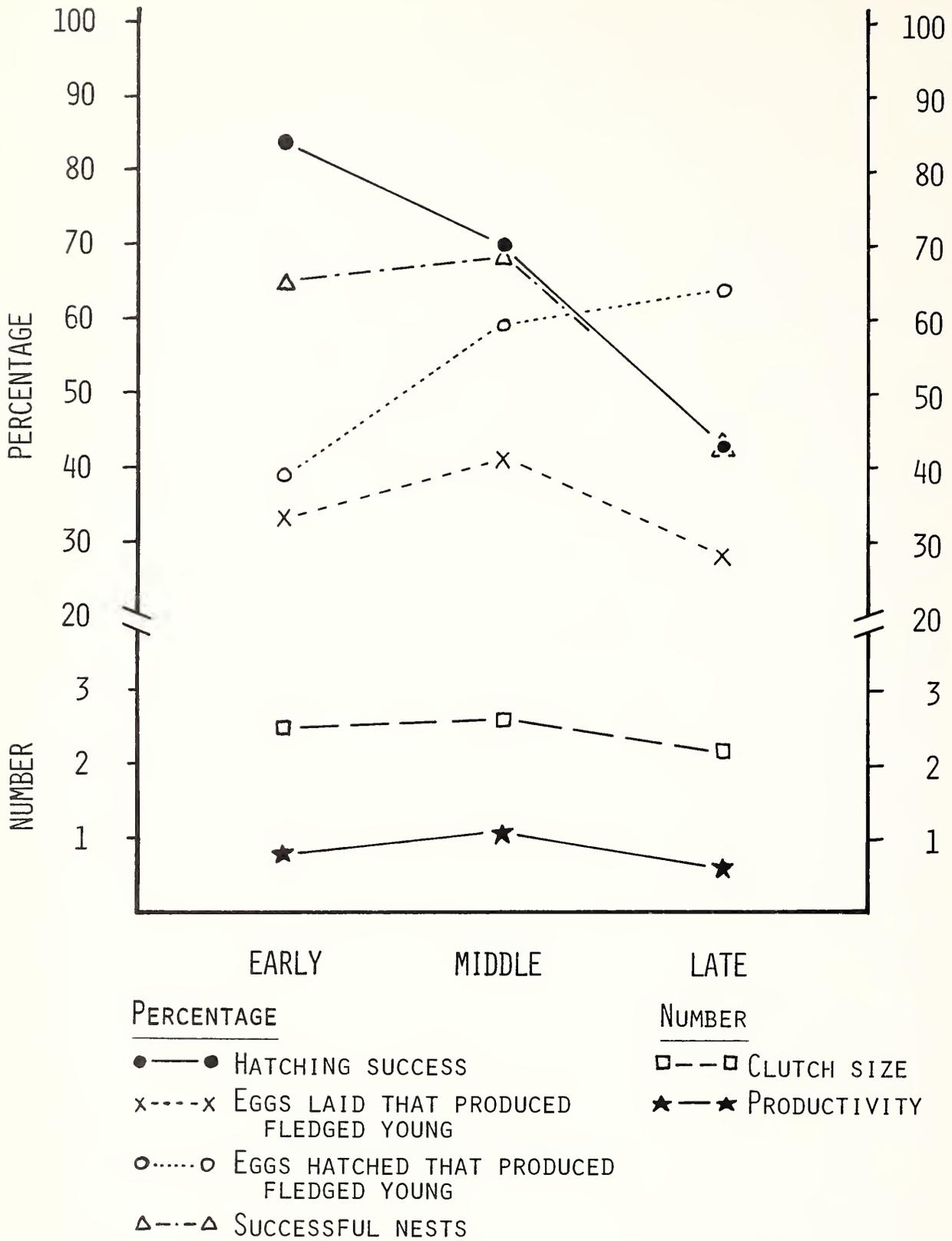


FIGURE 2. Seasonal pattern in clutch size, hatching success, and productivity.

clutch size through the season in the White Pelican (*Pelecanus erythrorhynchos*). He suggested that late breeders were younger birds (Knopf and Street 1974).

Conventional ornithological thought indicates seasonal changes in reproductive success. However, other than the seasonal effects on clutch size, with larger clutches formed early and at the peak of laying, seasonal changes in reproductive success have actually been demonstrated in few species. In those species for which data are available, indications are that these seasonal changes are related to the age or experience of the nesting birds. Clearly, more data are needed on the subject.

A seasonal pattern of late nests being less successful than early and middle period nests is well established in this colony of Brown Pelicans. Nesters at the peak of laying were the most successful. Early and middle period nesting birds not only have larger clutches, but they are also most successful in producing fledglings.

Blus and Keahey (1978) noted that the few subadult plumaged Brown Pelicans nesting in South Carolina in 1975 did so later than full adult plumaged birds. Keith (1978) by contrast, found no tendency for subadult plumaged birds to nest late in the season in Baja California. Unfortunately, I know nothing about the precise ages of the breeding birds in this study in Florida. However, no birds in subadult plumage bred in my study units. It is impossible to age the adults that did nest (Schreiber *in preparation*) and few data are available on nesting success related to precise age in this species.

I have demonstrated an investigator bias on reproductive success and distinct seasonal fluctuations in those parameters in this species. With those two factors in mind, I next consider the year to year fluctuations in productivity that are superimposed on the seasonal differences in reproductive success.

ANNUAL FLUCTUATIONS IN REPRODUCTIVE SUCCESS (based on marked nests)

In Table 12, I present data on various reproductive parameters measured in a consistent manner for 328 nests during eight years in one unit of the colony. The data in this table do not include nests in which relaying occurred or "nests" that did not receive an egg (see Tables 13 and 14).

CLUTCH SIZE: Varied between 2.8 (1969, with few nests) and 2.5 (1971) with a mean for all eight years of 2.6 eggs per nest (Table 12). This figure is lower than the 2.95 mean clutch size given from museum collections by Anderson and Hickey (1970) but that sample includes four egg clutches and is known to be biased toward a larger clutch size (Kiff *personal communication*). Blus and Keahey (1978) reported a clutch size of 2.85 for 89 nests of adults in South Carolina in 1975. They reported the presence of a small percentage of four and five egg clutches in a large sample of nests in that state between 1969 and 1975. I examined over 4,000 nests in Florida between 1969 and 1978 and did not see a four or five egg clutch. Bent (1922) and Palmer (1964) give three and occasionally two as the usual clutch size in this species. I believe that the data available indicate that two or three eggs constitute the normal clutch of the Brown Pelican.

HATCHING SUCCESS: (For individual eggs) varied from 89% (1969) to 53% (1973) with a mean of 71%. The percentage of eggs that produced a fledgling varied between 59% (1969) and

12% (1974) with a mean of 37%. The percentage of eggs hatched that produced a fledgling varied between 77% (1971) and 16% (1974) with a mean of 52%. The percentage of nests that were successful varied between 100% (1969) and 33% (1974) with a mean of 65%. Fledglings per successful nest varied between 1.7 (1971) and 1.0 (1974) with a mean of 1.5. Fledglings per total nest varied between 1.7 (1969) and 0.31 (1974) with a mean of 0.97.

These data clearly indicate that while clutch size and hatching success varied little between years, important differences did occur between years in reproductive success as measured by fledglings produced. Obviously, the figure for fledglings per successful nests will be higher than fledglings per total nests. I consider the figure for fledglings per successful nest as of little value for comparative purposes. The measurement of fledglings per total nests formed in a colony is the only useful measurement of productivity.

In three years (1971, 1972, and 1975) productivity was 1.2 to 1.3 young per nest. In 1969, fledging success in 13 nests was 1.7, a high figure that probably would not have been reached with a larger sample size (see Table 23). In 1970, productivity was one young per total nest. In 1973, 0.6 young fledged per nest. However, in 1974 and 1976 productivity was very low, at 0.3 and 0.4 young per nest.

RE-LAYING: In Table 13, I present an estimate of re-laying in marked nests. This estimate is not based on individually marked birds but on the following information: Several nests were constructed and received one or more eggs. On a later survey the eggs were gone, but the nest was still in undisturbed condition. The adults apparently continued to occupy it and in several instances I observed adults sitting on these empty nests. Unoccupied nests are rapidly destroyed by male pelicans gathering nest material (Schreiber 1977, and *unpublished data*). Thus, I believe it correct to assume that if a nest remained intact, and at a later date had eggs present, the original pair of pelicans had remained together on the site and the female re-layed there.

The amount of re-laying varied considerably between years, with none some years (1970), to as high as in 26% of the nests in 1973. Clutch size in the initial nests was slightly lower than in the re-laying attempt (2.4 vs. 2.5 eggs). Both were somewhat lower than in nests in which only an initial set was laid (2.6). The total number of eggs laid for replacement clutches was considerably greater than in "normal" clutches (4.6 eggs per nest). Only 28% of these eggs hatched (from none to 38% in different years). But of the eggs that hatched, 85% produced a fledgling, a figure significantly greater than for eggs laid in first clutches ($P < 0.01$, *t* test). Additionally, the 1.2 young fledged per total nest in which re-laying occurred is also higher than in non-replacement nests, although not significantly so.

With a sample of only 30 nests in which re-laying occurred during this eight year study, it is impossible to generalize on its occurrence. Re-laying does occur more in nests initiated early in the season; however, re-laying can occur throughout the season. In 25 of 30 nests in which re-laying occurred, the initial clutch was laid during the first four weeks of the season, probably reflecting the inability of females to recycle later in the nesting season. In my sample, re-laying was not significantly more prevalent in years with longer laying seasons, although more re-laying did occur in 1973 when the season lasted the longest into the summer (see Table 18 and Appendix 14).

Re-laying has occurred in nests from which eggs were lost

TABLE 12

Reproductive success of the Brown Pelican 1969–1976. All nests checked weekly in each year. Does not include nests in which re-laying occurred or "nests" that did not receive eggs.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests	13	25	39	86	23	61	52	29	328
Number of eggs laid	37	64	99	224	59	164	137	76	860
Clutch size	2.85	2.56	2.54	2.60	2.56	2.69	2.63	2.62	2.62
Number of eggs that hatched	31	45	61	152	31	128	114	48	610
Eggs hatched per nest	2.54	1.80	1.56	1.77	1.34	2.10	2.19	1.65	1.86
Percentage of nests in which eggs hatched	100%	76%	74%	85%	61%	85%	94%	76%	82%
Hatching success	89%	70%	62%	68%	53%	78%	83%	63%	71%
Number of young that fledged	22	26	47	109	16	20	67	11	318
Percentage of eggs laid from which young fledged	59%	41%	47%	49%	27%	12%	49%	14%	37%
Percentage of eggs hatched from which young fledged	67%	58%	77%	72%	52%	16%	59%	23%	52%
Number of successful nests (fledged one or more young)	13	21	27	67	13	20	43	10	214
Percentage of successful nests	100%	84%	69%	78%	56%	33%	83%	34%	65%
Fledglings per successful nest	1.69	1.24	1.74	1.63	1.23	1.00	1.56	1.10	1.48
Productivity (fledglings per total nests)	1.69	1.04	1.21	1.26	0.70	0.33	1.29	0.38	0.97

TABLE 13

Re-laying in the Brown Pelican, 1969–1976. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of additional nests in which re-laying occurred	1	0	3	12	6	3	2	3	30
Percentage of nesting attempts in which re-laying occurred	8%	0	8%	14%	26%	5%	4%	10%	9%
In nests in which re-laying occurred:									
Number of eggs laid	5	0	12	59	31	14	11	7	139
First attempt	3	0	6	28	15	8	5	3	68
Second attempt	2	0	6	31	16	6	6	4	71
Number of eggs hatched	1	0	3	23	7	3	2	0	39
Percentage of eggs laid that hatched	20%	0	25%	39%	22%	21%	18%	0	28%
Number of young fledged	1	0	3	19	5	3	2	0	33
Percentage of eggs laid that fledged	20%	0	25%	32%	16%	21%	18%	0	24%
Percentage of eggs hatched that fledged	100%	0	100%	83%	71%	100%	100%	0	85%
Number of young that fledged per total nests in which re-laying occurred	1.0	0	1.0	1.6	0.8	1.0	1.0	0	1.1

either early or late in the incubation period (14 in the first and 10 in the second half of incubation). Re-laying also occurred four times in nests in which one or more nestlings died within ten days of hatching. No re-laying was found in nests in which nestlings died at an older age. With my nest checks occurring only once a week, it was impossible to determine precisely the interval between loss of eggs or small nestlings and re-laying of the first egg of the replacement clutch. However, none was found in less

than two or more than four weeks. Replacement after loss of nestlings apparently took no longer than after egg loss, possibly indicating that re-laying is less likely to occur after loss of nestlings. This perhaps also reflects the inability of the female or the pair to recycle once the season has progressed.

No other published data exist on re-laying in Brown Pelicans.

While I have no data on the energy demands of egg production in the Florida Brown Pelicans, individual eggs initially weigh 98

TABLE 14

Aspects of reproductive success in the Brown Pelican: Nests not receiving eggs, fate of eggs that did not hatch, and nestling loss after hatching. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of nests that did not receive an egg	0	0	0	0	6	5	7	0	18
Percentage of nests that did not receive an egg	0	0	0	0	21%	7%	12%	0	5%
Number of nests that failed to hatch any eggs	0	6	10	13	9	9	3	7	57
Percentage of nests that failed to hatch any eggs	0	4%	26%	16%	39%	13%	6%	34%	17%
Number of eggs that did not hatch	6	19	39	72	28	32	22	34	252
Fate and age at which eggs disappeared									
Crushed in nest — Number	0	1	0	1	1	0	0	0	3
Percentage	0	5%	0	1%	4%	0	0	0	1%
Up to 10 days — Number	1	4	10	11	7	2	4	8	47
Percentage	17%	21%	26%	10%	25%	6%	18%	24%	19%
11 to 20 days — Number	1	3	2	9	4	2	2	10	33
Percentage	17%	16%	5%	12%	14%	6%	9%	29%	13%
21 to 30 days — Number	1	1	7	6	8	8	5	5	41
Percentage	17%	5%	18%	8%	29%	25%	23%	15%	16%
30+ days, Unhatched — Number	3	10	17	38	6	9	5	5	93
Percentage	50%	53%	44%	53%	21%	28%	23%	15%	37%
30+ days, Unknown — Number	0	0	3	11	2	11	8	0	35
Percentage	0	0	8%	15%	7%	34%	36%	0	14%
Number of nests that failed to fledge any young after one or more egg hatched	0	3	2	5	1	33	6	9	59
Percentage of nests that failed to fledge any young after one or more egg hatched	0	12%	5%	6%	4%	54%	11%	31%	18%

g ($n = 51$), less than 3.5% of the female weight of 2900 g ($n = 30$). Females accumulate massive amounts of subcutaneous and perivisceral fat prior to the onset of the nesting season. I suspect that producing the four to six eggs involved in a first and second laying is not an important energy drain on the female. Since a replacement clutch generally produces a fledgling, and has an even higher probability of doing so than single clutches, it is adaptively significant to produce the replacement clutch.

NESTS NOT RECEIVING EGGS: In Tables 14 and 15, I consider additional data from the nest surveys. Only 5% of all nests judged to be fully constructed did not receive an egg and all these occurred in only three years, 1973, 1974, and 1975 (Table 14). Nests remaining occupied during at least three weekly surveys were included here. Several other structures were started but were present on only one survey, and by the next a well-formed nest was present within a meter of the incomplete structure. I did not consider these structures as nests in which no eggs were laid but rather as the result of preliminary efforts that were later shifted to the actual nest. The number of nests that did not receive any eggs *does* effect computation of total reproductive success of the population (see Table 16).

EGG LOSS AND HATCHING FAILURE: Data on loss of eggs in different stages of incubation are presented in Table 14. Essentially all egg losses reported here resulted from the disappearance of eggs between my visits, except for those listed as "30+ days, unhatched" which were eggs that remained in nests for at least 30, and usually 35 to 40 days. The normal incubation

period is 30 days. Only three eggs, one each in 1970, 1972, and 1973, were found crushed in the nest. This was 1% of the total eggs that failed to hatch in the study area and only 0.0035% of the total eggs laid in the study nests.

Egg loss during incubation was essentially equally distributed within 10-day periods of the 30-day incubation period with 19%, 13%, and 16% lost during each interval. Thirty-seven percent (93 of 252) of all egg losses resulted from eggs that did not hatch. Most remained in nests only 32–35 days, but I recorded 27 in nests between 38 and 60 days and one remained in a nest a minimum of 88 days. At least 12 of these eggs were in nests in which one or more eggs had hatched and the unhatched eggs remained in the nest with the chick(s).

I recorded four dead embryos that piped the shell which was somehow then crushed or broken around it. Also, the shells remained intact but the embryo did not break out of the piped shell in eight cases.

During incubation, the whole clutch disappeared from 27 nests between two of my weekly visits; while in 76 nests the eggs were lost one at a time. I believe the loss of the whole clutch represented eggs predated while the others were lost one at a time due to the activity of the adults.

No eggs hatched in 17% of the total nests which received eggs (Table 14). This was highest in 1973 and 1976, years of low productivity. Few nests failed to hatch any eggs in 1974, also a year of low production. No clear relationship exists between productivity and the number of nests that failed to hatch any eggs. In

TABLE 15

Aspects of reproductive success in the Brown Pelican. Numbers of young fledged per nest and age at which nestlings died. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of nests that fledged three young	2	0	2	3	0	0	1	0	8
Percentage of nests that fledged three young	15%	0	7%	4%	0	0	2%	0	4%
Number of nests that fledged two young	5	5	16	36	3	0	22	1	88
Percentage of nests that fledged two young	38%	24%	59%	54%	23%	0	51%	10%	41%
Number of nests that fledged one young	6	16	9	28	10	20	20	9	118
Percentage of nests that fledged one young	46%	76%	33%	42%	77%	100%	47%	90%	55%
Number of successful nests	13	21	27	67	13	20	52	10	214
Number of young that died	9	19	13	42	15	102	46	35	281
Age at which young died									
Up to 10 days old — Number	4	5	10	13	4	24	14	15	89
— Percentage	44%	26%	77%	31%	27%	14%	30%	43%	31%
11 to 20 days old — Number	3	9	1	13	3	24	15	13	81
— Percentage	33%	47%	8%	31%	20%	24%	33%	37%	29%
21 to 30 days old — Number	2	5	2	10	7	38	13	4	81
— Percentage	22%	26%	15%	24%	47%	37%	28%	11%	29%
31 to 40 days old — Number	0	0	0	6	0	16	4	1	27
— Percentage	0	0	0	14%	0	15%	9%	3%	10%
Over 40 days old — Number	0	0	0	0	1	0	0	2	3
— Percentage	0	0	0	0	6%	0	0	6%	1%

years of low productivity, and especially 1974 and 1976, a high number of nests failed to fledge young after successfully hatching eggs (Table 14). In general, loss of young was more important to nesting failure (48%) than loss of eggs (29%).

NESTLING MORTALITY: Mortality of nestlings was essentially equally distributed within the first 30 days of life and 89% of all nestlings that died did so during that period (Table 15). Only 30 of 281 nestlings survived 31 to 40 days and then died and only three nestlings survived over 40 days and subsequently died: one in 1973 and two in 1976. In 1971, the majority of the nestlings that died did so before 10 days of age (77%). In 1974 heavy mortality occurred, being quite low in the first 10 days (14%) and then increasing during the next 20 days (24% and 37% in the ten-day intervals) and continuing through a nestling age of 31–40 days (15%). In 1972 and 1973, several nestlings died at 31–40 days of age.

FLEDGLINGS PER NEST: During this eight year study, when low production occurred, it was primarily due to losses during the nestling stage and not during the incubation period. Years of low production were years in which a small percent of young survived to fledging (1973, 1974, and 1976; Table 15). In all years, only 4% of all nests fledged three young, from eight total nests distributed in 1969, 1971, 1972, and 1975, the years of highest productivity (Table 15). Forty-one percent of all nests fledged two young; 1969, 1971, 1972, and 1975 had high numbers of these nests while 1974 had none and 1976 had only one. Conversely, in years of low production, such as 1974 and 1976 and to a lesser extent 1973 and 1970, the nests which were successful fledged only one young. In 1974, when productivity was lowest, no nest fledged more than one young, and less than one-

third of all nests that received eggs produced one young (Table 14). In 1976, of 29 nests only ten were successful; nine produced one young each, one produced two young.

SUMMARY: To summarize data on reproductive success in this study for all eight years, a total of 376 nests were constructed during 1969 through 1976 (Table 16), including nests which did not receive eggs. Of the 376 nests, 18 (4.8%) did not receive any eggs, which occurred only in 1973, 1974, and 1975. Re-laying occurred in 30 nests (8.0%). One or more were recorded in every year, but the most were found in 1972 (12 = 14%) and in 1973 (6 = 26%). Both 1972 and 1973 were unusual years with long laying periods. The length of the nesting season and the amount of re-laying are undoubtedly related in some manner.

Reproductive success ranged from 1.7 young fledged per total nests in 1969, to 0.33 and 0.34 young per nest in 1974 and 1976, with a calculated mean for all 8 years of 0.93 young per nest ($n = 376$).

PRODUCTIVITY: This study has clearly demonstrated that: (1) in the Brown Pelican wide differences occur in reproductive success between years; (2) a long-term study is necessary to derive a reasonably accurate figure for productivity; and (3) using different methods of interpreting reproductive success gives different results. Depending on the method of calculation, and the questions being asked in the study, whether from marked nests, whether a nest is defined as simply a structure or a structure that received eggs, and whether re-laying is included in the calculations, important differences will occur in figures derived. In this species, in this colony, re-laying appears to be advantageous since replacement clutches generally produced a fledgling and eggs laid as replacements were significantly more successful at

TABLE 16

Reproductive success of the Brown Pelican, 1969–1976. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of nests that did not receive eggs	0	0	0	0	6	5	7	0	18
Number of nests in which re-laying occurred	1	0	3	12	6	3	2	3	30
Total nests	14	25	42	98	35	69	61	32	376
Number of young that fledged from all nests	24	26	50	128	21	23	69	11	351
Productivity (fledglings per total nests)	1.71	1.04	1.19	1.31	0.60	0.33	1.13	0.34	0.93

fledging than were eggs laid in "normal" clutches.

During this study only 5% of the fully formed nests did not receive an egg but this low percentage does represent an important reduction in measuring productivity. Of the nests that received eggs, none hatched in 17%, but the relationship between colony productivity and the number of nests that failed to hatch any eggs is not impressive. Clutch size and hatching success varied little but productivity varied considerably between years. However, years of low productivity were years in which large numbers of nests failed to fledge any young after one or more eggs hatched, indicating that the factors contributing to nesting failure operated on the nestlings rather than during incubation.

Data on fish available to Brown Pelicans during this study do not exist. However, in October through December 1973 fish kills occurred in the Gulf of Mexico in the feeding range of the pelicans nesting in this colony and from January through April and May 1974 fish kills occurred in Boca Ciega Bay and Tampa Bay, surrounding the Tarpon Key area. These fish kills were caused by red tide (*Gymnodinium breve*; Quick and Henderson 1975) and essentially all fish in the region died. These massive fish kills undoubtedly caused the poor reproductive success of Brown Pelicans in this colony in 1974 but no direct data exist on fish for other years. I have examined commercial fish catch records and no relevant data are contained therein that correlate with colony productivity.

One line of evidence indicating that fish availability is related to productivity is the amount of regurgitation that occurred in the colony while I checked nests. In 1969 through 1972, and 1975 (years of high reproductive success), many birds, both adults and nestlings, regurgitated. However, during 1973, 1974, and 1976 (years of relatively low reproductive success) I was unable to gather any food samples from the birds. This is indirect evidence that they were capturing insufficient food, or at least had little in their stomachs or esophagae to stimulate regurgitation as a fright response. Discussion with local fishermen indicated in a general way that "bait fish" were not available in 1973 and 1976 but that information is impossible to quantify. No "bait fish" were available in 1974 during the entire nesting season.

Brown Pelican populations have been decimated by the "crashes" of the Anchovy (*Engraulis gingens*) in Peru for years (Murphy 1936; Schaefer 1970 and references therein) but other than the complete failure of nesting attempts, those studies have not related reproductive success to relative food availability. Keith (1978) after a long term study of Brown Pelicans (*Pele-*

canus occidentalis californicus) nesting in the Sea of Cortez, Mexico, documented reproductive success and had good circumstantial evidence that lack of food contributed to low reproductive success in some years but he also had no direct evidence on fish abundance. Blus, et al. (1974), studying Brown Pelicans in South Carolina, showed annual fluctuations in productivity, but also had no evidence for fish availability. Such data are probably impossible to generate since the pelicans feed over such a wide region; eat so many species of fish (40 in Florida: Fogarty, et al. *in press*; Schreiber *unpublished data*); and, most importantly, because it is virtually impossible to quantitatively sample fish stocks in the marine environment. To measure actual fish availability to a surface diving bird is even more difficult. Pelicans probably do not catch fish deeper than a meter and they are probably dependent on predaceous fish (i.e. mackerel, *Scomberomorus sp.*, etc.) and marine animals (*Tursiops sp.*) to drive the fish close to the water surface and thus make them available for capture by the birds (Ashmole 1971; Schreiber, et al. 1975). Thus we must rely on circumstantial evidence for food availability and are unable to adequately describe the ultimate and proximate factors controlling the reproductive success in the species.

I believe the contrast in age at which nestlings died between the years of lowest productivity (1974 and 1976), and the other six years are quite instructive as to these ultimate causes of mortality in pelicans: more old nestlings died in poor reproductive years. In 1974 mortality increased through the first 40 days of nestling life, indicating that the causation probably began and occurred all the way through the nestling period. In 1976, mortality was highest in the early to middle periods, but continued throughout the nestling period, indicating that probably the mortality factor or factors were in effect prior to hatching but were not as severe as during 1974. The high mortality in the 21–30 day period, the middle of nestling life, in 1973 probably indicates the action of the causative agent(s) in the midst of the nestling period. I believe these nestling mortalities reflect the food situation for the adults and the timing of the starvation of the nestlings indicates that the adults were unable to capture sufficient fish to feed them.

In an earlier paper (1976a) I discussed mortality as related to growth of nestlings in this colony and presented data that clearly demonstrated the ability of nestlings to survive long periods of starvation. I also showed that brood size reduction occurs through starvation of nestlings, usually of the third and then second to hatch. The first nestling to hatch has the greatest chance to sur-

TABLE 17

Reproductive success in relation to clutch size of the Brown Pelican, 1969–1976. All nests checked weekly in each year.

	3 Egg Clutch	2 Egg Clutch	1 Egg Clutch
Number of nests	223	87	18
Percentage of total nests	68%	26%	5%
Clutch size	669	173	18
Number of eggs hatched	497	108	5
Number of young fledged	252	61	5
Hatching success	74%	61%	28%
Percentage of eggs laid from which young fledged	38%	35%	28%
Percentage of eggs hatched from which young fledged	51%	57%	100%
Percentage of total nests that fledged one or more young	72%	55%	28%
Fledglings per successful nest	1.58	1.27	1.00
Productivity (fledglings per total nests)	1.14	0.70	0.28

live, and late hatchlings survive only in years of apparent abundant food. Unfortunately, growth data were collected in this colony only during four years (1969–1972), only one of which (1970) was a relatively low reproductive year. I have no growth data for the less successful years of 1973, 1974, and 1976. However, my impression is that the same pattern existed in those years: the first nestling to hatch was the only one to survive in years when adults apparently were unable to capture sufficient food to adequately feed a full brood.

In this study 89% of all young that died did so during their first 30 days of nestling life. The contrasts between 1974 and 1976 vs. the other six years, and the differences between 1973 and 1974–1976 are most instructive: 1973 was the poorest year in the first consecutive five years of this study and hatching success (53%) was the lowest of all eight years, indicating that for some reason adults abandoned nests early in that year. However, although total fledging success was low, in terms of nests in which eggs hatched, 1973 was a relatively successful year. 1973 was also the year in which the greatest number of “nests” did not receive an egg, again indicating that adults may have abandoned nesting attempts. Also in 1973, a late nest was successful in fledging a young, the only year in which this occurred. In 1974 few nests failed to hatch any eggs but more than half of them failed to fledge young. No nests in 1974 fledged more than one young and few did so in 1973 and 1976, while in the other five years several nests did so.

The sum of these circumstantial data indicate that 1973 but especially 1974 and 1976 were years of decreased food availability that caused lower reproductive success.

PRODUCTIVITY RELATED TO CLUTCH SIZE: With the data collected I was able to examine the relation between reproductive success and clutch size (Table 17). Three egg clutches were the most common and hatching success of individual eggs was significantly higher ($P < 0.01$, *t* test) in these larger clutches than in one-egg clutches. The percentage of all eggs laid that fledged young declined in smaller clutches (but not significantly so) and the percentage of hatched eggs that fledged young was

higher in the one-egg clutches (100%) than in the two or three egg clutches, which were similar (57% and 51%). The chance of a chick surviving from a one-egg nest is greater because it has no siblings to compete with for food. The number of young fledged per clutch increases significantly with increased clutch size. Less than one-third of the one-egg clutches produced one young. In Schreiber (1976a) I presented data from another unit of this colony showing that survival decreased importantly in the second and third eggs in a clutch.

Blus and Keahey (1978) found in the South Carolina Brown Pelicans in 1975 that adults laid larger clutches and had better reproductive success to the “downy young” stage than did “immature” plumaged birds. The only one-egg clutches in their sample were laid by immatures. In my study no immature plumaged birds were involved. However, young or less experienced “adults” could have been involved.

In another study Blus, et al. (1974) attempted to measure success (to the downy young stage) in nests from which one egg was collected to measure pollution levels. Both Skutch (1966) and Mayfield (1961) have strongly made the point that studies of breeding success should be based on nests found for that purpose only, and it is now generally accepted by ornithologists that nest success cannot be measured when eggs have been removed from a clutch. I in no way want to denigrate the Blus, et al. studies of pollution effects, especially of DDE and egg shell thinning in pelicans. However, it is obvious from the data in Table 17 that an unbiased measure of nesting success cannot be obtained using nests from which an egg has been removed, and especially when mortality during the full length of the nestling period is not determined.

TIMING OF THE NESTING SEASON

In addition to the productivity parameters obtained from marked nests presented above, which I consider the only true measure of productivity obtained during this study, I also counted

TABLE 19

Production based on counts of nestlings in each visible nest for Brown Pelicans on Tarpon Key, Pinellas County, Florida. Counts made from mid-lagoon.

DATE	NUMBER OF NESTLINGS PER NEST			TOTAL NESTLINGS TOTAL NESTS	COMPUTED NUMBER OF NESTLINGS PER NEST
	3	2	1		
1970					
15 June	0	33	93	159/126	1.3
1971					
5 June	0	17	13	47/30	1.6
12 June	0	56	48	160/104	1.5
27 June	2	31	27	95/60	1.6
1972					
26 March	0	6	5	17/11	1.5
30 March	0	5	5	15/10	1.5
13 April	0	9	4	22/13	1.7
18 April	0	8	8	24/16	1.5
1973					
3 June	0	6	65	77/71	1.1
10 June	1	6	72	87/79	1.1
9 July	0	0	195	195/195	1.0
1974					
30 April	1	8	13	32/22	1.4
5 May	0	73	67	213/140	1.5
13 May	1	66	129	264/196	1.4
18 May	0	41	172	254/213	1.2
25 May	0	26	229	281/255	1.1
2 June	0	34	238	306/272	1.1
8 June	0	20	284	324/304	1.0
1975					
12 April	11	88	33	242/132	1.8
20 April	7	145	89	400/241	1.7
29 April	3	154	91	408/248	1.6
5 May	0	155	147	457/302	1.5
12 May	2	167	179	513/328	1.6
18 May	0	37	37	111/74	1.5
24 May	1	92	95	282/181	1.5
1976					
11 April	1	10	8	31/19	1.6
22 April	0	15	27	57/42	1.4
29 April	0	29	79	137/108	1.3
4 May	1	34	102	173/137	1.3
13 May	0	24	126	174/150	1.2
22 May	0	25	136	186/161	1.2
27 May	0	25	205	255/230	1.1

TABLE 20

Production based on counts of maximum number of nests and the maximum number of Brown Pelican nestlings visible. Counts made from mid-lagoon.

YEAR	MAXIMUM NUMBER OF NESTS COUNTED (RANGE)	DATES	MAXIMUM NUMBER NESTLINGS COUNTED	DATES	CALCULATED NUMBER OF NESTLINGS PER NEST
1970	200 (194-207)	6-27 May	266	29 June	1.3 - 1.4
1971	inside 250 (236-259) outside 20	2-25 May 13 March - 28 April	257 24-26	27 June 25 May - 10 June	1.0 1.2 - 1.4
1972	inside 260 (247-270) outside 22-24	1-18 April 29 February - 13 April	371-417 30-32	12-23 June 27 May - 12 June	1.4 - 1.6 1.3 - 1.5
1973	305 (289-320)	19-26 June	310	4 August	1.0
1974	400	13-20 April	304	8 June	0.8
1975	625 (610-636)	21 March - 12 April	675-747	24 May - 28 June	1.4 - 1.7
1976	inside 420 (417-428) Whale 36-38 outside 11-13	30 March - 11 April 24 February - 11 April 2 March - 27 May	230 30-32 11	27 May 22-27 May 27 May	0.6 0.8 1.0 -

easily visible units give similar results to those obtained for the larger sample of nests in the main colony.

These data clearly reflect the differences in production within the colony between years of high and low reproductive success.

COUNTS MADE DURING BEHAVIOR OBSERVATIONS:

During 1970 and 1971 I made behavior observations in one unit of the colony from an observation tower ca. 2 m high and 25 + m from the mangrove and the nearest nest (Schreiber 1977). Observations of 19 nests in the unit, from initial courtship activity through fledging of the young, provide a fledging success figure for those years (Table 21). In 1970 all four nests were successful with a total of five fledglings produced, or 1.2 young per nest. In 1971, four of 15 nests were unsuccessful and the 11 others produced 18 young or 1.6 young per successful nest and 1.2 per total nests. These figures are similar to those obtained by other measurements of production in those years.

REPRODUCTIVE SUCCESS MEASURED DURING GROWTH AND DEVELOPMENT STUDIES

In 1969 through 1972 I measured growth and development of nestlings in one unit of this colony (Schreiber 1976a). In Table 22, I compile figures on reproductive success from nests in the unit used to carry out these measurements. In this table, for each

year the number of nests, the number of fledglings, and a calculated figure for young per nest are presented, with the figures above the dashed line for the nests in which growth and development of nestlings was actually measured (see Table 1, p. 20,

TABLE 21

Productivity based on observations of undisturbed nests.

YEAR	NESTS	YOUNG PRODUCED	PRODUCTIVITY (fledglings per total nests)
1970	4	5	1.2
1971	11 (successful)	18	1.6 (per successful nest)
	4 (unsuccessful)	0	0
	18 (total)	18	1.2

TABLE 22

Productivity based on individually marked nests used to measure growth and development of nestlings. Nests visited on average more than once per week.¹

YEAR	NESTS	YOUNG PRODUCED	PRODUCTIVITY (fledglings per total nests)
1969	11	18	1.6
	33	43	1.3 (per successful nest)
	53	43	0.8
1970	15	19	1.3
	37	44	1.1 (per successful nest)
	52	44	0.9
1971	17	27	1.6
	26	45	1.7 (per successful nest)
	41	45	1.1
1972	13	17	1.3
	23	40	1.7 (per successful nest)
	26	40	1.5

¹For each year the data above the dashed line are the nests used for growth and development studies and thus the nestlings were handled on each visit. The data below the line are for all the nests which formed in this study unit.

Schreiber 1976a). The figures below the dashed line include all nests and young in this study unit. This unit was visited essentially weekly and for about 1.5 hours on each visit.

Earlier (Table 2) I indicated that no significant differences existed in the parameters of the 1972 data between the growth and development unit and the weekly nest check unit. Similarly, in 1970 and 1971 no statistical differences existed between units in either young per successful or total nests.

The reproductive success figures obtained during the growth and development studies exhibit annual fluctuations similar to those obtained when nests are disturbed on the same frequency but for a shorter period of time on each visit. I conclude that carrying out these growth studies does not hinder the pelicans. The additional data gathered on growth of nestlings make this a worthwhile effort if colonies are being disturbed to measure productivity.

COMPARISON OF METHODS OF MEASURING REPRODUCTIVE PERFORMANCE

In Table 23 I summarize five methods of computing reproductive performance. Four points emerge from these data:

1. Important year to year fluctuations in production occurred in this colony. All five methods reflect these fluctuations. Only a study of several years will generate sufficient data to accurately reflect the reproductive performance in a colony.

2. Important differences exist between calculations of young fledged per successful nest and young fledged per total nests. The former is essentially a useless datum and only data on productivity (young fledged per total nests attempted) are biologically useful.

3. The figures, however, derived from weekly nest checks were similar to the figures derived from observations of the colony from a distance. Thus, the data from counts of nestlings per nest and of the maximum number of nests and nestlings present can be used to assess productivity only if corrected downward with additional data on the number of nests that failed early in the nesting season. These additional data can only be gathered by studying individual nests.

4. A comparison between years (and between studies in different regions) using the figures garnered from any one methodology is valid but comparison between methods (i.e., productivity measured by weekly nest checks vs. production measured by counts of nestlings or maximum nests and nestlings) is invalid. Only data collected in a similar manner can be compared. Only the figures for young per total nest attempts should be used in discussions of population stability.

ESTIMATES OF PRODUCTION: I know of no manipulations that will relate the various production figures obtained from different techniques of data capture and presentation. Years of high and low productivity are easily separable using any one of the data collection methods, however, counts from a distance of nestlings per nest and an estimate of the maximum number of nests

TABLE 23

Comparison of reproductive performance measurements computed from five techniques used to census the colony of Brown Pelicans.

DATE	COUNTS OF NESTLINGS PER NEST	MAXIMUM NESTLINGS ² MAXIMUM NESTS	OBSERVATION ³		GROWTH AND ⁴ DEVELOPMENT		WEEKLY INDIVIDUAL ⁵ NEST CHECKS	
			Succ. nests	Total nests	Succ. nests	Total nests	Succ. nests	Total nests (Productivity)
1969	—	—	—	—	1.3	0.8	1.7	1.7
1970	1.3	1.3–1.4	1.2	1.2	1.1	0.9	1.2	1.0
1971	1.5–1.6	1.0	1.2	1.6	1.7	1.1	1.7	1.2
1972	1.5–1.7	1.4–1.6	—	—	1.7	1.5	1.7	1.3
1973	1.0–1.1	1.0	—	—	—	—	1.2	0.6
1974	1.1	0.8–0.9	—	—	—	—	1.0	0.3
1975	1.5	1.4–1.7	—	—	—	—	1.6	1.1
1976	1.0–1.2	0.6–1.0	—	—	—	—	1.1	0.3

¹Based on counts of nestlings per nest during the nesting season — see Table 19

²Based on counts of maximum number of nests and maximum number of nestlings present just prior to first fledging — see Table 20.

³Based on nests used for behavioral studies — see Schreiber 1977, and Table 21.

⁴Based on nests used for growth and development studies — see Schreiber 1976a, and Table 22.

⁵Based on individually marked nests checked weekly throughout the nesting season — see Tables 11–16.

formed during a season give the most accurate measure of production in the colony. Obtaining these data requires at least six to eight or more visits to the colony during the nesting season.

The production figures based on two other methods, a) counts of maximum number of nestlings and nests and b) counts of brood size from a distance in the colony, give essentially similar results for all eight years of this study.

PRODUCTIVITY: The only measure of productivity obtained in this study is based on weekly counts of young per individual nest (whether from nests used solely for that or to also measure growth and development). This is the lowest figure obtained by the methods presented here. It is the only one that actually measures productivity since it accounts for nests in which no eggs are laid, in which no eggs hatch or the young die at less than two to three weeks of age, and because of the additional information gained from knowing the details of individual nests. The other methods merely present interesting additional information. Weekly nest checks of individually marked nests requires considerable time and energy to obtain results, but because of the additional data obtainable with that method, it is the most useful type of study to carry out.

CONCLUSION AND SUMMARY

I believe that for this species, *Pelecanus occidentalis*, in these mangrove colonies, a reasonably accurate figure for reproductive performance can be obtained by making weekly surveys of the colony and checking contents of individually marked nests. Years of high and low productivity are easily separable but periodic, frequent visits throughout the nesting season are necessary. Only

two or three visits to the colony, even if spaced over a two or three month period, will not yield results comparable between colonies or between years. Comparison of productivity with other colonies of pelicans studied by other workers using different techniques of data collection seem quite futile. I believe it is impossible to generalize on productivity from year to year, but the mean figure derived for young per breeding pair from a reasonably long period of study (six to ten years) is a reasonably accurate measure. However, this mean is of less interest than the year to year variability in productivity and its underlying causes.

Henny (1972) calculated a theoretical recruitment standard of 1.51 to 1.87 young per breeding female necessary to maintain a stable population of Brown Pelicans in North and South Carolina. He noted this standard as too high, based on the clutch size of Brown Pelicans and the productivity of Great White Pelicans (*Pelecanus onocrotalus*) in Africa; and since band loss occurs in the Brown Pelicans the calculated mortality rate estimates for his sample would be inflated. He thus arbitrarily revised downward the recruitment standard as "more closely approximates the range of 1.2 to 1.5 young per breeding pair" but does not indicate how this range was determined. Henny's figures of 1.2 to 1.5 are oft-quoted (Blus, et al. 1977, and references therein) but with serious reservations as to its usefulness (Anderson, et al. 1975).

King, et al. (1977a), recorded 0.87 young per nest in Corpus Christi Bay, Texas, in 1964 through 1973 and noted that this was a "poor" rate "comparable to that of declining populations in South Carolina" (based on Blus, et al. 1974) although that figure is very similar to what Blus found in South Carolina (Blus, et al. 1977). King, et al. (1977b), also noted that nine young fledged from 11 nests in the same area in 1975, or 0.82 young per nest, by birds that may have been reneesting late in the season.

Blus, et al. (1977) reported reproductive success in two colonies in South Carolina from 1969 through 1973 as 0.78, 0.85, 0.92, 0.69, and 1.66 although the methods used to derive these figures are not clearly stated and data for independent analysis in that paper or earlier publications are not presented or are difficult to interpret. In 1975 Blus and Keahey (1978) recorded successful nests as those in which one or more downy young survived to leave the nest at four to five weeks of age and recorded 0.89 young per nest for adults and 0.11 young per nest for immature plumaged nesting birds. The colony was visited once or twice a week throughout the season, which probably reduced nesting success to an unknown extent, especially in light of suggested disturbance of up to one hour in the colony, apparently with the adults off of their nests the whole time. In 1976 production of 1.43 fledglings per nest was recorded in this colony (Stickel 1977). While productivity was definitely lower in the 1969–1972 period than in later years, production of 0.92 young per nest from 9370 total nests (8590 young) for those seven years is remarkably close to the mean figure of 0.93 young per nest derived from marked nests in Florida (this study) in the same time span. Blus, et al. (1974 and references therein) note the Florida population as stable. Comparison of Florida and South Carolina data is virtually impossible because of the lack of control on bias caused by human disturbance. However, I would expect the South Carolina birds to exhibit somewhat lower total reproductive success since the large number of young birds breeding in the population would have lower nesting success and because the population is on the northern extreme of the range for the species. Yet even in 1977 reliance by Blus, et al. (1974) on the Henny recruitment standard occurs with the indication that productivity in South Carolina is subnormal. The South Carolina birds spend the winter in Florida (Schreiber 1976b) and the Brown Pelican population of the east coast of Florida has not declined in the past 20 years (Schreiber and Schreiber 1973). It is interesting that Blus, et al. have consistently ignored these Florida Christmas Count data when they claim a population decline in South Carolina. Significant egg shell thinning has occurred in South Carolina but I suggest that the population decline has actually not been as severe as claimed. Production has been erratic and fluctuating in South Carolina but that is characteristic for this species.

Keith (1978), during a detailed study of the largest colonies in North America on the San Lorenzo Island group of the Sea of Cortez, Mexico, in 1970–1977, despite severe difficulties of access and fully cognizant of the sensitivity of the pelicans to human disturbance, noted distinct annual fluctuations in productivity, primarily from starvation of nestlings and desertion of nests by adults during incubation. He also found wide fluctuations in the number of breeding attempts. Using detailed counts of total young produced and total nests present, Keith found low productivity of 0.43 to 0.23 young per total nests with an average of 0.30 young per nest attempt in 1973 through 1976. Keith also discusses the biases in the Henny (1972) recruitment standard, especially as regards non-breeding by adult birds, and finds it not a useful comparison.

I believe that the data are now overwhelming that "normal" nesting success of Brown Pelicans fluctuates, with the mean centering around or slightly below one young fledged per nesting pair per year. It is time to abandon the theoretical recruitment standard of Henny (1972) in favor of productivity based on field data in a stable population. Only further analysis of banding data, utilizing the greatly increased number of recoveries in the past

decade, will provide a test of whether banding data can provide an accurate index to mortality rates and production necessary for population maintenance in this species (Schreiber *in preparation*).

The fluctuations in productivity between years noted in all studies thus far carried out on Brown Pelicans (Blus, et al. in South Carolina, Anderson and Keith in Baja California and California, King in Texas, and my data for Florida) clearly indicate that only a long term study, probably on the order of 20 years or the reproductive span of an adult female Brown Pelican, whatever that may be, carried out by the same individuals using precise methods and who are fully cognizant of the effects of human disturbance on measurement of reproductive success, will be adequate to determine the long term population trends of this endangered species.

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APPENDIX 1

1969 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	16-31 March	1-15 April	16-30 April	Total
Number of nests	4	7	2	13
Percentage of total nests	31%	54%	15%	100%
Number of eggs laid	11	20	6	37
Clutch size	2.8	2.9	3.0	2.9
Number of eggs that hatched	8	19	4	31
Eggs hatched per total nests	2.0	2.7	2.0	2.5
Number of nests in which eggs hatched	4	7	2	13
Hatching success	73%	95%	67%	89%
Number of young that fledged	5	14	3	22
Percentage of eggs laid from which young fledged	45%	70%	50%	59%
Percentage of eggs hatched from which young fledged	63%	74%	75%	67%
Number of successful nests (fledged one or more young)	4	7	2	13
Percentage of successful nests	100%	100%	100%	100%
Fledglings per successful nest	1.2	2.0	1.5	1.7
Productivity (fledglings per total nests)	1.2	2.0	1.5	1.7

APPENDIX 2

1970 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	1-15 March	16-31 March	1-15 April	16-30 April	Total
Number of nests	4	5	11	5	25
Percentage of total nests	16%	20%	44%	20%	100%
Number of eggs laid	12	13	27	12	64
Clutch size	3.0	2.6	2.4	2.4	2.6
Number of eggs that hatched	8	10	18	9	45
Eggs hatched per total nests	2.0	2.0	1.6	1.8	1.8
Number of nests in which eggs hatched	4	5	10	5	24
Hatching success	67%	77%	67%	75%	70%
Number of young that fledged	6	5	11	4	26
Percentage of eggs laid from which young fledged	50%	38%	41%	33%	41%
Percentage of eggs hatched from which young fledged	75%	50%	61%	44%	58%
Number of successful nests (fledged one or more young)	4	4	9	4	21
Percentage of successful nests	100%	80%	82%	80%	84%
Fledglings per successful nest	1.5	1.3	1.2	1.0	1.2
Productivity (fledglings per total nests)	1.5	1.0	1.0	0.8	1.0

APPENDIX 3

1971 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	2	8	19	8	2	39
Percentage of total nests	5%	20%	49%	20%	5%	100%
Number of eggs laid	4	23	48	21	3	99
Clutch size	2.0	2.9	2.5	2.6	1.5	2.5
Number of eggs that hatched	3	17	28	13	0	61
Eggs hatched per total nests	1.5	2.1	1.5	1.6	0	1.6
Number of nests in which eggs hatched	2	8	13	6	0	29
Hatching success	75%	74%	58%	62%	0	62%
Number of young that fledged	2	15	20	10	0	47
Percentage of eggs laid from which young fledged	50%	65%	42%	48%	0	47%
Percentage of eggs hatched from which young fledged	67%	88%	71%	77%	0	77%
Number of successful nests (fledged one or more young)	2	8	12	5	0	27
Percentage of successful nests	100%	100%	63%	62%	0	69%
Fledglings per successful nest	1.0	1.9	1.7	2.0	0	1.7
Productivity (fledglings per total nests)	1.0	1.9	1.1	1.2	0	1.2

APPENDIX 4

1972 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	1-15 February	16-19 February	1-15 March	16-31 March	1-15 April	16-30 April	Total
Number of nests	5	7	23	35	12	4	86
Percentage of total nests	6%	8%	26%	41%	14%	5%	100%
Number of eggs laid	12	18	65	95	27	7	224
Clutch size	2.4	2.6	2.8	2.7	2.2	1.8	2.6
Number of eggs that hatched	8	11	54	65	14	0	152
Eggs hatched per total nests	1.6	1.6	2.4	1.9	1.2	0	1.8
Number of nests in which eggs hatched	4	7	23	32	7	0	73
Hatching success	66%	61%	83%	68%	52%	0	68%
Number of young that fledged	6	8	33	52	10	0	109
Percentage of eggs laid from which young fledged	50%	44%	51%	55%	37%	0	49%
Percentage of eggs hatched from which young fledged	75%	73%	61%	80%	71%	0	72%
Number of successful nests (fledged one or more young)	4	6	19	31	7	0	67
Percentage of successful nests	80%	86%	83%	88%	58%	0	78%
Fledglings per successful nest	1.5	1.3	1.7	1.7	1.4	0	1.6
Productivity (fledglings per total nests)	1.2	1.1	1.4	1.5	0.8	0	1.3

APPENDIX 5

1973 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	15-30 March	1-15 April	16-30 April	1-15 May	16-31 May	1-15 June	16-31 June	Total
Number of nests	7	2	2	10	1	0	1	23
Percentage of total nests	30%	9%	9%	43%	4%	—	4%	100%
Number of eggs laid	18	5	5	26	3	—	2	59
Clutch size	2.6	2.5	2.5	2.6	3.0	—	2.0	2.6
Number of eggs that hatched	4	2	2	22	0	—	1	31
Eggs hatched per total nests	0.6	1.0	1.0	2.2	0	—	1.0	1.3
Number of nests in which eggs hatched	2	1	1	9	0	—	1	14
Hatching success	22%	40%	40%	85%	0	—	50%	53%
Number of young that fledged	2	1	1	11	0	—	1	16
Percentage of eggs laid from which young fledged	11%	20%	20%	42%	0	—	50%	27%
Percentage of eggs hatched from which young fledged	50%	50%	50%	50%	0	—	100%	52%
Number of successful nests (fledged one or more young)	2	1	1	8	0	—	1	13
Percentage of successful nests	28%	50%	50%	80%	0	—	100%	56%
Fledglings per successful nest	1.0	1.0	1.0	1.4	0	—	1.0	1.2
Productivity (fledglings per total nests)	0.3	0.5	0.5	1.1	0	—	1.0	0.7

APPENDIX 6

1974 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	16-29 February	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	11	18	20	10	1	1	61
Percentage of total nests	18%	30%	33%	16%	2%	2%	100%
Number of eggs laid	33	50	56	22	2	1	164
Clutch size	3.0	2.8	2.8	2.2	2.0	1.0	2.7
Number of eggs that hatched	30	44	41	13	0	0	128
Eggs hatched per total nests	2.7	2.4	2.0	1.3	0	0	2.1
Number of nests in which eggs hatched	11	18	17	6	0	0	52
Hatching success	91%	88%	73%	59%	0	0	78%
Number of young that fledged	7	8	3	2	0	0	20
Percentage of eggs laid from which young fledged	21%	16%	5%	9%	0	0	12%
Percentage of eggs hatched from which young fledged	23%	18%	7%	15%	0	0	16%
Number of successful nests (fledged one or more young)	7	8	3	2	0	0	20
Percentage of successful nests	64%	44%	15%	20%	0	0	33%
Fledglings per successful nest	1.0	1.0	1.0	1.0	0	0	1.0
Productivity (fledglings per total nests)	0.6	0.4	0.2	0.2	0	0	0.3

APPENDIX 7

1975 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date of first egg laid. Does not include nests in which relaying occurred or "nests" that did not receive any eggs.

	1-15 February	16-29 Feb.	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	9	19	8	0	8	4	4	52
Percentage of total nests	17%	36%	15%	—	15%	8%	8%	100%
Number of eggs laid	27	29	23	—	20	9	9	137
Clutch size	3.0	2.6	2.9	—	2.5	2.2	2.2	2.6
Number of eggs that hatched	26	47	19	—	15	3	4	114
Eggs hatched per total nests	2.9	2.5	2.4	—	1.9	0.8	0.8	2.2
Number of nests in which eggs hatched	9	19	8	—	8	2	3	49
Hatching success	96%	96%	83%	—	75%	33%	44%	83%
Number of young that fledged	11	25	16	—	11	2	2	67
Percentage of eggs laid from which young fledged	41%	51%	70%	—	55%	22%	22%	49%
Percentage of eggs hatched from which young fledged	42%	53%	84%	—	73%	66%	50%	59%
Number of successful nests (fledged one or more young)	8	16	8	—	8	1	2	43
Percentage of successful nests	88%	84%	100%	—	100%	25%	50%	83%
Fledglings per successful nest	1.4	1.6	2.0	—	1.4	2.0	1.0	1.6
Productivity (fledglings per total nests)	1.2	1.3	2.0	—	1.4	0.5	0.5	1.3

APPENDIX 8

1976 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	25-29 February	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	3	13	4	6	2	1	29
Percentage of total nests	10%	45%	14%	21%	7%	3%	100%
Number of eggs laid	9	37	10	14	4	2	76
Clutch size	3	2.9	2.5	2.7	2.0	2.0	2.6
Number of eggs that hatched	9	23	5	9	0	0	48
Eggs hatched per total nests	3.0	1.8	1.2	1.5	0	2.0	1.6
Number of nests in which eggs hatched	3	10	4	4	0	1	22
Hatching success	100%	62%	50%	65%	0	100%	64%
Number of young that fledged	2	5	2	2	0	0	11
Percentage of eggs laid from which young fledged	22%	14%	20%	14%	0	0	14%
Percentage of eggs hatched from which young fledged	22%	22%	40%	22%	0	0	23%
Number of successful nests (fledged one or more young)	2	4	2	2	0	0	10
Percentage of successful nests	67%	31%	50%	33%	0	0	34%
Fledglings per successful nest	1.0	1.2	1.0	1.0	0	0	1.1
Productivity (fledglings per total nests)	0.7	0.4	0.5	0.3	0	0	0.4

APPENDIX 9

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible from the observation tower.

1970 North Area										
DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	3	2	1		
					CHICKS	CHICKS	CHICK			
13 Feb	0									
7 Mar	193	0								
9 Mar	157	0								
19 Mar	155	24	6.4/1							
30 Mar	257	75	2.4/1							
1 Apr	290	78	2.7/1							
5 Apr	295	88	2.5/1							
7 Apr	340	105	3.2/1							
11 Apr	356	127	2.8/1							
14 Apr	304	—	—							
19 Apr	—	—	—							
24 Apr	290	173	1.7/1							
6 May	308	194	1.6/1	—	11					
11 May	230	—	—	—	29					
17 May	210	204	1.0/1	—	44 nestlings visible					
22 May	257	207	1.2/1	—	53					
27 May	205	203	1.0/1	—	96 nestlings visible					
3 June	204	—	—	—	132 nestlings visible					
10 June	108	—	—	—	181 nestlings visible					
15 June	84	—	—	First fledglings	0	33	93	159/126 =	1.26	
22 June	94	—	—	—	188 nestlings visible					
29 June	62	—	—	—	228 nestlings and 38 young of the year					
2 July	28	—	—	—	281 nestlings and young of the year					
17 July	21	—	—	Major number of young of the year away from Tarpon Key						
30 July	18	—	—	—						

APPENDIX 10

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible from the observation tower.

1971 North Area

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS			TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST	
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS			2 CHICKS
28 Feb	141	—							
2 Mar	172	—							
5 Mar	143	—							
13 Mar	128	—							
24 Mar	224	—							
27 Mar	225	—							
29 Mar	279	—							
31 Mar	264	—							
12 Apr	206	—	—		First nestlings heard				
16 Apr	250	—	—		First nestlings visible				
21 Apr	270	—	—						
2 May	255	259	1/1						
4 May	267	253	1/1						
17 May	245	241	1/1	—	—	—	—	85/56 = 1.52	
25 May	232	236	1/1	—	118 nestlings visible				
5 June	155	—	—	—	126 nestlings visible				
					a sample =	0	17	13	47/30 = 1.57
12 June	133	—	—	—	—	0	56	48	160/104 = 1.54
27 June	118	—	—	—	257 nestlings visible				
					a sample =	2	31	27	95/60 = 1.58
6 July	—	—	—		First fledglings				
10 Aug	—	—	—	—	52 nestlings visible				
24 Aug	—	—	—	—	15 nestlings visible				
2 Sept	—	—	—	—	3 nestlings visible				

APPENDIX 11

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible in the north outside area of the colony, 1971.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH				
						3	2	1		
						CHICKS	CHICKS	CHICK		
16 Feb	0									
27 Feb	45	2	22.5							
2 Mar	43	8	5.3							
5 Mar	36	17	2.1							
13 Mar	21	19	1.1							
27 Mar	13	13	1.0							
29 Mar	29	16	1.8							
31 Mar	22	17	1.3							
12 Apr	20	17	1.2	First nestlings heard (at least in 2 nests)						
16 Apr	27	18	1.5	15	3					
28 Apr	28	20	1.4	10	10					
8 May	19	17	1.1	8	9	3	3	3	18/9 =	2.0
20 May	14	16	0.87	4	12	1	6	5	20/12 =	1.67
25 May	14	18	0.77	4	14	2	8	4	26/14 =	1.86
10 June	14	18	0.77	3	15	1	7	7	24/15 =	1.60
27 June	14	—	—	First fledgings						
3 July	13	—	—	0	2	0	1	1	3/2 =	1.5
8 July	12	—	—	0	2	0	2	0	4/2 =	2.0
23 July	2	—	—	0	0	0	2	0	4/2 =	2.0
17 Aug	0	—	—	0	0					

APPENDIX 12

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1972 Inside, Northeast, West, and Southeast areas.

DATE	ADULTS	NESTS	ADULT/NEST RATIO		
4 Jan	199	courtship activity ongoing			
9 Jan	378	"	"		
19 Jan	267	"	"		
25 Jan	266	102	2.6/1		
4 Feb	284	143	2.0/1		
7 Feb	228	136	1.7/1		
22 Feb	194	90	2.2/1		
29 Feb	293	118	2.5/1	First nestlings heard	
11 Mar	361	148	2.4/1		
18 Mar	365	214	1.7/1	First nestlings visible	
21 Mar	445	229	1.9/1		
1 Apr	338	247	1.4/1		
4 Apr	327	261	1.2/1		
13 Apr	348	270	1.3/1	Nestlings visible in 38 nests	
18 Apr	370	259	1.4/1	Nestlings visible in 41 nests	
25 Apr	336	216	1.6/1	Nestlings visible in 55 nests	
				First fledglings	
2 May	313	231	1.4/1	Nestlings visible in 78 nests	
14 May	312	231	1.3/1	Nestlings visible in 118 nests	
		Adults on nests	Nestlings	Fledglings	
21 May	261	118	207	25	119 nestlings in 69 nests = 1.7 chick/nest
26 May	226	143	240	53	
12 June	232	—	344	45	
23 June	93	—	372 (49 downy)	45	
27 June	93	—	293	114	First influx of birds of the year away from Tarpon Key
8 July	48	—	224	147	
16 July	56	—	226 (33 downy)	149	
22 July	47	—	173 (16 downy)		
30 July	101	—	150		
7 Aug	38	—	64		
13 Aug	23	—	72		
26 Aug	7	—	36		
31 Aug	20	—	22		
8 Sept	13	—	12		
26 Sept	5	—	7		
30 Sept	14	—	2		
7 Oct	4	—	1		
15 Oct	8	—	0		
20 Oct	3	—	0		14 fledglings still present
12 Nov	0	—	0		No fledglings present

APPENDIX 13

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1972 Outside Northeast.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH				
						3	2	1		
						CHICKS	CHICKS	CHICK		
4 Jan	26	10	2.6/1							
19 Jan	26	16	1.6/1							
4 Feb	18	17	1.0/1							
22 Feb	22	18	1.2/1							
29 Feb	53	22	2.4/1							
11 Mar	34	23	1.5/1	15	8					
18 Mar	28	23	1.2/1	14	9	1	6	2	17/9 =	1.9
21 Mar	35	24	1.4/1	13	11	—	—	—		
26 Mar	28	23	1.4/1	12	11	0	6	5	17/11 =	1.5
30 Mar	26	24	1.1/1	14	10	0	5	5	15/10 =	1.5
4 Apr	10	24	0.4/1	11	13	—	—	—		
13 Apr	22	23	0.9/1	10	13	0	9	4	22/13 =	1.7
18 Apr	19	27	0.7/1	11	16	0	8	8	24/16 =	1.5
2 May	17	—	—	7	—	—	—	—	27	
14 May	17	—	—	—	—	—	—	—	29 (15 ready to fly)	
27 May	12	—	—	—	—	—	—	—	28 + 4 fledglings	
12 June	5	—	—	—	—	2	10	4	30/16 =	1.9
									+ 8 fledglings	
27 June	2	—	—	—	—	—	—	—	19	
8 July	1	—	—	—	—	—	—	—	18	
22 July	0	—	—	—	—	—	—	—	8	
30 July	0	—	—	—	—	—	—	—	3	
13 Aug	0	—	—	—	—	—	—	—	0	

APPENDIX 14

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1973 Inside.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	
21 Feb	0			
27 Feb	—	Pairs together and active courtship		
17 Mar	442	150	2.9/1	
31 Mar	195	140	1.4/1	
5 Apr	275	143	1.9/1	First nestling heard
14 Apr	380	217	1.7/1	First nestling seen
21 Apr	435	246	1.8/1	
28 Apr	414	235	1.8/1	Nests with chicks visible
5 May	476	255	1.9/1	7
12 May	491	278	1.8/1	35
19 May	510	320	1.6/1	42 (all 1 chick per nest)
25 May	492	306	1.6/1	40 3 Ch. 2 Ch. 1. Ch.
3 June	487	304	1.6/1	71 0 6 65 = 77ch/71 nests = 1.08 ch/nest
10 June	450	305	1.5/1	79 1 6 72 = 87/79 = 1.10 ch/nest
16 June	377	289	1.3/1	83
23 June	340	290	1.2/1	77
9 July	290	—	—	195 total nestlings, all 1 inch per nest. First fledglings
14 July	255	209	1.2/1	239 total, all 1 chick per nest
21 July	172	—	—	282 total, all 1 chick per nest
4 Aug	97	—	—	310 total, 1 two chick nest, and 51 fledglings
				<u>nestlings + fledglings = total</u>
12 Aug	127	—	—	270 + 95 = 361
19 Aug	122	—	—	242 + 153 = 365
24 Aug	104	—	—	208 + 160 = 395
3 Sept	167	—	—	242 + 127 = 369
9 Sept	93	—	—	123 + 108 = 231
15 Sept	44	—	—	87 + 126 = 213
23 Sept	144	—	—	86 + 91 = 177
29 Sept	67	—	—	32 + 78 = 110
25 Oct	51	—	—	10 + 40 = 50
10 Nov	22	—	—	2 + 5 = 7
18 Nov	0	—	—	0 0

APPENDIX 15

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1974 Inside										
DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK		
14 Feb	143	0								
23 Feb	626	25	25.0/1							
28 Feb	558	76	7.3/1							
3 Mar	631	105	6.0/1							
11 Mar	655	194	3.4/1							
17 Mar	693	—	—							
25 Mar	873	201	4.3/1							
3 Apr	773	343	2.3/1							
7 Apr	702	388	1.8/1							
13 Apr	636	403	1.6/1							
20 Apr	666	423	1.6/1							
30 Apr	558	—	—		223	1	8	13	32/22 = 1.45	
5 May	542	—	—		140	0	73	67	213/140 = 1.52	
13 May	331	322	1.0/1		196	1	66	129	264/196 = 1.35	
18 May	315	—	—		213	0	41	172	254/213 = 1.19	
25 May	295	328	0.9/1	83	255	0	26	229	281/255 = 1.10	
2 June	324	330	0.9/1	70	272	0	34	238	306/272 = 1.13	
8 June	227	—	—	18	304	0	20	284	324/304 = 1.06	
28 June	89	—	—	—					352+2 fledglings	
9 July	119	—	—	—					333+24 fledglings	
19 July	103	—	—	—					170+206 fledglings	
27 July	85	—	—	—					82+265 fledglings	
3 Aug	40	—	—	—		1	2	—	80+196 fledglings	
11 Aug	11	—	—	—		0	1	27	29+153 fledglings	
18 Aug	19	—	—	—		0	3	24	30+103 fledglings	
31 Aug	11	—	—	—		0	4	3	11+28 fledglings	
16 Sept	—	—	—	—		0	5	0	10+32 fledglings	
26 Sept	8	—	—	—		0	1	3	5+24 fledglings	
29 Oct	1	—	—	—		0	0	0	0+0	

APPENDIX 16

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1975 Inside.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH				
						3	2	1		
						CHICKS	CHICKS	CHICK		
19 Jan	63									
27 Jan	267									
29 Jan	356	2+								
1 Feb	598	—								
8 Feb	492	111	4.3/1							
16 Feb	591	269	2.2/1							
25 Feb	552	384	1.4/1							
3 Mar	551	400	1.4/1							
11 Mar	631	460	1.4/1							
16 Mar	689	565	1.2/1							
21 Mar	832	610	1.4/1							
29 Mar	871	625	1.4/1							
6 Apr	696	636	1.1/1							
12 Apr	733	626	1.2/1	—	132	11	88	33	242/132 =	1.83
20 Apr	526	564	0.9/1	—	241	7	145	89	400/241 =	1.66
29 Apr	608	525	1.2/1	277	248	3	154	91	408/248 =	1.64
5 May	617	540	1.1/1	238	302	0	155	147	457/302 =	1.51
12 May	593	—	—	—	328	2	167	179	513/328 =	1.56
18 May	428	—	—	—	—	0	37	37	111/74 =	1.50
24 May	381	—	—	186	713 nestlings	(1	92	95	282/181 =	1.48
31 May	329	—	—	176	747 nestlings	—	—	—	816 total young	
7 June	294	—	—	138	675 nestlings	—	—	—	904 (159 downy)	
12 June	245	—	—	—	680 " (69 downy young in 44 nests)	—	—	—	1029 (179 downy)	
28 June	188	—	—	46	688 nestlings	—	—	—	830 (75 downy)	
6 July	140	—	—	—	453 nestlings	—	—	—	606 total young	
10 July	146	—	—	30	373 nestlings	—	—	—	503 total young	
19 July	66	—	—	27	328 nestlings	—	—	—	602 total young	
4 Aug	20	—	—	—	250 nestlings	—	—	—	463 total young	
10 Aug	11	—	—	11	186 nestlings	—	—	—	493 total young	
18 Aug	22	—	—	8	79 nestlings (9 downy)	—	—	—	303 total young	
7 Sept	0	—	—	0	35 nestlings	—	—	—	214 total young	
19 Sept	0	—	—	0	18 nestlings	—	—	—	160 total young	
5 Oct	0	—	—	0	10 nestlings	—	—	—	144 total young	
16 Nov	0	—	—	0	0	—	—	—	0	

APPENDIX 17

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible from mid-lagoon.

1976 total inside colony.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	3	2	1		
4 Feb	96	1	—							
10 Feb	65	21	3/1							
15 Feb	382	36	10/1							
24 Feb	486	152+	46 pairs courting	A/N = 3.2/1						
2 Mar	496	226	2.2/1							
8 Mar	607	329	1.8/1							First nestlings heard
15 Mar	527	332	1.6/1							
21 Mar	586	381	1.5/1							First downy nestlings visible
30 Mar	586	428	1.4/1							
4 Apr	539	421	1.3/1							
11 Apr	518	417	1.2/1	398	19	1	10	8	31/19 =	1.63
22 Apr	485	374	1.5/1	332	42	0	15	27	57/42 =	1.36
29 Apr	513	337	1.5/1	229	108	0	29	79	137/108 =	1.27
4 May	401	351	1.1/1	214	137	1	34	102	173/137 =	1.26
13 May	407	350	1.2/1	200	150	0	24	126	174/150 =	1.16
22 May	374	309	1.2/1	148	161	0	25	136	186/161 =	1.15
27 May	252	324	0.77/1	94	230	0	25	205	255/230 =	1.11
										(downy young)
11 June	—	—	—						257 (45)	
18 June	—	—	—						220 (41)	
26 June	—	—	—						166 (22)	
7 July	—	—	—						125 (27)	
13 July	—	—	—		140				155/140 =	1.11
21 July	—	—	—						151 (32)	
28 July	—	—	—						117 (44 in 23 nests)	
21 Aug	—	—	—						67 (28 in 15 nests)	
8 Sept	—	—	—						35 (9)	
25 Sept	—	—	—						5/3 =	1.67
24 Oct	—	—	—						0	

APPENDIX 18

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

Outside southeast 1976.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH				
						3	2	1		
						CHICKS	CHICKS	CHICK		
10 Feb	0									
13 Feb	21	2	10.5/1							
15 Feb	22	8	2.8/1							
24 Feb	24	12	2/1							
28 Feb	18	5	3.6/1							
2 Mar	16	11	1.5/1							
8 Mar	18	13	1.4/1							
15 Mar	16	11	1.5/1							
21 Mar	27	12	2.2/1							
30 Mar	15	11	1.4/1							
4 Apr	16	11	1.5/1		First nestlings visible					
11 Apr	13	11	1.2/1	—	5	1	3	1	10/5 =	2.0
22 Apr	10	11	0.9/1	3	9	0	3	6	12/9 =	1.3
29 Apr	6	10	0.6/1	2	8	0	5	3	13/8 =	1.6
4 May	3	10	—	—	8	0	2	6	10/8 =	1.3
13 May	4	10	—	1	9	0	2	7	11/9 =	1.2
27 May	1	11	—	0	11	0	0	11	11/11 =	1.0
6 June	0	9	—	First fledglings		0	0	9	9/9 =	1.0
11 June	0	7	—	0	7	0	0	7	7/7 =	1.0
26 June	0	7	—	0	7	0	0	7	7/7 =	1.0
7 July	0	3	—	0	3	0	0	3	3/3	
13 July	0	2	—	0	2	0	0	2	2/2	
21 July	0	2	—	—	2	0	0	2	2/2	
28 July	0	1	—	—	1	0	0	1	1/1	
21 Aug	0	0	—	—	0	0	0	0		

APPENDIX 19

Brown Pelicans. Whale Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1976												
DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST		
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH						
						3 CHICKS	2 CHICKS	1 CHICK				
11 Jan	8											
20 Jan	14											
28 Jan	57											
4 Feb	40											
10 Feb	37	15	2.5/1									
13 Feb	65	26	2.5/1									
15 Feb	71	26	2.7/1									
24 Feb	67	36	1.9/1									
28 Feb	50	37	1.4/1									
2 May	55	33	1.3/1									
8 May	76	33	2.3/1									
13 May	63	37	1.5/1									
15 May	44	38	1.3/1									
21 May	49	35	1.4/1									
30 May	36	33	1.1/1									
				First nestlings visible								
4 Apr	33	36	0.9/1	9	8	1	7	0	17/8 =	2.1		
11 Apr	31	37	0.8/1	—	17	1	7	6	23/14 =	1.6		
22 Apr	35	—	—	—	19	0	7	8	22/17 =	1.3		
29 Apr	29	32	—	—	25	1	7	17	34/25 =	1.4		
4 May	13	28	—	—	28	0	8	20	36/28 =	1.1		
13 May	6	—	—	—	27	0	3	24	30/27 =	1.1		
22 May	15	—	—	—	30	0	3	27	33/30 =	1.1		
27 May	10	—	—	—	32	0	3	29	35/32 =	1.1		
6 June	—	—	—	First fledglings							36	
11 June	—	—	—	—	—	—	—	—	36 (3 downy)			
18 June	—	—	—	—	—	—	—	—	26 (3 downy)			
26 June	—	—	—	—	—	—	—	—	18			
7 July	—	—	—	—	—	—	—	—	12			
13 July	—	—	—	—	—	—	—	—	12			
21 July	—	—	—	—	—	—	—	—	3			
28 July	—	—	—	—	—	—	—	—	0			

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FOSSIL ENALIARCTINE PINNIPEDS (MAMMALIA: OTARIIDAE)
FROM PYRAMID HILL, KERN COUNTY, CALIFORNIA

By Lawrence G. Barnes



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FOSSIL ENALIARCTINE PINNIPEDS (MAMMALIA: OTARIIDAE) FROM PYRAMID HILL, KERN COUNTY, CALIFORNIA^{1, 2}

By Lawrence G. Barnes³

ABSTRACT: Including *Enaliarctos mealsi*, a total of three named fossil species of enaliarctine pinnipeds in the carnivore family Otariidae are now known by skulls from latest Oligocene to earliest Miocene rocks in California. Two of these species are new: *Enaliarctos mitchelli*, new species, and *Pinnarctidion bishopi*, new genus and species. Most of the published fossils are from two strata in the lower part of the Pyramid Hill Sand Member of the Jewett Sand that is exposed at Pyramid Hill in the southern part of the San Joaquin Valley in Kern County. Increasing aquatic adaptation relative to *E. mealsi* and adaptive and phylogenetic diversity within the subfamily Enaliarctinae are demonstrated by these new taxa. The two known genera have different skull proportions and dental and basicranial characters.

In the past, *E. mealsi* has been thought to be a possible otariine (modern sea lions, fur seals) ancestor. *P. bishopi*, on the other hand, shares many characters with extinct species of *Allodesmus*, particularly with *A. packardi*. Therefore, the subfamily Enaliarctinae, as defined in this study, apparently gave rise to at least two other otariid subfamilies; the Allodesminae and the Otariinae. The other otariid subfamilies (Desmatophocinae, Imagotariinae, and Odobeninae) also may have been derived from the Enaliarctinae, but there is no published paleontological proof of this. Rather than classify each enaliarctine genus within its apparently descendent subfamily, I propose the continued recognition of one basal group, the subfamily Enaliarctinae. This classification joins in one subfamily the primitive otariids that have a similar stage of evolution. I believe that the morphological diversity and apparent phylogenetic relationships of the six above named subfamilies warrant their inclusion in only one carnivore family, the Otariidae.

INTRODUCTION

Our knowledge of the evolutionary history of sea lions, fur seals, and walruses has increased greatly in recent years. Most of the new evolutionary information derives from fossil evidence and has been recently reviewed by Mitchell (1968, 1975), Repenning (1975, 1976), Repenning and Tedford (1977), and by Tedford (1976). These reviews include phylogenies, classifications, and a cladistic analysis. Such interpretations of the fossil record of these animals were not attempted prior to the mid-1960's. The classification of the sea lions, fur seals, walruses, and their extinct relatives is presently a matter of controversy, as evidenced by the diversity of opinions in recent studies.

Most mammalogists have traditionally placed the modern walruses in the family Odobenidae, and the modern sea lions and fur seals in the family Otariidae. A majority of authors have recognized that these two families are more closely related to each other than either is to the true seals of the family Phocidae. In recognition of this closer relationship, the Otariidae and Odobenidae are therefore classified by some authors together in the superfamily Otarioidea. Most of the named fossil pinnipeds showing affinities with sea lions or walruses were placed by their original describers in either the Otariidae or the Odobenidae. Early departures from this classification were the naming of the

families Desmatophocidae Hay 1930 and Allodesmidae Kellogg 1931. These two families were not generally accepted, however.

Mitchell (1968) emphasized that most known fossil otariid species were not clearly members of either modern lineage, but belonged to other lineages, some of which shared characters in various combinations both with modern sea lions and with walruses. His classification had six subfamilies, including the subfamily Odobeninae (walruses) as a new rank, in one family, the Otariidae. A seventh subfamily, the primitive Enaliarctinae, was later added to the family Otariidae (Mitchell and Tedford 1973;

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Mitchell 1975). In their studies, Repenning and Tedford have recognized most of the subfamilies in Mitchell's classifications, but have put them in four different families. They kept the Odobenidae and Otariidae at family rank and recognized two additional families; the Enaliarctidae and the Desmatophocidae (Repenning 1975, 1976; Repenning and Tedford 1977). Tedford's (1976) cladistically inspired classification is still different in placing *Enaliarctos* Mitchell and Tedford 1973 in the family Enaliarctidae and the Odobeninae (and presumably some or all of the other subfamilies recognized by Mitchell (1968)) in the family Otariidae.

The classification that I adopt in this study (see p. 38) consists of one family, the Otariidae, that includes the subfamilies Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, and Odobeninae. It is a middle ground between the above-mentioned classifications, but is closest to that of Mitchell (1968, 1975), and does not include Dusignathinae.

Enaliarctos mealsi Mitchell and Tedford 1973 is geologically the oldest and morphologically the most primitive named fossil otariid. Authors (Mitchell and Tedford 1973; Repenning 1975, 1976; Repenning and Tedford 1977; Tedford 1976), therefore, have considered the monotypic subfamily Enaliarctinae (or in some classifications family Enaliarctidae) to be ancestral to most or all of the later otariids, and to be transitional in morphology between fissiped and otariid pinniped carnivores. Mitchell (1975:19), Repenning (1975:29; 1976:376–377), Ray (1976:429), Tedford (1976:369), and Repenning and Tedford (1977:77, 79) have indicated that other fossils referable to the Enaliarctinae exist in collections but are not yet described.

The holotype and referred specimens of *Enaliarctos mealsi* were collected from rocks of late Oligocene or early Miocene age at Pyramid Hill which is in Kern County in the southeast part of California's San Joaquin Valley (see Addicott 1970:fig. 3; Mitchell and Tedford 1973:figs. 1, 4). The purpose of the present paper is to describe additional fossils of *Enaliarctos mealsi*, skull parts of a new species of *Enaliarctos*, and skull parts of another, more advanced new genus and species of pinniped from the same localities and rock sequence at Pyramid Hill, to compare them with those specimens studied by Mitchell and Tedford (1973), and to place them in evolutionary and stratigraphic perspective. The fossils from Pyramid Hill document the first described wide diversity of primitive otariids in late Oligocene or early Miocene time.

Many postcranial bones of primitive otariids have been collected from rocks at Pyramid Hill and elsewhere. Until associated or articulated skeletons are described, however, the referral of any of these isolated postcranial bones to any of the species based upon skulls will be tenuous. Some additional bones will be described by myself and Edward Mitchell in a separate study.

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Peggy Zeadow, Daphne Cowan, and Doris Pickering aided in manuscript preparation. The photographs were prepared by Armando Solis (Figs. 2, 14–21), and Lawrence Reynolds (Figs. 3, 4, 6, 8) of the Natural History Museum of Los Angeles County. Some of the drawings were prepared by David Cook (Figs. 7, 9, 10) and by J. Patricia Lufkin (Figs. 5, 11–13), both staff artists of the University of California Department of Paleontology, Berkeley. The remaining illustrations are by the author.

ABBREVIATIONS

Institutional acronyms for specimens cited in the text are:

- CIT: California Institute of Technology, Pasadena; collections and records now held by Natural History Museum of Los Angeles County.
 LACM: Natural History Museum of Los Angeles County, Section of Vertebrate Paleontology, Los Angeles, California, U.S.A.
 SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.
 UCMP: University of California Museum of Paleontology, Berkeley, California, U.S.A.

METHODS

Most of the mammal bones from the Pyramid Hill Sand Member of the Jewett Sand are in concretionary sandstone that is harder than the enclosed bone. Mechanical preparation using pneumatic, air-abrasive, and grinding tools is satisfactory for removing bulk matrix, but destroys the outer surface of the bone. Acetic acid (CH₃CO₂H) or formic acid (HCO₂H) in a dilute aqueous solution (10 to 20 percent) dissolves the sandstone matrix but not the bone. The bone surface that is exposed by acid must be periodically removed from the solution, rinsed with water, neutralized with a base, rinsed again with water, dried thoroughly, and coated with diluted resin or with a plastic cement similarly diluted with acetone.

A pinniped palate described in this paper (UCMP 80943), was found as the sole remaining part of a shattered skull that was at one time complete and enclosed in a nodule. The teeth and ventral surface of the palate were buried in the matrix and the visible surface was the bone of the dorsal surface of the palate within the nasal chamber. Polyester resin and fiberglass cloth were applied to the exposed broken surface of the bone and acetic acid and air-abrasive tools were used to remove the matrix from the occlusal surface of the palate. As a result, the prepared specimen consists of a thin layer of bone laminated on a fiberglass and resin base.

Most of the skull measurements given in Table 3 were made following the instructions given by Sivertsen (1954:18–20) and by Barnes (1972:3). Mitchell and Tedford (1973:table 2) also used several of the measurements explained by Sivertsen, and

some additional ones. Some of the values I recorded for measurements of the specimens of *Enaliarctos mealsi* differ from those recorded by Mitchell and Tedford, and are indicated by an asterisk in my Table 3. For these questionable values, I have attempted to duplicate the measurement method shown in Sivertsen's (1954) figures 5 through 7. For example, I have measured the zygomatic root of the maxilla, Sivertsen's (1954:20, fig. 6) measurement 14, across the narrowest span to the ventral lip of the infraorbital foramen. Measurements not defined by Sivertsen, such as the length of the tooth row from C to M², the width between the infraorbital foramina, the point of greatest intertemporal constriction, the width of the palate across the anterior roots of P⁴, and the greatest width of the anterior nares are explained in Barnes 1972:fig. 1. The post-palatal length (palatal notch to basion), used in this study and by Mitchell and Tedford (1973), was considered by Sivertsen (1954:20) to be unserviceable, but is useful as a measure of anteroposterior length for the mostly fragmentary enaliarctine skulls at hand.

Among the measurements not previously defined by Sivertsen or Barnes, and used in this report and/or by Mitchell and Tedford (1973), the post-palatal length is measured from the basion to the posterior point of Sivertsen's (1954:fig.6) measurement 10, and the paroccipital width is measured across the lateral extremities of the paroccipital processes. The width across the occipital condyles is measured from the lateral edges of the articular surfaces. Measurements of the nares, foramen magnum, and infraorbital foramen are straightforward. With the exceptions of the measurement from the basion to the anterior end of the zygomatic root and the width of the zygomatic root of the maxilla, all measurements are in sagittal, frontal, vertical, or transverse planes of the skull. Most of the estimated transverse measurements are half-skull measurements multiplied by two.

GEOLOGIC AND PALEONTOLOGIC CONTEXT

The Tertiary marine rocks that are exposed in Kern County just west of California's Sierra Nevada contain a sequence of invertebrate and vertebrate fossil assemblages that is of great importance to studies of marine vertebrate evolution and of Tertiary chronology. The marine rocks crop out in low hills in a northwest to southeast trending belt between the Sierra Nevada and the area of the city of Bakersfield (Addicott 1970:fig. 1). Addicott (1970) has provided a recent review of the Tertiary marine rock units in the region. Mitchell and Tedford (1973) have also discussed the regional geology, with emphasis upon the marine rocks that are exposed at Pyramid Hill.

The specimens that were used in the original description of the oldest named fossil otariid pinniped, *Enaliarctos mealsi* Mitchell and Tedford 1973, were collected at Pyramid Hill (see Addicott 1970:fig. 3; Mitchell and Tedford 1973:fig. 1) from the basal part of the Pyramid Hill Sand Member of the Jewett Sand. This is the oldest marine rock unit exposed on the south face of Pyramid Hill where it unconformably overlies the non-marine Walker Formation (Addicott 1970:10; Mitchell and Tedford 1973:fig. 4). Elsewhere in the Bakersfield area, the Pyramid Hill Sand Member either is separated from the underlying Walker Formation by the intervening Vedder Sand, or lies unconformably directly upon the basement complex of the Sierra Nevada (Addicott 1970:9, 12).

With the exception of the isolated teeth, all of the pinniped fossils described in this report were in concretions from Pyramid Hill. Within the lower part of the Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill, there are two fossiliferous, concentration-bearing beds (Mitchell and Tedford 1973:figs. 2, 4; Fig. 1, this report).

The age and depositional differences between these two beds are not yet clearly understood, but indications are that their fossil species compositions are different. I therefore consider it very important to distinguish from which bed each fossil was derived. The lowest of these two beds (including localities LACM 1603, 1626, 1627, UCMP V7032) is at the very base of the Pyramid Hill Sand Member, contains pebbles, rounded black chert grains, angular quartz clasts, and is referred to as the "grit zone" by some geologists (Addicott 1970:12). The Pyramid Hill Local Fauna named and characterized by Mitchell and Tedford (1973:216, 268–272) should be strictly limited to the fossil assemblage from the "grit zone."

I concur with Mitchell and Tedford (1973:220–221, fig. 2) that the holotype (LACM 4321) of *Enaliarctos mealsi*, found loose on the hillside, probably originally came from the lower concretion bed (LACM locality 1627) in the "grit zone." The coarse sandstone that remains within the skull is typical of concretions from this lower bed. The isolated teeth referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973) and in this report, and those identified only as *Enaliarctos* sp. in this report, were collected from a nearby locality toward the west end of Pyramid Hill (LACM locality 1626 = UCMP locality V7032) which is also in the "grit zone" (Mitchell and Tedford 1973:fig. 2, table 4). The skull (LACM [CIT] 5303) that was referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973:229) is in a finer matrix such as is found in higher beds, but the color of the bone is characteristic of those from the lower bed. The exact source of this referred specimen is still uncertain, but I believe it was derived from the lower bed. Its museum locality is given as CIT locality 481, a designation which records that the specimen was discovered as a loose item at the base of Pyramid Hill with no source bed implied. Fossils in UCMP that have the locality designation V6618 were found under similar circumstances.

The upper fossiliferous, concretion-bearing bed (LACM locality 1628 = UCMP locality V6916) on the south face of Pyramid Hill is 40 to 50 feet stratigraphically above the lower "grit zone" (Mitchell and Tedford 1973:figs. 2, 4), and the concretions in this upper bed are characteristically finer grained, stained reddish-brown on the outside by iron oxide, and are gray internally (Addicott 1970:12; and personal observations). The holotype skull (UCMP 86334) of *Pinmarctidion bishopi*, new genus and species, was collected *in situ* from this upper bed in a concretion fitting the above description.

The endocranial cast (LACM [CIT] 5302) referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973:229–232) and referred herein on new morphological evidence to *Pinmarctidion bishopi*, new genus and species, and the holotype (UCMP 100391) and paratype (UCMP 80943) of *Enaliarctos mitchelli*, new species, have bone color and matrix characteristic of the upper concretion bed, and are presumed to have rolled down Pyramid Hill from that level (= LACM locality 1628 = UCMP locality V6916). Their listed museum locality numbers (CIT 481 = UCMP V6618), however, indicate that they were discovered as loose specimens on the lower slopes of Pyramid Hill.

The interstitial matrix surrounding the fine-grained concretions

in the upper bed is a very different coarse quartz sand containing mollusk shells and other fossils. Some of the bones are exposed at the surfaces of the enclosing concretions and appear to have become so exposed by erosion. In the case of the holotype of *Pinnarctidion bishopi*, new genus and species, the right zygomatic arch and the end of the rostrum were exposed at the surface of the enclosing concretion and worn away, but the coarser matrix surrounding the concretion was in contact with the exposed bone surface. These facts suggest that the fine-grained, bone-bearing concretions were derived from some other, probably older source rock, and were re-deposited in coarse sand when the upper concretion-bearing bed was laid down. At the present time, it is not known how much older than the surrounding coarse sand matrix these bone-bearing concretions might be, but I believe they are undoubtedly younger than the lower basal "grit zone." Fossils from this upper bed should not be included as part of the Pyramid Hill Local Fauna of Mitchell and Tedford (1973).

In summary (see Fig. 1), the stratigraphic distribution of fossil pinnipeds now known from the Pyramid Hill Sand Member of the Jewett Sand exposed at Pyramid Hill is as follows: *Enaliarctos mealsi* is probably from the lowest fossil-bearing horizon (LACM locality 1627) in the "grit zone." The holotype of *Pinnarctidion bishopi*, new genus and species, is definitely from the upper fossil-bearing concretion bed (LACM locality 1628 = UCMP locality V6916). Based on lithology and bone color the referred specimen of that species and the holotype and paratype of *Enaliarctos mitchelli*, new species, were probably originally from the same upper bed. Bones in the upper bed were probably redeposited when that bed was formed, but probably are none-the-less still geologically younger than the basal "grit zone."

Addicott (1970:33–34, fig. 2) and Mitchell and Tedford (1973:214–217, 220, 272) agreed by stating that based on paleontological evidence the age of the Pyramid Hill Sand Member of the Jewett Sand is early Miocene. This is roughly consistent with ages and correlations derived from various sources, but should not be accepted without some qualification. For example, based on its contained fossil mollusks, the Jewett Sand falls within the "Vaqueros" provisional California provincial molluscan stage as used by Addicott (1972:8–10; 1976), which he called early Miocene in the California chronology. Mitchell and Tedford (1973:272) believed that teeth of the horse, *Anchitherium* sp., from the "grit zone" are most similar to those of *A. agatense* (Osborn 1918) of Arikareean age from the Harrison Formation of Nebraska, and, therefore, they (1973:217, 220, fig. 3) correlated the "grit zone" with the Arikareean North American Land Mammal Age. Evernden, Savage, Curtis, and James (1964:165) reported a radiometric date of 21.3 million years from the Agate Ash in the Harrison Formation.

The holotype of the odontocete *Argyrosetus joaquinensis* Kellogg 1932 undoubtedly was derived from the Pyramid Hill Sand Member of the Jewett Sand (Mitchell and Tedford 1973:268; Barnes 1976:325) despite information presented by Kellogg (1932:1) that it was derived from the older "Vedder zone." The matrix adhering to the holotype of *A. joaquinensis* is similar to that on the holotype of *Enaliarctos mealsi*, and I conclude that both specimens are from the basal "grit zone" of the Jewett Sand. Most of the molluscan species listed by Kellogg (1932:1) from the type locality of *A. joaquinensis*, are also listed by Addicott (1972:9) as representative of the "Vaqueros" provisional California provincial molluscan stage. The type species of *Argy-*

rosetus Lydekker 1894, *A. patagonicus* Lydekker 1894, is from the early Miocene Patagonian marine formation in Argentina. I have compared (Barnes 1976:325, 335) the grade of evolution of the aggregate cetacean assemblage from the Jewett Sand with that of odontocetes from the early Miocene deposits at Belluno, Italy (see Dal Piaz 1977 for summary of cetacean assemblage there).

The Jewett Sand has been assigned by various workers to the upper Zemorrian, the upper Zemorrian and lower Saucesian, or the Saucesian foraminiferal stages (see Addicott 1970:33 for summary). There is some disagreement, however, among authors as to how these foraminiferal stages correlate with the European sequence and with the radiometric time scale. Evernden, et al. (1964:167) and Turner (1970:97, 100–101, table 1, fig. 4) showed the Zemorrian-Saucesian boundary equivalent to the late Arikareean Land Mammal Age and at about 22 or 22.5 million years ago, but avoided epoch correlations. Berggren and Van Couvering (1974:fig. 12) showed the Oligocene-Miocene epoch boundary at 22.5 million years ago. Bandy and Ingle (1970:fig. 2), however, showed the Oligocene-Miocene boundary between 24.1 and 25 million years ago and also correlative with the Zemorrian-Saucesian boundary. Lipps (1967:fig. 4) placed the Zemorrian-Saucesian boundary slightly younger than the Oligocene-Miocene boundary. Most consistent information, therefore is that the Zemorrian-Saucesian boundary is about 22.5 million years old and correlates with the Oligocene-Miocene boundary. The foraminiferal stage assignments for the Jewett Sand quoted above, therefore, would allow no more accurate epoch assignment for this rock unit than latest Oligocene to early Miocene. This would be roughly 21 to 23 million years ago (Turner 1970, Berggren and Van Couvering 1974:fig. 12).

Mitchell and Tedford (1973) discussed the other fossils found associated in the same rock sequence with the fossil otariids at Pyramid Hill. Additionally, Bishop (1969) has commented on the diverse shark assemblages in both the lower "grit zone" and the upper concretion-bearing bed.

Wilson (1935) described fossil bones of primitive pinnipeds that were collected from outcrops of the Jewett Sand (Addicott 1970:9) northwest of Pyramid Hill and west of the small town of Woody. Some of these bones were identified by Wilson as phocids (true seals). In their survey of previously described primitive pinniped bones, Mitchell and Tedford (1973:267–268, 272–275) suggested that Wilson's phocid identifications were incorrect and that all the bones belonged to primitive otariid pinnipeds of an "otter like" grade of evolution. Mitchell (1966:20, pl. 24) and Barnes and Mitchell (1975:34) have also discussed the identities of some of the bones originally described by Wilson.

It is my belief that there is presently no firm evidence for or against the statement that the exposures of the Jewett Sand near Woody differ chronologically from the exposures at Pyramid Hill (as suggested by Mitchell and Tedford 1973:216–217, 272). The absence of documented invertebrate fossils in the outcrops near Woody will make it necessary to rely on stratigraphic and vertebrate fossil evidence to resolve the problem. The possibility does exist that some of the pinniped bones comprising the Woody Local Fauna of Mitchell and Tedford (1973), belong to the same species of otariids described in this report. This matter will be investigated in a separate study by Edward Mitchell and myself (in preparation).

The Jewett Sand is overlain by middle and late Miocene rock units that are best exposed farther to the west. These younger,

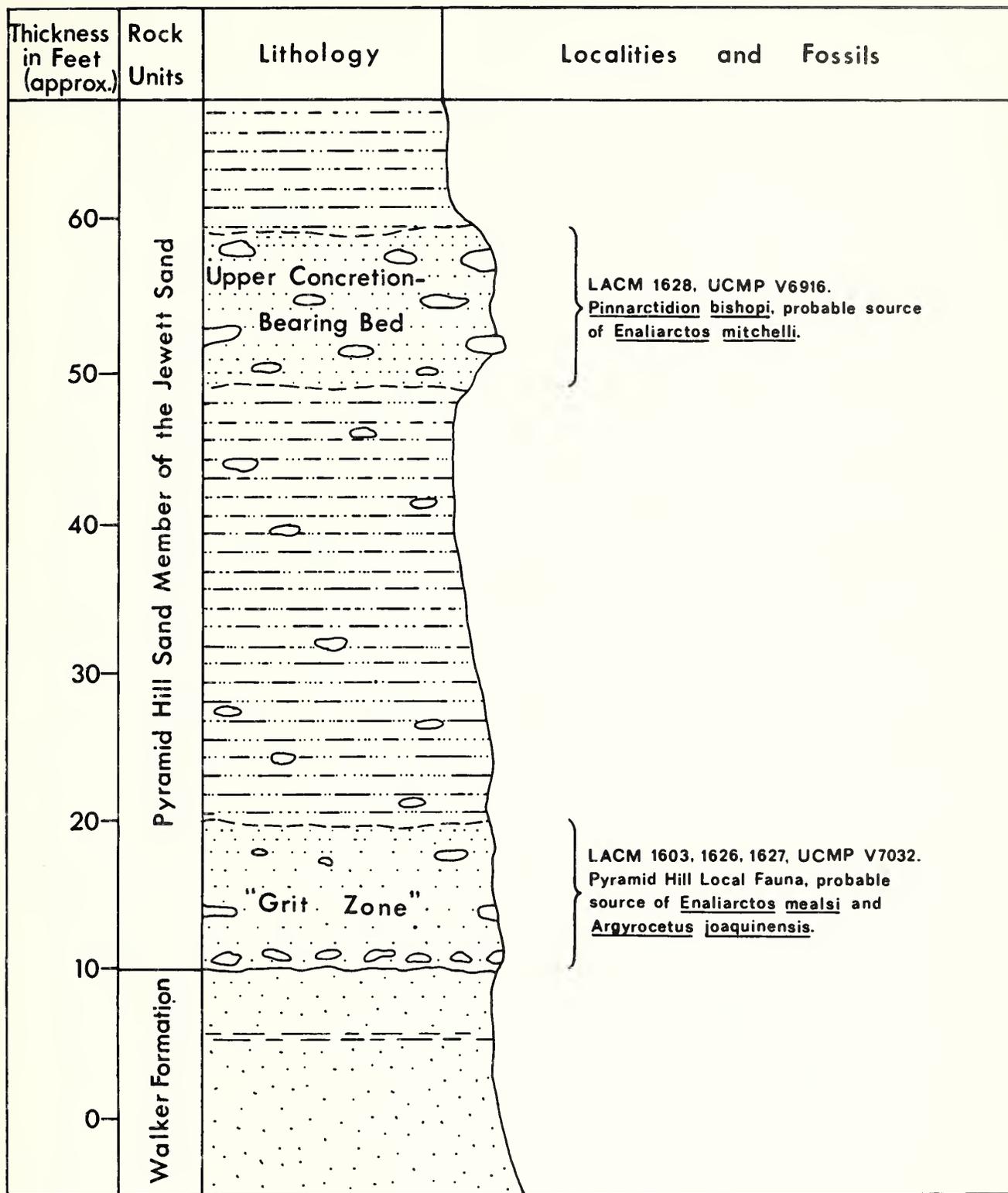


FIGURE 1. Generalized columnar section of the top of the Walker Formation and the base of the Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill. The sources of fossils, including enaliarctine otariids, and positions of vertebrate fossil localities are shown. (Derived in part from Mitchell and Tedford 1973: figs. 2, 4, table 4; and Addicott 1970.)

overlying rocks include the Round Mountain Silt which contains in its upper part the important Sharktooth Hill Bonebed, the source of abundant marine vertebrate fossils. I have (Barnes 1976, and see literature cited there) summarized the sequence of known fossil cetaceans in these overlying marine rock units and in the Jewett Sand.

SYSTEMATICS

CLASS MAMMALIA Linnaeus 1758

Order CARNIVORA Bowdich 1821

Family Otariidae Gill 1866

Trichecidae Gray 1821:302; invalid, based on *Trichechus* Linnaeus 1766 (walrus), *nec Trichechus* Linnaeus 1758 (manatees, family Trichechidae Gill 1872).

Otariina Gray 1825:340; as a tribe of the family Phocidae, to include *Otaria* Péron 1816.

Otariidae Brookes 1828:37; improperly formed name.

Otariidae Gill 1866:7, 10, (sea lions and fur seals).

Rosmaridae Gill 1866:7, 11, invalid, based on *Rosmarus* Scopoli 1777=*Rosmarus* Brünnich 1772=*Odobenus* Brisson 1762, (walrus).

Odobenidae Allen 1880:5, 17; originally spelled Odobaenidae, emended by Palmer 1904:833 (walrus).

Desmatophocidae Hay 1930:557; for *Desmatophoca oregonensis* Condon 1906, only.

Allodesmidae Kellogg 1931:227; inclusion of *Neotherium mirum* Kellogg 1931 uncertain.

Otariidae, *sensu lato*. Mitchell 1968:1844, including Odobeninae, Desmatophocinae, Allodesminae, etc.

Enaliarctidae. Tedford 1976:367 (caption for fig. 2), 372 (table 1); Repenning 1976:376; including *Enaliarctos* and undescribed taxa.

Enaliarctidae. Arnason 1977:241, ?typographic error.

TYPE GENUS: *Otaria* Péron 1816.

INCLUDED SUBFAMILIES: Enaliarctinae Mitchell and Tedford 1973; Desmatophocinae Hay 1930; Allodesminae Kellogg 1931; Imagotariinae Mitchell 1968; Odobeninae Allen 1880; Otariinae Gill 1866.

Subfamily Enaliarctinae Mitchell and Tedford 1973

Enaliarctinae Mitchell and Tedford 1973:218; Mitchell 1975:19 fig. 1.

"Common Ancestral Group." Repenning 1975:29, fig. 11.

Enaliarctidae. Tedford 1976:367 (caption for fig. 2), 372 (table 1); Repenning 1976:376; Repenning and Tedford 1977:11.

Enaliarctidae. Arnason 1977:241, ?typog. error.

EMENDED DIAGNOSIS OF SUBFAMILY: A subfamily of the family Otariidae differing from Allodesminae, Desmatophocinae, Imagotariinae, Odobeninae and Otariinae by having carnassial teeth and a protocone or a protocone shelf on P⁴, and by having a nasolabialis fossa; differing from Allodesminae, Odobeninae, and Otariinae by having three roots on P⁴, a smooth and inflated bulla, and no large orbital vacuity; differing from Imagotariinae and Odobeninae by having a large paroccipital-mastoid crest; differing from Allodesminae and Otariinae by having a larger tympanic membrane; differing from Desmatophocinae, Imagotariinae, Odobeninae, and Otariinae by having a prominent sulcus on cranium corresponding to pseudosylvian fissure of brain; differing from Odobeninae by having a narrow interorbital region; differing from Allodesminae and Desmatophocinae by having an antorbital process; differing from Odobeninae and Otariinae by having a lacrimal foramen; and differ-

ing from Otariinae by lacking a large supraorbital process of the frontal.

TYPE GENUS: *Enaliarctos* Mitchell and Tedford 1973.

INCLUDED GENERA: *Enaliarctos* Mitchell and Tedford 1973, and *Pinnarctidion*, new genus.

Enaliarctos Mitchell and Tedford 1973

Enaliarctos Mitchell and Tedford 1973:218.

EMENDED DIAGNOSIS OF GENUS: A genus of the subfamily Enaliarctinae differing from *Pinnarctidion*, new genus, by having a skull with a wider interorbital region, a smaller orbit, smaller antorbital processes, external openings of optic foramina located relatively higher on the anterior wall of the brain case, narrower and more arched palate, smaller infraorbital palatal plate of maxilla, cheek teeth proportionally larger and more closely spaced, deep embrasure pit for M₁ on palate between P⁴ and M¹, protocone shelf of P⁴ larger and positioned more anteriorly on the tooth, anterolabial corner of M¹ large, posterior narial opening higher and narrower, strut between palate and braincase less concave lateral to pterygoid hamulus, tympanic cavity smaller, paroccipital process smaller and joined to mastoid process by only a low paroccipital-mastoid crest, and occipital condyles nearly parallel in posterior view rather than diverging dorsally.

TYPE SPECIES: *Enaliarctos mealsi* Mitchell and Tedford 1973; type by original designation.

INCLUDED SPECIES: *Enaliarctos mealsi* Mitchell and Tedford 1973, and *Enaliarctos mitchelli*, new species.

Enaliarctos mealsi Mitchell and Tedford 1973

Figures 2a–q, 16a, 18a, 20a

Enaliarctos mealsi Mitchell and Tedford 1973:220.

EMENDED DIAGNOSIS OF SPECIES: A species of *Enaliarctos* differing from *E. mitchelli*, new species, by having a skull with a wider and more dorsoventrally compressed rostrum, a dorsoventrally compressed anterior narial opening that is oval in anterior view, longer nasal bones, zygomatic arches that are more greatly arched at midpoint, ventral surface of zygomatic arch ventral to the infraorbital foramen steeply inclined both anteriorly and laterally, interorbital region relatively wider, at least four pair of posterior palatine foramina instead of one, posterolabial root of P⁴ more widely separated from the other two roots of the same tooth, and the posterior root of M¹ clearly posterior to the posterior margin of the zygomatic arch.

HOLOTYPE: LACM 4321, skull, as described by Mitchell and Tedford 1973, probably from the lower nodule-bearing "grit zone" at Pyramid Hill, LACM locality 1627; collected by Harold S. Meals, 8 January 1961.

PREVIOUSLY REFERRED SPECIMENS: LACM (CIT) 5303, incomplete skull from CIT locality 481, found loose on the slopes of Pyramid Hill and probably derived from the "grit zone," collected by Chester Stock, 1950; LACM 4364, left P⁴ from LACM locality 1626, collected by Harold Meals, March 1961; LACM 4574, left M₁, LACM 4575, left dP₄, and LACM 4576, protocone of left P⁴, all from LACM locality 1626, a locality west of Pyramid Hill correlated with the "grit zone," col-

lected by Joseph F. Arndt, 1960; LACM 17036, left M_1 lacking roots, LACM 20517, right M^2 , both from LACM locality 1626, collected by Richard C. Bishop, 1965.

ADDITIONAL REFERRED SPECIMENS: LACM 4365, left P^3 from LACM locality 1626, collected by Harold Meals, March 1961; LACM 17035, right P_3 or P_4 from LACM locality 1626, collected by Richard C. Bishop; LACM 72383, left M_1 from LACM locality 1626, collected by Michael K. Hammer, 16 January 1966; LACM 72733, left P_3 or P_4 from LACM locality 1626; UCMP 86211, right M^1 from UCMP locality V7032 (=LACM locality 1626), collected by Mark A. Roeder, December 1969.

DISCUSSION: The isolated endocranial cast, LACM (CIT) 5302, previously referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973) is reidentified here as belonging to *Pinnarctidion bishopi*, new genus and species. This restricts the known anatomy of the endocranial cast of *E. mealsi* to the other referred skull, LACM (CIT) 5303. The anterior end of the rostrum of that other skull (LACM [CIT] 5303) referred to *E. mealsi* by Mitchell and Tedford (1973) is broken off in a transverse plane exposing two anteriorly facing holes which Mitchell and Tedford (1973:234, see their fig. 12b) interpreted as alveoli for incisors. The more complete rostrum described herein of *Enaliarctos michelli*, new species, demonstrates that these holes in LACM (CIT) 5303 are not incisor alveoli, but are the cross sections of the incisive foramina (palatine fissures). The alveoli for the incisors were still farther anterior to these foramina. In the reconstructions of *Enaliarctos mealsi* in this study (Figs. 16a, 18a, 20a), the incisive foramina and rostral extremity are based on *E. michelli*. In my previous description of the holotype of *Allodesmus packardi* Barnes 1972, I also misinterpreted (pp. 48–49) the exposed cross sections of the incisive foramina as medial incisor alveoli. In *A. packardi*, the great lengths of the roots of I^3 are emphasized by the extension of their alveoli posteriorly to a point lateral to the incisive foramina (see Barnes 1972:fig. 18). There is, therefore, no evidence for the existence of only four rather than the usual six upper incisors as I previously restored the skull of *A. packardi* (Barnes 1972:fig. 19). In the present study I have restored the rostrum of *A. packardi* (Fig. 21b) as it is in *A. kernensis* Kellogg 1922. The incisive foramina of *A. kernensis* are small and appear on the palate merged into a single small foramen. This condition in *Allodesmus* Kellogg 1922 is unique among pinnipeds, which usually have large, paired palatal openings of the incisive foramina as do fissiped carnivores.

Because of the incompleteness of some of the bone in the area of the anterior lacerate foramina (orbital fissures) on the holotype of *E. mealsi*, it is difficult to interpret the precise relationship between the foramen rotundum and the alisphenoid canal. In species of Canidae and Ursidae, the foramen rotundum is in the medial wall of the alisphenoid canal, and is separated from the anterior lacerate foramen by a wide bony septum. In contrast, in the modern Otariinae, the foramen rotundum is merged with the anterior lacerate foramen forming one large aperture, and this is separated from the anterior end of the alisphenoid canal by a bony septum. I judge this to be a derived character. On the left side of the holotype of *E. mealsi*, the posterior wall of the partly obliterated foramen rotundum forms a semicircular notch in the medial wall of the alisphenoid canal. There is, however, no anterior wall of the foramen rotundum that would have separated it from the anterior lacerate foramen, as in canids and ursids. In this respect, *E. mealsi* is intermediate in structure between the

latter and modern otariines, and is morphologically closer to the condition in otariines.

It appears that *E. mealsi* had an inferior petrosal sinus that was enlarged as an embayment in the lateral edge of the basioccipital medial to the bulla which Hunt has shown (1974a:36; 1974b:1038, pl. 1; 1977:830, 837, fig. 2, pls. 1–3) is a structure shared by modern bears and fossil Amphicyonidae. Hunt assumed that the embayment in the extinct amphicyonids served the same function as in modern ursids: to hold an elongate loop of the median branch of the internal carotid artery. Both the holotype (LACM 4321) and referred specimen (LACM [CIT] 5303) of *E. mealsi* show evidence of a relatively small embayment in each side of the basioccipital. It is ventrally located within a rounded tuberosity in the probable area of insertion of the rectus capitis ventralis muscle. On the holotype, the tuberosity on the left side is broken through to reveal the sinus (see Mitchell and Tedford 1973:fig. 5a). On the endocast of the referred specimen (see Mitchell and Tedford 1973:fig. 12a) the bone forming the basioccipital tuberosities is mostly broken away to reveal hemispherical, matrix-filled recesses in the basioccipital. Each sinus, lying medial to the petrosal, is approximately 8 mm wide. The left one is larger than the right. Similar sinuses occur in *Allodesmus packardi* and in *Pinnarctidion bishopi*, new genus and species, and are discussed in further detail under the description of the latter species.

Mitchell and Tedford (1973:228) described the tympanic crest of *E. mealsi* as being of small diameter. This has been cited (Repenning and Tedford 1977:11) as diagnostic for the subfamily Enaliarctinae (=their family Enaliarctidae). Compared with species of the Otariinae and Allodesminae, however, the tympanic crest of *E. mealsi* is of relatively wide diameter. It measures approximately 7 mm across as compared to 9.3 mm by 7.5 mm across in the much larger holotype skull of *Imagotaria downsi* Mitchell 1968 (see also Repenning and Tedford 1977:32).

Mitchell and Tedford (1973:229) described the M^1 of the holotype of *E. mealsi* as having "three roots of which the lingual root is the largest; the labial roots are smaller and crowded together." Repenning and Tedford (1977:11) cited this character as diagnostic for their family Enaliarctidae. I disagree with this interpretation. I base my observations upon the holotype, the referred skull (LACM [CIT] 5303), and a referred isolated right M^1 (UCMP 86211). The M^1 has only two roots. The anterior, labial root is circular in cross section and separate. The remnant of the formerly separate posterior labial root is fused with the likewise formerly separate lingual root which is above the protocone. These two fused roots form one posterolingually placed root that is bilobed in cross section, and has its long cross-sectional axis anterolabial to posterolingual. The root structure of the M^1 in *E. mealsi* is, therefore, homologous with that of the holotype of *Desmatophoca oregonensis* Condon 1906 (see Mitchell 1975:fig. 2) and of a specimen (USNM 184060) referred to *Imagotaria downsi* by Repenning and Tedford (1977:pl. 8, fig. 1), and exemplifies a probable evolutionary step in the development of the two nearly equal-sized roots on the M^1 of some late Cenozoic and Recent species of Otariinae (e.g. Repenning and Tedford 1977: pl. 19, figs. 3, 4; pl. 20; pl. 22, fig. 2; pl. 23, fig. 12).

The M^1 (UCMP 86211) which I refer to *E. mealsi* (Fig. 2j), was collected from the same locality (LACM 1626 = UCMP V7032) as were all the other isolated teeth referred to *E. mealsi* in this report and by Mitchell and Tedford (1973). The structure and proportions of the crown and root of UCMP 86211 cor-

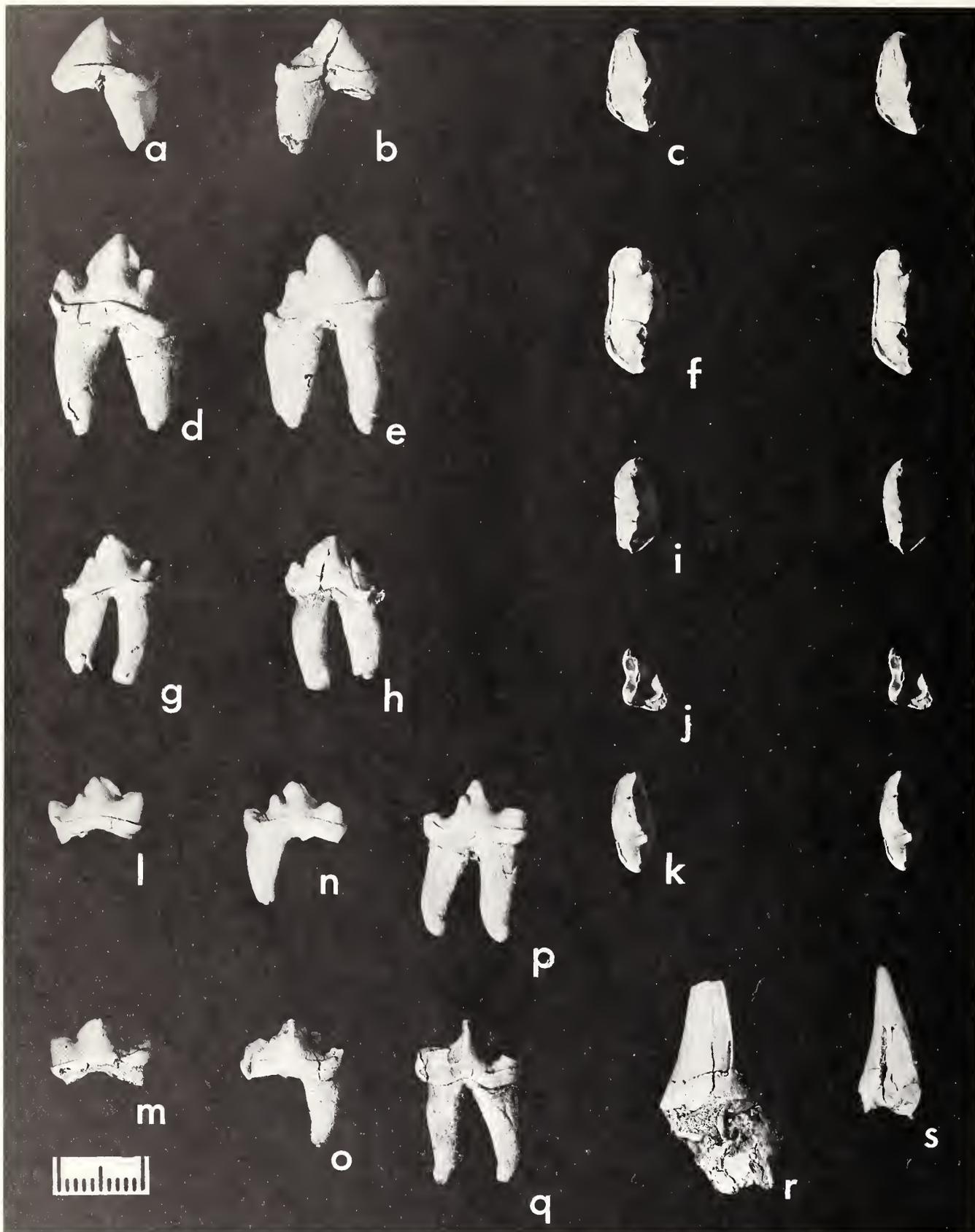


FIGURE 2. *Enaliarctos mealsi* Mitchell and Tedford 1973, referred teeth. LACM 4365, left P³; *a*, lingual view; *b*, labial view; *c*, stereophotograph of occlusal view; LACM 17035, possible right P₃ or P₄ of male; *d*, lingual view; *e*, labial view; *f*, stereophotograph of occlusal view; LACM 72733, possible left P₃ or P₄ of female; *g*, lingual view; *h*, labial view; *i*, stereophotograph of occlusal view; *j*, UCMP 86211, stereophotograph of occlusal view of right M¹; LACM 17036, unworn left M₁ lacking roots; *k*, stereophotograph of occlusal view; *l*, lingual view; *m*, labial view; LACM 72383, moderately worn left M₁ lacking anterior root; *n*, lingual view; *o*, labial view; LACM 4574, heavily worn left M₁; *p*, lingual view; *q*, labial view; *Enaliarctos* sp., referred right upper canine crowns; *r*, LACM 72381, possible male; *s*, LACM 30540, possible female; all from LACM locality 1626 (= UCMP locality V7032); all 1.5 x natural size, scale equals 10 mm.

respond with the left M^1 in the holotype skull, but the isolated tooth is 19 percent smaller than the M^1 in the holotype. Disparate sizes of other specimens referred to *E. mealsi* are noted in the following text.

The referral of an isolated left P^4 with a nearly complete crown (LACM 4364) to *E. mealsi* by Mitchell and Tedford (1973:241–242, fig. 15) was based on similarities between that tooth and the broken fourth premolars in the holotype of the species. The isolated P^4 is about 1 mm shorter than those in the holotype, however, and could have belonged to an individual the size of the referred skull, LACM (CIT) 5303.

The referral by Mitchell and Tedford of the isolated right M^2 (LACM 20517) to the species is supported by the shape of the M^2 alveolus in the holotype skull, but should now be qualified by the knowledge that other enaliarctine species, whose second molars are unknown, occur in the same rock unit.

An isolated tooth (LACM 4365) which I identify as a left P^3 of *E. mealsi* (Figs. 2a–c) probably is from an animal comparable in size to the one that had the left P^4 , LACM 4364. The crown of this P^3 is comprised of one main cusp, the paracone, which is shaped much like the same cusp on the P^4 , LACM 4364. The metacone is reduced to a small cusp on the posterior side of the paracone. A cingulum surrounds the entire crown and is elevated into a posterior cingular cusp. The crown bulges slightly posterolingually. The posterior root of the tooth is bilobed, and its lingual lobe is above the posterolingual bulge of the crown. The anterior root is broken off, but was originally of smaller diameter than the posterior one. This tooth was apparently used by Mitchell and Tedford (1973) in the preparation of their figure 17, but was not further described or illustrated.

Mitchell and Tedford (1973:242, fig. 16) referred two isolated left M_1 's to *E. mealsi* based upon their proper occlusal relationships with the P^4 and M^1 in the holotype. I have no reason to doubt these referrals, and refer an additional left M_1 , LACM 72383, to the species. All three of these teeth are probably from smaller individuals than the holotype of *E. mealsi*. It is assumed that in life the paraconid of M_1 occluded with the protocone shelf of P^4 and that the hypoconid of M_1 occluded with the protocone shelf of M^1 (see Mitchell and Tedford 1973:242). None of the three referred M_1 's is large enough to occlude with both upper teeth of the holotype at the same time. All three M_1 's are illustrated here (Figs. 2k–q) to show variation. These teeth resemble the M_1 in a mandible (UCMP 114474) from the Skooner Gulch Formation at Point Arena in northern California. I had previously (Barnes in Phillips, Welton, and Welton 1976:152) identified that mandible as an enaliarctine otariid. I now tentatively identify it as *Enaliarctos* sp. based on the similarities between the M_1 in the mandible and the M_1 's referred to *E. mealsi*.

Two isolated cheek teeth (Figs. 2d–i) from Pyramid Hill (LACM locality 1626) resemble the P_3 or P_4 in the same mandible from Point Arena, and I identify them as P_3 or P_4 of *E. mealsi*. These two teeth are of different sizes. The smaller one, LACM 72733, is 25 percent smaller than the other one, LACM 17035, and is the same size as the P_4 in the mandible (UCMP 114474) from Point Arena. Each tooth has two roots and a crown with three main cusps and a lingual and labial cingulum. The cingulum curves dorsally at the middle of both the labial and lingual sides and at the anterior and posterior ends of the crown.

There is a small posterior cingular cusp. The three main cusps are aligned anteroposteriorly and are apparently homologous with the paraconid, protoconid, and metaconid described on the M_1 of *E. mealsi* by Mitchell and Tedford (1973:242). The paraconid is slightly lingual to the anteroposterior axis of the crown. Anteriorly it is confluent with the cingulum and separated from the protoconid by a deep notch. The protoconid is the largest cusp, and in a manner similar to the same cusp on M_1 , is expanded anteriorly by a larger and posteriorly by a smaller narrow crest. The metaconid is close to the posterior side of the protoconid, and is separated from it by a shallow notch. Compared to the paraconid, the metaconid is smaller, but is higher on the tooth.

Mitchell and Tedford (1973:243) discussed the possibility but did not conclude that the size differences between skulls of *E. mealsi* represented sexual dimorphism. Repenning (1976:379) believed there was no evidence for sexual size dimorphism in *E. mealsi* and suggested that the species did not form rookeries as do Recent gregarious otariid species, in which the males are larger than the females. The referred skull, LACM (CIT) 5303, is approximately 9 percent smaller than the holotype. In the foregoing descriptions I have noted size disparities among some of the teeth referred to *E. mealsi*. An isolated M^1 (UCMP 86211, Fig. 2j) is 19 percent smaller than that on the holotype. The three isolated lower first molars are apparently from smaller individuals than the holotype. One referred P_3 or P_4 (LACM 72733) is 25 percent smaller than another (LACM 17035). Since crowns of mammalian teeth do not increase in size during ontogeny, these size ranges may indicate; 1) that more than one species is represented; 2) that *E. mealsi* teeth exhibited wide individual variability; or 3) that the species was sexually size dimorphic. Among Recent species of Otariidae males are larger than females. The present fossil evidence indicates that sexual dimorphism in *E. mealsi* cannot be ruled out.

Regarding the ontogenetic age of the individual animal represented by the holotype skull of *E. mealsi*, I used the sutures and closure values set out for otariids by Sivertsen (1954). Of nine sutures listed by Sivertsen, only one, number IX, the premaxillary-maxillary suture is not preserved on the holotype. All the other eight areas of sutures are preserved and those sutures show maximum closure for values of four each. The suture age of the specimen, therefore, is a minimum of 32, and this would place it in Sivertsen's Group I, adults. The preserved areas of sutures on the referred specimen (LACM [CIT] 5303) indicate essentially equal maturity, except that the interfrontal suture appears not to be entirely closed.

In this paper I present new reconstructions of the skull of *E. mealsi* (Figs. 16a, 18a, and 20a) that are modified from those of Mitchell and Tedford (1973) on the basis of new material and re-interpretations of previously published specimens. The rostral extremity and canine are based upon *E. mitchelli*, new species, but the facial angle is shown as less, based upon the referred specimen of *E. mealsi* (LACM [CIT] 5303). Based upon observations of the holotype (LACM 4321), I have shown a wider lambdoid crest, a smaller paroccipital process, a notch between the articular surfaces of the condyles ventrally, and no notch in the dorsal articular surfaces. I believe the skull originally had a hamular process of the pterygoid as in other fossil and Recent otariids. The P^3 is based on an isolated tooth LACM 4365.

Enaliarctos mitchelli NEW SPECIES

Figures 3–5, 16b, 18b, 20b

DIAGNOSIS OF SPECIES: A species of *Enaliarctos* differing from *Enaliarctos mealsi* by having a skull with a narrower but higher rostrum, a higher anterior narial opening that is more nearly circular in anterior view, shorter nasal bones, zygomatic arches relatively lower on skull and not as greatly arched at midpoint, ventral surface of zygomatic arch ventral to the infraorbital foramen more nearly horizontal and not as steeply inclined anteriorly, interorbital region relatively narrower, only one pair of posterior palatine foramina, roots of P⁴ relatively closer together and forming a nearly equilateral triangle in ventral aspect, both roots of M¹ anterior to posterior margin of zygomatic arch.

HOLOTYPE: UCMP 100391, anterior half of skull, lacking teeth, collected by Dr. Daryl P. Domning, 6 May 1972.

TYPE LOCALITY: UCMP V6618 (=CIT 481). The specimen was found in a loose rock on the south face of Pyramid Hill. It could have fallen from either of the fossiliferous beds upslope, but the fine grained matrix and reddish bone color match those of specimens that are known to have been collected in the upper fossiliferous concretion-bearing bed, LACM 1628 = UCMP V6916. I believe it came from the upper bed.

PARATYPE: UCMP 80943, palatal remnants of a skull, bearing parts of both canines, collected by Dr. J. Howard Hutchison, 18 May 1968. This specimen was collected from the same locality (UCMP V6618) as the holotype. It has similar adhering lithology and is of similar color and is also presumed to have fallen from the upper fossiliferous concretion-bearing bed, UCMP V6916 (=LACM 1628).

ETYMOLOGY: The species is named in honor of Dr. Edward D. Mitchell, Jr., who stimulated renewed interest in the study of fossil otariids, and who collected and studied some of the specimens that are described in this report.

DESCRIPTION: The anterior end of the holotype skull (UCMP 100391) of *Enaliarctos mitchelli* is broken obliquely through the postorbital region (Fig. 3). It was found in one-half of a concretion by Daryl Domning, and was broken by prior human activity or by natural weathering. The posterior part of the skull has not been located at Pyramid Hill. The specimen lacks teeth, and the anterior margin of the rostrum and parts of the incisor alveoli are weathered away. All sutures in the rostrum are fused, including those bordering the nasal bones. The squamosal-jugal suture on the zygomatic arch was, expectedly, not fused. The animal would undoubtedly be considered to be an adult following Sivertsen's (1954) suture age method.

The paratype (UCMP 80943) of *Enaliarctos mitchelli* is a palate discovered by Howard Hutchison adhering to a piece of concretionary matrix after someone had hammered off the rest of the skull. This palate (Figs. 4–5) is not preserved as far anteriorly as is the holotype, but it does contain parts of both canine teeth and is preserved farther posteriorly. It is otherwise directly comparable with the palate of the holotype. As with the holotype of *E. mitchelli*, all the bones of the paratype are fused, obliterating the sutures, and it is also believed to have been from an adult individual.

The following description is partly a composite based upon both the holotype, UCMP 100391, and the paratype, UCMP 80943, which reveal the anatomy of the skull from the tip of the snout to the postorbital area. The skulls of *E. mitchelli* are both smaller than the holotype and referred skulls of *Enaliarctos*

mealsi. With the present specimens, I cannot definitely determine the sex of either skull of *E. mitchelli*, nor determine if this species was sexually dimorphic; however, the small canine of the paratype is consistent for that of a suspected female dimorph (see Table 2).

E. mitchelli differs from *E. mealsi* in having a rostrum that is relatively wider and deeper dorsoventrally. These differences result in its having a more circular external bony narial opening that is higher than wide. The referred skull (LACM [CIT] 5303) of *E. mealsi*, conversely, has a narial opening that is wider than high. The nasal bones of *E. mitchelli* do not extend as far anteriorly nor do they slope as steeply anteroventrally as in *E. mealsi*. Fusion has obscured the sutures surrounding the nasal bones, so it is impossible to see if they contact the frontals posteriorly in the same manner as in *E. mealsi*. Compared with *E. mealsi*, the lateral margins of the narial opening are more steeply inclined in *E. mitchelli*, giving the latter a more blunt snout in lateral view. Its facial angle (as defined by Repenning, Peterson, and Hubbs 1971) is undoubtedly less than in the referred specimen of *E. mealsi*, but the latter is not complete enough to make such a measurement. In *E. mealsi*, the maxillae bow outward on the lateral surfaces of the rostrum more than in *E. mitchelli*. I am convinced that these differences in rostral shape are actual and are not caused by geologic distortion.

The zygomatic arches depart from the skull in a manner different than in *E. mealsi*. Compared with the latter, the anterior end of the zygomatic arch in *E. mitchelli* makes a more acute angle in the horizontal plane where it joins the skull, and curves less dorsally in the sagittal plane at its midpoint. Consequently the postorbital process of the jugal is lower on the skull in *E. mitchelli* (compare Figs. 18a and 18b). The orbit of *E. mitchelli*, therefore, faces more laterally and is positioned lower on the skull than in *E. mealsi*. The nasolabialis fossa, described by Mitchell and Tedford (1973:232, 234) on the side of the snout anterior to the orbit of *E. mealsi*, is more pronounced in *E. mitchelli*. Consistent with the different slope of the lateral surface of the snout, the surface of the nasolabialis fossa is oriented more vertically in *E. mitchelli*. The antorbital process bordering the posterior margin of the fossa, and the eminence at the anterior margin of the fossa are both larger than in *E. mealsi*.

The dorsal surface of the skull upon the nasal bones and anterior to the sagittal crest is flatter, shorter, and proportionally wider than on the skull referred to *E. mealsi*. The intertemporal constriction is relatively narrower, and the sagittal crest, while present, is lower than in *E. mealsi*.

The interorbital septum of the holotype of *E. mitchelli* was entirely broken away prior to fossilization. The lacrimal foramina are also missing. The orbital aperture of the posterior palatine foramen is in a position slightly anterior of its location on the holotype of *E. mealsi*. The opening of the infraorbital foramen within the orbit in *E. mitchelli* is floored by a relatively wider and flatter surface of the maxilla than in the holotype of *E. mealsi*, but is more like the structure in the skull (LACM [CIT] 5303) referred to *E. mealsi* by Mitchell and Tedford (1973).

The palate of both the holotype and paratype of *E. mitchelli* may be compared with both the holotype and referred skull of *E. mealsi*, and there are several differences between the two species. Of the teeth, only P⁴ and M¹ are preserved in place on specimens of *E. mealsi*, and only the canines are known for *E. mitchelli*. Both specimens of *E. mitchelli* are smaller than those of *E. mealsi*. The species are similar in both having heterodont dentition, a

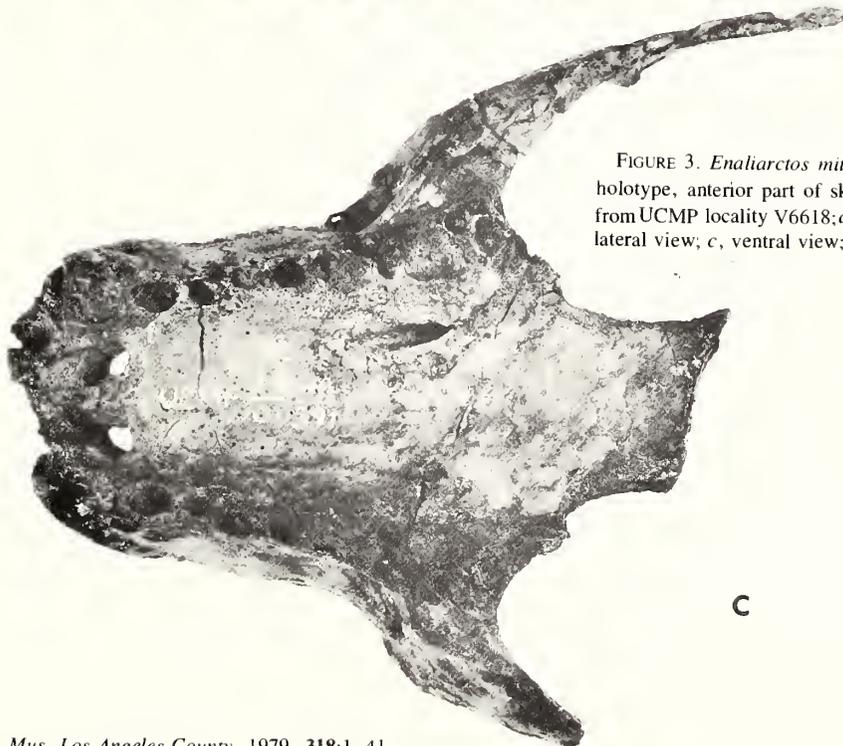
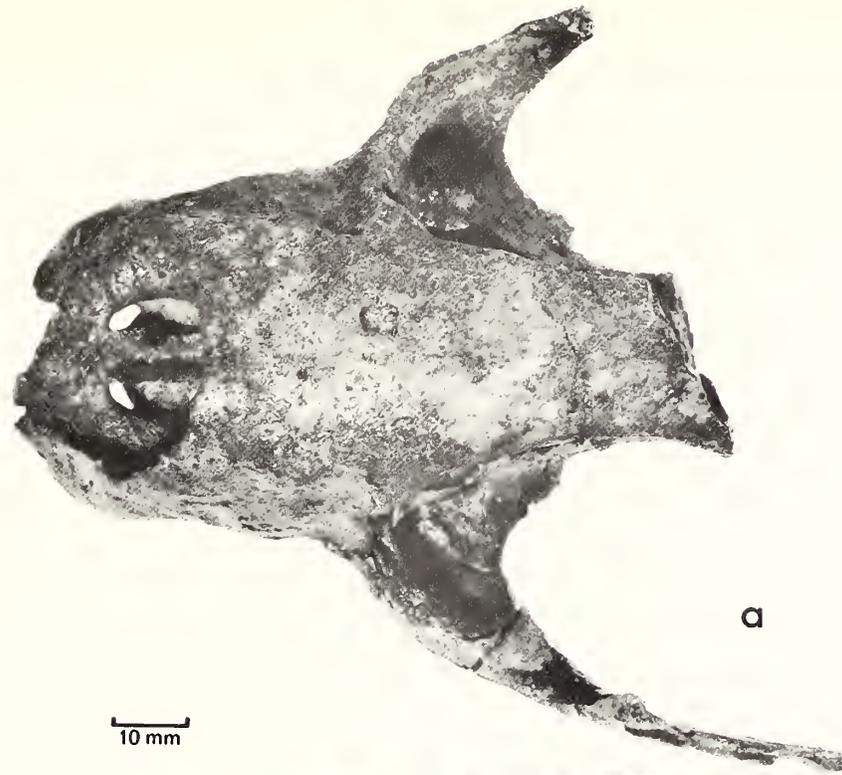


FIGURE 3. *Enaliarctos mitchelli*, new species, holotype, anterior part of skull, UCMP 100391 from UCMP locality V6618; a, dorsal view; b, left lateral view; c, ventral view; natural size.



FIGURE 4. *Enaliarctos mitchelli*, new species, paratype, palate with canines, UCMP 80943 from UCMP locality V6618, ventral view, natural size.

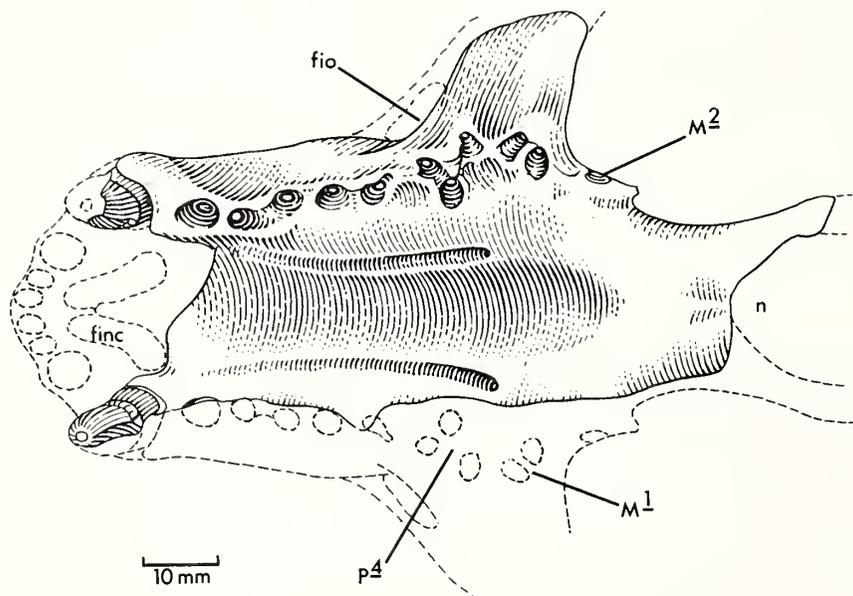


FIGURE 5. *Enaliarctos mitchelli*, new species, paratype, palate with canines, UCMP 80943 from UCMP locality V6618, ventral view with rostral extremity restored from holotype, UCMP 100391, natural size. Abbreviations: *finc* — incisive foramen; *fio* — anterior end of infraorbital foramen; *n* — posterior narial opening; *P*⁴, *M*¹, *M*² — alveoli for fourth upper premolar and first and second upper molars, respectively.

TABLE 1

Differences between *Enaliarctos mealsi* Mitchell and Tedford 1973 and *Enaliarctos mitchelli* new species.

<i>Enaliarctos mealsi</i>	<i>Enaliarctos mitchelli</i>
1. Four posterior palatine foramina on each side of palate.	1. One foramen on each side of palate.
2. Ventral surface of zygomatic arch beneath infraorbital foramen is inclined antero-dorsally and lacks fossa.	2. Surface more horizontal, with fossa
3. Anterior narial opening wide and low, nearly oval in anterior view.	3. Anterior narial opening higher, nearly circular in anterior view.
4. Lateral (cheek) surface of maxilla strongly convex.	4. Lateral surface more vertical, less convex.
5. Posterior border of zygomatic arch joins palate opposite middle of M ¹ .	5. Posterior border joins palate opposite space between M ¹ and M ² .
6. Rostrum flattened dorsoventrally.	6. Rostrum arched dorsoventrally.
7. Posterolabial root of P ⁴ widely separated from the other two roots.	7. Three roots of P ⁴ nearly equidistant and forming nearly equilateral triangle.
8. Nasal bones slope anteroventrally.	8. Nasal bones not sloping, nearly horizontal.
9. Zygomatic arch has continuous dorsal curvature in lateral view.	9. Zygomatic arch flatter, not curved dorsally as much as in <i>E. mealsi</i> .

fossa on the palate between P⁴ and M¹ to receive the crown of the lower carnassial, a posteriorly projecting palatine process, and a constricted posterior palatal extension surrounding the posterior nares. An upper carnassial is inferred but not proven to exist in *E. mitchelli*. As in *E. mealsi*, the palate narrows anteriorly and is transversely arched between the cheek tooth rows. Both species have a median eminence at the posterior end of the palate directly anterior to the posterior narial opening.

The holotype of *E. mealsi* has four posterior palatine foramina on each side of the palate (see Mitchell and Tedford 1973:figs. 5a, 17c). In that species the anterior-most foramen on each side is the largest. It is located medial to the anterior edge of P⁴ and is continuous with an elongate, anteriorly directed palatine sulcus. On both specimens of *E. mitchelli*, there are no smaller posterior palatine foramina; only the one large one (Fig. 5) on each side of the palate that is supposedly homologous with the anterior-most foramen in *E. mealsi*. On both specimens of *E. mitchelli*, the foramina are located farther posterior, being medial to the anterior edge of M¹. There is, obviously, no way to test the significance of this difference in position, but it is consistent in both specimens of *E. mitchelli*. As in *E. mealsi*, each foramen in *E. mitchelli* is continuous anteriorly with a palatine sulcus, which is longer and deeper in the paratype of *E. mitchelli* (UCMP 80943) than in the holotype of the species. The sulcus ends medial to P².

The relationships between the ventral parts of the zygomatic arches and the palates differ between the two species of *Enaliarctos*. On both specimens of *E. mitchelli*, the ventral surface of the zygomatic portion of the maxilla ventral to the infraorbital foramen is more nearly in the same plane as the palate than in *E. mealsi*. Also the ventral surface of the zygomatic arch does not rise dorsolaterally from the side of the skull at such a steep angle as in *E. mealsi*. Lateral to the space between P⁴ and M¹ in *E.*

mitchelli, there is a fossa on the ventral side of the zygomatic arch. This fossa is adjacent to the cheek tooth row. In *E. mealsi* there is no such fossa, and on both known skulls of that species, the uninterrupted ventral surface of the zygomatic arch rises abruptly anterodorsally toward the ventral lip of the infraorbital foramen.

Although no cheek teeth are known for *E. mitchelli*, most of the alveoli for the cheek teeth of both known specimens are in the same positions as on both specimens of *E. mealsi*. The left cheek tooth row on the paratype (UCMP 80943) contains well-preserved alveoli for P¹⁻⁴ and M¹⁻². The following description is based on both that specimen and the holotype (UCMP 100391). The alveolus for P¹ is 2 mm posterior to the canine alveolus, procumbent, and about 4 mm in diameter. P¹ had a single large, round root. P²⁻³ each had two roots aligned in the anteroposterior axis of the cheek tooth row. The two widely diverging roots of P² span approximately 10 mm across their maximum anteroposterior dimension. The anterior root was longer than the posterior one. The two roots of P³ were similarly spread, but on this tooth the posterior root was the longer of the two. P⁴ had three roots, of which the labial two are in the anteroposterior axis of the cheek tooth row. The medial or protocone root of this tooth on the paratype (UCMP 80943) is larger than the two labial roots and is oval-shaped, being expanded in a transverse plane. The three roots of P⁴ on the holotype (UCMP 100391) are of nearly equal size.

There are major differences between the two species of *Enaliarctos* in the positions of roots of P⁴. Compared with both specimens of *E. mealsi*, both specimens of *E. mitchelli* have the three roots of P⁴ relatively closer together and their alveoli are arranged on the palate in a more nearly equilateral triangle (compare Figs. 20a and 20b). This is due to the slightly more posterior

position of the medial or protocone root, and a more antero-medial position of the posterior or talon root in *E. mitchelli*. The striking differences in the P⁴ roots of the two species are very evident when the isolated P⁴ (LACM 4364) referred to *E. mealsi* is compared with the alveoli of either specimen of *E. mitchelli*. It may be implied from the positions of the alveoli for the roots, that the P⁴ in *E. mitchelli*, in comparison with that in *E. mealsi*, had a crown that was relatively smaller, more triangular in occlusal view, and probably less like a carnassial.

In *E. mitchelli*, the posterior labial root of P⁴ and the anterior root of M¹ are not positioned as far laterally upon the base of the zygomatic arch as in *E. mealsi* (see Fig. 20). The more medial location of these labial alveoli demonstrates that in *E. mitchelli* the tooth row was in a straighter line than in *E. mealsi*. Modern otariinae have nearly straight cheek tooth rows, and the approach toward this condition in *E. mitchelli* indicates an apparent increase in aquatic adaptation.

In *E. mitchelli*, M¹ had two roots, the posterior one of which was located lingual to the anteroposterior axis of the cheek tooth row. The posterior root was bilobed as shown by the shape of its alveolus, and was probably formed by the fusion of the originally separate lingual and posterior labial roots. The separate, anterior labial root was circular in cross section. The shapes and evolutionary origin of the roots of M¹ are presumably the same as described in preceding text for *E. mealsi*.

M² was apparently very small and had a single, bilobed root measuring only 4 mm by 2 mm. It was located at the margin of the palate near the posterior palatine process.

Parts of both canines are preserved on the paratype of *E. mitchelli* (UCMP 80943), and between these two teeth only the proximal anterior part of the crown is not represented. The canine is relatively small, slightly compressed transversely, and has a somewhat recurved conical crown. The complete tip of the right canine is preserved and it is conical with a flat wear facet at its apex. On the posterior side of the crown a vertical crest extends from near the apex proximally to meet the cingulum. The cingulum extends anteriorly to the middle part of the lingual side of the crown. At that point the cingulum ends and merges with another vertical crest that extends half way toward the apex on the lingual side of the crown. On the anteromedial side of the right canine, and interrupted by a break, is a slight vestige of a wear facet that was caused by occlusion with the lower canine. The enamel is smooth and is relatively thin. The overall structure of these canines of *E. mitchelli* is similar to canines of modern Otariinae, especially *Zalophus californianus* (Lesson 1828), but differs from canines of *Allodesmus* spp. which have procumbent, conical crowns that lack vertical crests and have thick, finely rugose enamel.

Enaliarctos sp.

Figures 2 r-s

REFERRED SPECIMENS: LACM 30540, crown of right upper canine collected by E.D. Mitchell, J.H. Lipps, and H. Meals, 26 February 1961; LACM 72381, incomplete crown of right upper canine collected by E.D. Mitchell, 1961 or 1962; both from LACM locality 1626, a locality west of Pyramid Hill correlated with the "grit zone" on the south face of Pyramid Hill.

DESCRIPTION: These two fragmentary canines represent a large (LACM 72381) and a small (LACM 30540) individual. Both are similar in morphology and both are from the same local-

ity (LACM I626 = UCMP locality V7032) that produced the isolated cheek teeth referred to *Enaliarctos mealsi* in the present paper, and by Mitchell and Tedford (1973). This locality was correlated by Mitchell and Tedford (1973:Fig. 2) with the lower fossil-bearing bed in the "grit zone" on the south face of Pyramid Hill, the probable source of the holotype of *E. mealsi*. These two canines may actually belong to *E. mealsi*, but there is no way to prove this with the known fossils. They resemble the canines of the paratype of *Enaliarctos mitchelli*, and for the purposes of the present study I identify them only as *Enaliarctos* sp. I have included their morphology in the restorations of both *E. mealsi* and *E. mitchelli* (Fig. 18a, b). The canines of these two species were probably similar, if not essentially identical.

Both canine crowns resemble those of the paratype (UCMP 80943) of *E. mitchelli* by being conical, slightly recurved, and by having an irregular posterolingual cingulum that extends between the proximal ends of both a posterior and a medial vertical crest. Both canines have a vertically oriented wear facet on the distal anteromedial part of the crown caused by shearing occlusion with the posterior side of the lower canine. The wear facet on the larger canine, LACM 72381, is faint, but that on the smaller canine, LACM 30540, is more extensive and extends entirely through the enamel. The enamel on both of these canines is relatively thin. The enamel surface is nearly smooth with only slight irregularities.

The smaller of these two canines is approximately the size of the upper canines rooted in the palate of the paratype of *E. mitchelli* (see Table 2). These small canines are 20 to 32 percent smaller than the larger canine, LACM 72381. This disparity in canine size reinforces my previous suggestion, based upon cheek teeth referred to *E. mealsi*, that species of *Enaliarctos* may have been sexually size dimorphic.

Pinnarctidion NEW GENUS

DIAGNOSIS OF GENUS: A genus of the subfamily Enaliarctinae differing from *Enaliarctos* by having a skull with narrower interorbital region, larger orbit, larger antorbital processes, external openings of optic foramina located more ventrally and posteriorly, wider and flatter palate, larger infraorbital palatal plate of maxilla, cheek teeth proportionally smaller and more widely spaced, no embrasure pit for M₁ on palate between P⁴ and M¹, protocone shelf of P⁴, smaller and positioned more posteriorly on the tooth, anterolabial corner of M¹ reduced, posterior narial opening wider and lower, strut between palate and braincase deeply concave lateral to pterygoid hamulus, tympanic cavity larger, paroccipital process larger and joined to mastoid process by large paroccipital-mastoid crest, and occipital condyles more widely separated dorsally.

TYPE SPECIES: *Pinnarctidion bishopi*, new species.

ETYMOLOGY: *Pinna*, Latin, fin; *arktos*, Greek, bear; *idion*, Greek diminutive suffix; in reference to the apparent ursid or arctoid affinities of the subfamily to which this genus of small, aquatic carnivores belongs.

Pinnarctidion bishopi NEW SPECIES

Figures 6-15, 17a, 19a, 21a

Enaliarctos mealsi, part. Mitchell and Tedford 1973:229-232, 237-241, figs. 13, 14 (LACM (CIT) 5302, natural endocranial cast).

TABLE 2

Measurements (in mm) of canine tooth crowns of *Enaliarctos mitchelli* new species, and *Enaliarctos* sp. Estimated measurements are indicated by parentheses.

	<i>Enaliarctos mitchelli</i> both sides, possible female UCMP 80943 Paratype	<i>Enaliarctos</i> sp. LACM 30540 possible female	<i>Enaliarctos</i> sp. LACM 72381 possible male
Anteroposterior diameter at base of enamel	8.5	8.4	12.4
Transverse diameter at base of enamel	7.2	7.1	9.8
Total crown height	(14.2)	16.0	(20.0)

DIAGNOSIS OF SPECIES: Because the genus *Pinnarctidion* only contains one known species, the diagnoses of the genus and of the type species are identical.

HOLOTYPE: UCMP 86334, skull with left P⁴ and M¹, roots of left P³ and M², lacking anterior end of the rostrum, the right zygomatic arch, the right occipital condyle, and fragments of bone from the dorsal surface of the cranium, collected by Richard C. Bishop, November 1968. The specimen was found in a badly weathered nodule, and the natural matrix endocranial cast was free. The natural endocranial cast was molded and plaster reproductions were made of it, then the nodule was reassembled and I removed the surrounding matrix from the skull. A reproduction of the natural endocranial cast is catalogued under the same number in UCMP with the holotype.

TYPE LOCALITY: UCMP V6916 (= LACM locality 1628). The skull was collected in place from the upper fossiliferous concretion-bearing bed on the south face of Pyramid Hill. The adhering matrix is fine grained and the bone is reddish colored.

REFERRED SPECIMEN: LACM (CIT) 5302, natural endocranial cast with some bone adhering. This specimen was previously referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973). It was collected by the late Dr. Chester Stock in 1950 from CIT locality 481, as a loose specimen on the south face of Pyramid Hill, and its precise stratigraphic source is uncertain. The bone color and adhering matrix are like those of the holotype, and this specimen was possibly derived from the upper bed also.

ETYMOLOGY: The species name honors Mr. Richard C. Bishop. His father, the late Mr. Charles Bishop, Richard Bishop, and his sons, Charles, Patrick, Larry and Steve, three generations of one family, have collected from marine rocks in the vicinity of Bakersfield, California, many important fossils that are now in museum collections.

DESCRIPTION: The holotype skull (UCMP 86334) of *Pinnarctidion bishopi* was found in a weathered nodule that was cracked and partly exfoliated. Pre-depositional weathering of the concretion had removed part of the right side and the rostral extremity. Of the nine suture areas listed by Sivertsen (1954:11)

for age analysis, at least four and probably five exhibit maximum closure. The suture age based on eight preserved sutures of the nine listed, totals a suture age of at least 23, which would classify the animal as an adult, Group I, in Sivertsen's (1954:13) scheme. The presence of at least three open sutures, however, indicates this individual was younger than the ones described previously for *Enaliarctos mealsi* and *Enaliarctos mitchelli*.

The skull of *Pinnarctidion bishopi* is broad and low with a relatively large brain case, small snout, elongate interorbital region, and large orbits. The rostrum is not complete, but its profile in lateral view is not as high as in *E. mitchelli*, and is more like the low profile of *E. mealsi*. The original shape of the anterior narial opening is not discernible due to poor preservation, but appears to have been broad and relatively smaller than in species of *Enaliarctos*. The rostrum is fairly narrow and its sides are not bowed outward as in *Enaliarctos* spp. The nasal bones are almost entirely broken away, and their relationships to the frontals and maxillae are unknown. There are some interdigitating sutures on the top of the rostrum where the maxillae meet the frontals above the anterior edge of the orbit.

There is a nasolabialis fossa on the lateral surface of the rostrum anterior to the orbit as in both *E. mealsi* and *E. mitchelli*. The antorbital process (or lacrimal process) at the posterior edge of this fossa is larger, however, than in both species of *Enaliarctos*. The infraorbital foramen is continuous anteriorly with an elongate, double-grooved fossa dorsal to and paralleling the margin of the cheek tooth row. There is a relatively much smaller fossa in the same position in *Enaliarctos* spp., and it is not divided into two grooves.

The interorbital region of *P. bishopi* is comparatively narrower than in the holotype of *E. mealsi*. Along the midline, the frontals are split by a sagittal fissure that is up to 5 mm deep and extends along the interfrontal suture from the nasal bones to the anterior margin of the brain case. This fissure may be an anomaly or may be an artifact of preservation, but similar, relatively smaller fissures are present on some specimens of modern otariids, particularly adult males of *Otaria byronia* (de Blainville 1820) and females of *Eumetopias jubata* (Schreber 1776). There is a small

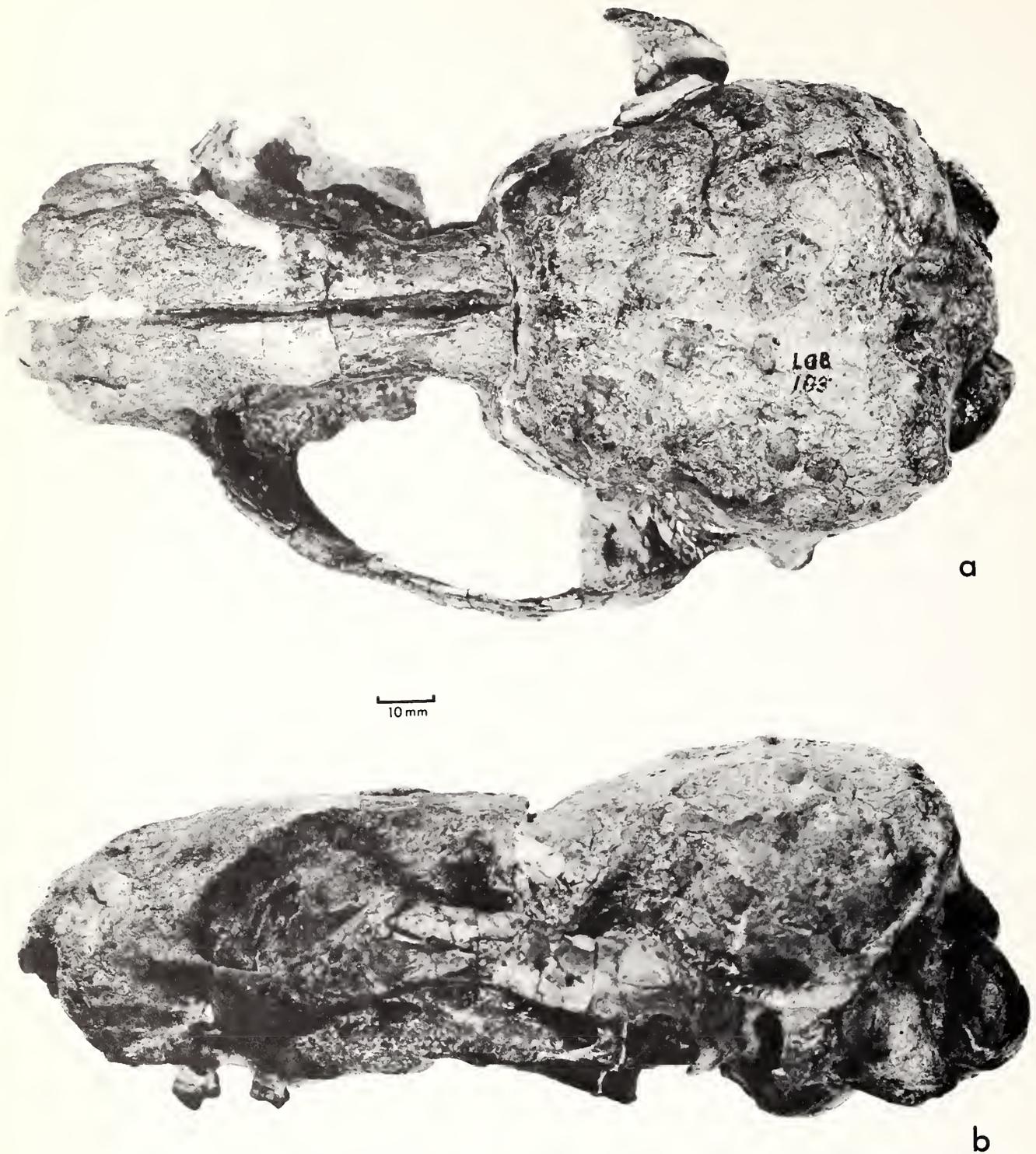


FIGURE 6. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916, a, dorsal view; b, left lateral view; natural size.

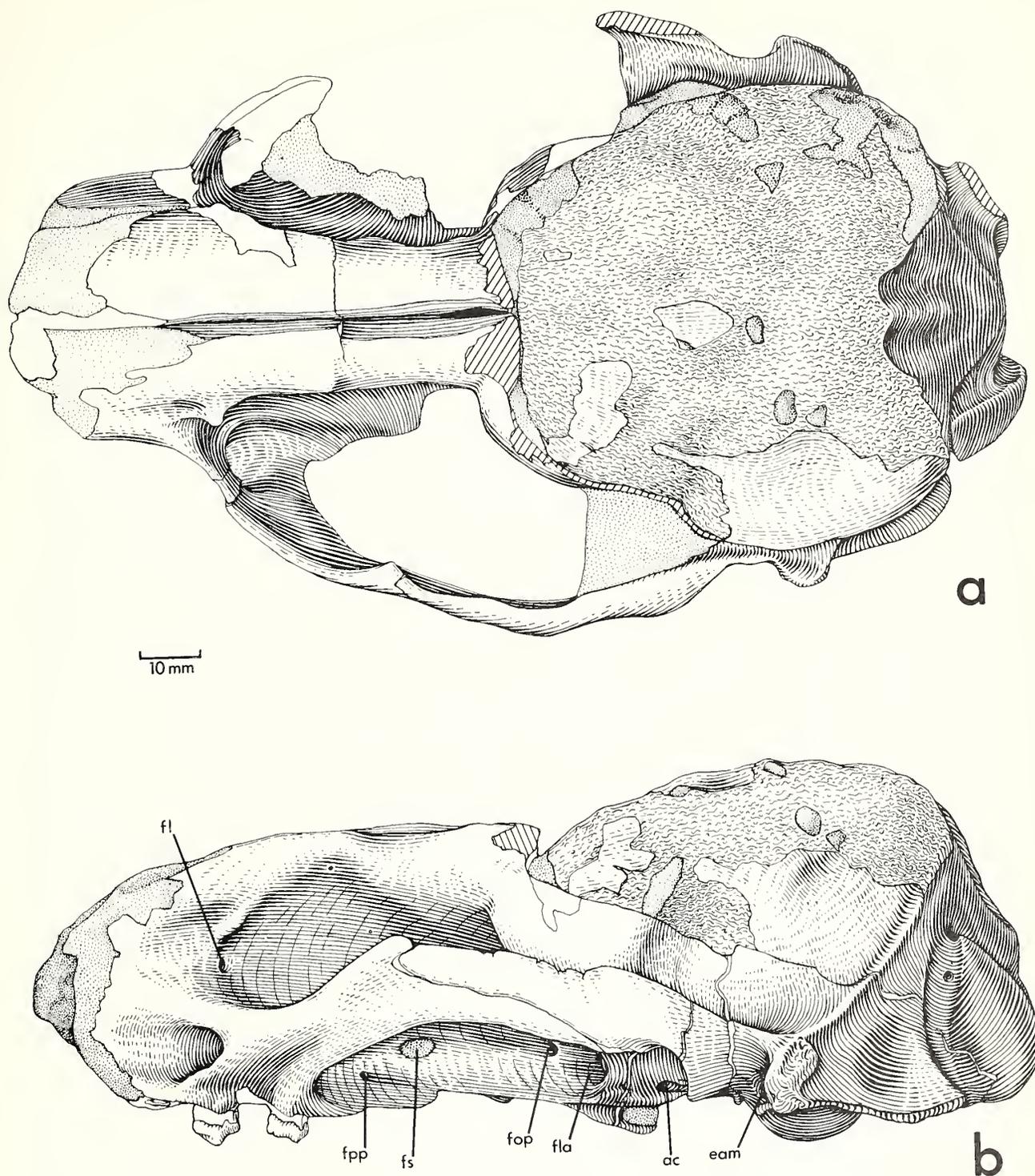


FIGURE 7. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916; *a*, dorsal view; *b*, left lateral view; natural size. Abbreviations: ac — posterior end of alisphenoid canal; eam — external acoustic meatus; fl — lacrimal foramen; fla — anterior lacerate foramen, anterior end of alisphenoid canal is in the same recess; fop — optic foramen; fpp — posterior end of canal from posterior palatine foramina; fs — sphenopalatine foramen.

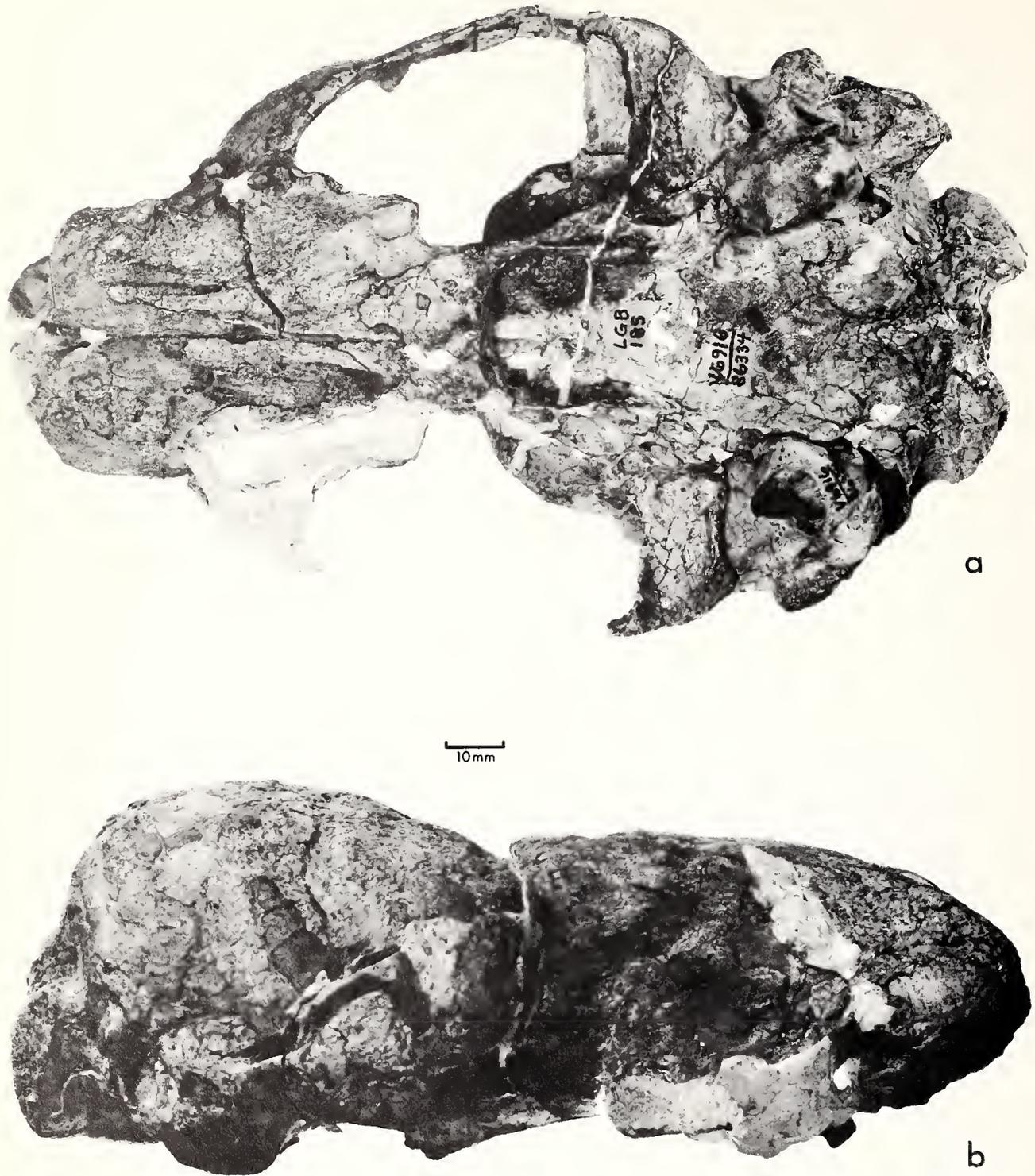


FIGURE 8. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916; *a*, ventral view; *b*, right lateral view; natural size.

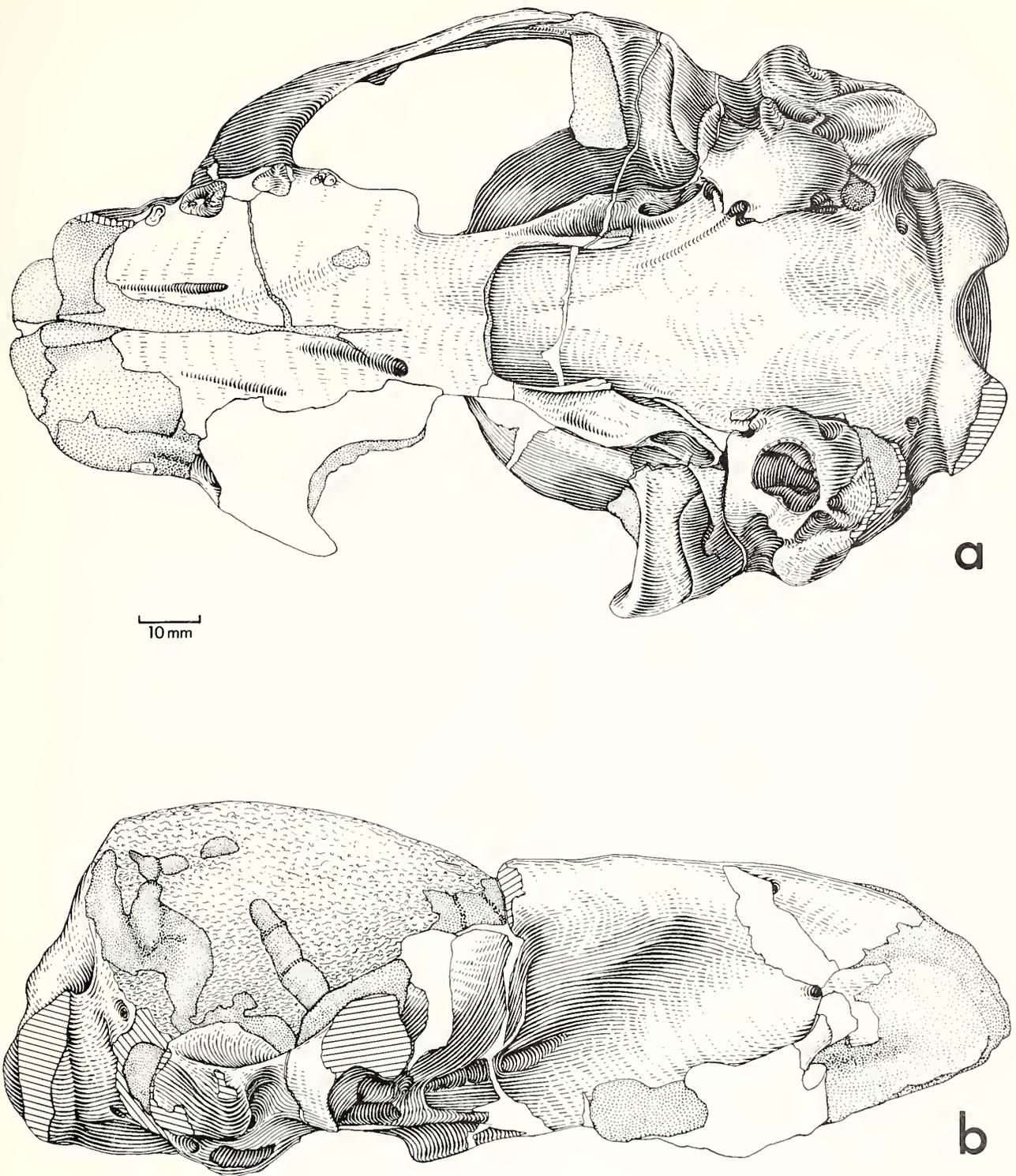


FIGURE 9. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916; a, ventral view; b, right lateral view; natural size.

supraorbital process, approximately the size of that of *Enaliarctos*, but located relatively farther posteriorly as in *Allodesmus* spp. On the right side of the interorbital region of the holotype of *P. bishopi* there is another small process posterior to the supraorbital process, and this is anterior to a fossa. These are only present on the right side and may be pathologic or anomalous.

The brain case is joined to the interorbital region differently in *E. mealsi* and *P. bishopi*. In *P. bishopi*, a sharper angle is formed by the junction between the interorbital region and the brain case than on the holotype of *E. mealsi*. The brain case of *P. bishopi* is proportionally broader across its anterior part, and the anterolateral corners of the brain case in the temporal fossae are more prominent. In *E. mealsi* the anterolateral corner of the brain case is low within the temporal fossa and the dorsal surface of the interorbital region slopes ventrolaterally toward it. In *P. bishopi* the anterolateral corner of the brain case is relatively higher, being nearly as high as the top of the interorbital region, the surface of which slopes only slightly laterally onto the brain case.

There is no indication of a sagittal crest in *P. bishopi*, but most of the surface of the brain case has been broken off. Along the midline of the brain case, the surface is elevated above the dorsal surface of the interorbital region, the reverse of the condition in *E. mealsi* in which the interorbital region is higher than the brain case. The top of the brain case in *P. bishopi* is irregular and relatively broader than in *E. mealsi*. The surfaces of the parietals in *P. bishopi* follow the contour of the brain and are not raised into a prominent lambdoidal crest as in *E. mealsi*. The supraoccipital is similarly shaped in both species, however it is lower and broader in *P. bishopi*. Both species have a prominent, vertically-oriented fossa on either side of the midline of the supraoccipital below the lambdoidal crest, a prominent strut extending from near the medial side of each condyle to the lamb-

doidal crest, and a deep fossa dorsal to the occipital condyle (Fig. 10). Both species have a prominent medial tuberosity on the supraoccipital at the dorsal margin of the foramen magnum, but this appears smaller in *E. mealsi* because it apparently has been partly chipped away.

In *P. bishopi* the occipital condyles are proportionally more widely spaced and are more divergent dorsally than in *E. mealsi*, in which the medial margins of the condyles are nearly parallel. With the present fossil sample, it is impossible to know whether these differences in the orientation of the condyles have taxonomic significance or represent individual variation as I have suggested (Barnes 1972) is the case in *Allodesmus kernensis*. The condyloid foramina of *P. bishopi* are in about the same location as in the holotype of *E. mealsi*, but are bilaterally asymmetrical. The right condyloid foramen is approximately 2.4 mm wide by 4.5 mm high. The left condyloid foramen is recessed more deeply within the foramen magnum, and is only about 1.5 mm in diameter. In *P. bishopi*, the intercondyloid incisure is approximately as wide as in *E. mealsi*, but is not as deep. In conformity with this shallower incisure, the articular surfaces on the condyles of *P. bishopi* do not curve as far anteriorly on their ventral and lateral sides as in *E. mealsi*. The condyles of *P. bishopi* do not project as far from the occipital shield as in *E. mealsi*, but are more distinctly demarcated ventrally from the basioccipital by a straight transverse sulcus (see Fig. 9a).

The surface of the exoccipital flares anteriorly and ventrolaterally toward the mastoid process (Fig. 7b) in a manner typical of modern Otariinae. The paroccipital process, however, is relatively larger than in otarine species, and is connected to the mastoid process via a large, flattened, paroccipital-mastoid crest. In contrast, the paroccipital process of *E. mealsi* is a small tuberosity and is joined to the mastoid process by only a low, rounded

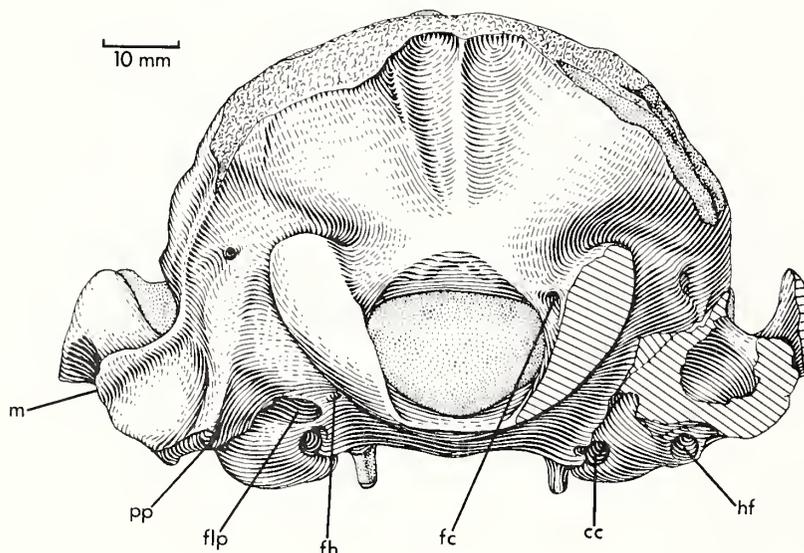


FIGURE 10. *Pinnarctidion bishopi*, new genus and species, holotype, skull, UCMP 86334 from UCMP locality V6916, posterior view, natural size. Abbreviations: cc — posterior carotid foramen; fc — condyloid foramen; fh — hypoglossal foramen; flp — posterior lacerate foramen; hf — tympanohyal pit; m — mastoid process; pp — paroccipital process.

crest. The lateral extension of the paroccipital-mastoid crest of *P. bishopi* enhances the large fossa dorsal to it in the lateral part of the exoccipital. The posterior-most margin of the paroccipital process is directed posteriorly and ventrolaterally, and is separated from the occipital condyle by a wide gap. Because the sutures are fused, it is not known in what proportion the squamosal and exoccipital bones contribute to the formation of the paroccipital process.

The entire structure of the paroccipital-mastoid crest is similar to, but proportionally larger than, the same structure in the modern California sea lion, *Zalophus californianus*, and in the fossil fur seal, *Thalassoleon mexicanus* Repenning and Tedford 1977. In *Allodesmus kernensis* both the paroccipital and mastoid processes are large, however, the crest connecting them is small.

The zygomatic arch of *P. bishopi* is positioned relatively closer to the skull than in *E. mealsi*, and in this respect more closely resembles the condition in *E. mitchelli*, as far as preserved in known specimens (compare Figs. 16a, b, and 17a). In *P. bishopi* the temporal fossa is more constricted posteriorly. This is partly because the brain case is more expanded laterally, and partly because the zygomatic arch does not curve so widely away from the skull, compared with *E. mealsi*. The zygomatic arch of *P. bishopi* is also lower on the skull and does not arch so high at midpoint, resembling *E. mitchelli*. The differences in the shape of the zygomatic arch are associated with the more lateral orientation of the orbit in *P. bishopi* than in *E. mealsi*.

The anterior part of the zygomatic arch that is dorsal to the infraorbital foramen is narrower and more vertically inclined than in either species of *Enaliarctos*. It is neither flared outward as in modern Otariinae, nor retracted and rounded as in *Allodesmus* spp. The anterior surface of the postorbital process of the jugal is inclined at approximately the same angle as in both species of *Enaliarctos*, but the process is relatively more expanded antero-posteriorly. The jugal extends posteriorly ventral to the squamosal as a thin, but relatively dorsoventrally deep process that reaches the anterolateral corner of the glenoid fossa.

The anterior end of the zygomatic process of the squamosal is unique among otariids in its shape and in its relationships with the jugal (see Fig. 7b). In *Enaliarctos* spp. and in species of Otariinae, as in fissiped carnivores, the part of the zygomatic process of the squamosal that is in contact with the jugal tapers anteriorly to a sharp point, and in nearly all individuals and taxa the squamosal does not touch the postorbital process of the jugal. In *P. bishopi*, the squamosal does not taper anteriorly, but ends in a blunt, vertically expanded tip. It not only touches the postorbital process of the jugal, but fits into the notch on its posterior side. This type of articulation was called "mortised" by Mitchell (1968:table V), and is more greatly developed in *Allodesmus* spp. and to a slightly lesser degree in species of Phocidae in which both the postorbital process of the jugal and the zygomatic process of the squamosal are more expanded dorsoventrally.

The margins of the round orbit form a circle approximately 37 mm in diameter. An antorbital (or lacrimal) process is at the anterior edge of the orbit. This process is not as broad-based as the same process in *Enaliarctos* spp., but protrudes farther from the side of the skull. Between this process and the dorsal surface of the zygomatic arch is a broad gap (not a lacrimal fossa) in the otherwise sharply defined border of the orbit. At this gap, the lateral surface of the rostrum is nearly continuous with the medial wall of the orbit. *E. mealsi* differs by having a well defined orbital crest marking this edge of the orbit. In *P. bishopi*, the

opening of the lacrimal canal is approximately 2 mm in diameter, and is located just within the margin of the orbit below the antorbital process.

The lateral extension of the palate is a much flatter and more extensive shelf beneath the orbit and posterior to the infraorbital foramen than in *Enaliarctos* spp. The ventral surface of the orbital opening of the infraorbital foramen is wide and nearly flat.

The medial wall of the orbit is flatter but more recessed than in *Enaliarctos* spp. The opposite walls of both orbits are more parallel than in *Enaliarctos* spp. and converge as closely as 6 mm apart posteriorly. On each side of the holotype of *P. bishopi*, there is a small perforation about 7 mm in diameter in the medial wall of the orbit. This may be homologous with the large orbital vacuities that are characteristic of more modern pinnipeds. Below this perforation and extending posteriorly from the dorsal margin of the infraorbital foramen is a prominent ridge. This ridge marks the medial margin of the infraorbital shelf of the maxilla, and is more prominent and more horizontal than a similar ridge in *E. mealsi* (see Mitchell and Tedford, 1973:222). Below this ridge in *P. bishopi* is the posterior opening of the posterior palatine foramen which is 2 mm in diameter. The foramen enters the bone in an anterior direction. Posterodorsal to this, at the posterior end of the ridge, is the exceptionally large sphenopalatine foramen. The left sphenopalatine foramen measures 7 mm wide and 4 mm high (see Fig. 17b).

The medial wall of the orbit abruptly meets the nearly vertical anterior wall of the brain case. The oblique crest in the postero-dorsal part of the orbital region that merges with the brain case is more prominent and more dorsally located than on the holotype of *E. mealsi*. There is an ethmoidal foramen below the posterior part of this crest in approximately the same location as in *E. mealsi*. The palate is wide and nearly flat, being arched neither anteroposteriorly nor transversely as much as in *Enaliarctos* spp. Compared with *E. mealsi*, the bony palate extends as far posteriorly relative to the anterior wall of the brain case, but is relatively wider and flatter posteriorly. In the place of the small posterior palatine processes of both species of *Enaliarctos*, *P. bishopi* has a wide, thin, squared posterolaterally projecting shelf of the palate beneath each orbit.

The posterior palatine foramina and their associated palatine sulci are more randomly positioned and variably developed than in either known species of *Enaliarctos*, and in this respect *P. bishopi* resembles *Allodesmus packardii*. On the left side of the palate of *P. bishopi*, the largest posterior palatine foramen is located medial to P⁴, slightly posterior to the location of such a foramen in *E. mealsi*, and a deep sulcus extends anteriorly from it. Posterior to this, medial to M², there are at least two sulci that may be associated with smaller foramina, but incomplete preservation of the palate there obscures the evidence. On the right side of the skull of *P. bishopi* there are two much larger foramina associated with sulci. One is medial to M² and the other is farther posterior.

Compared with the deep embrasure pit in species of *Enaliarctos* for the crown of M₁ in the palate between P⁴ and M¹, there is only a slight cavity in *P. bishopi*. This implies a reduced carnassial function of the lower teeth. The palate bears a small median tuberosity at its posterior margin, and this projects slightly posteriorly beneath the internal narial opening. The palatal or ventral margin of the internal narial opening is wider and less curved than in *Enaliarctos* spp. The ventral part of the

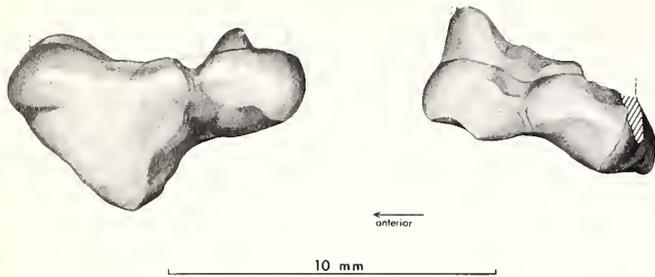


FIGURE 11. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, left P⁴ and M¹, labial view, slightly larger than 4 x natural size.

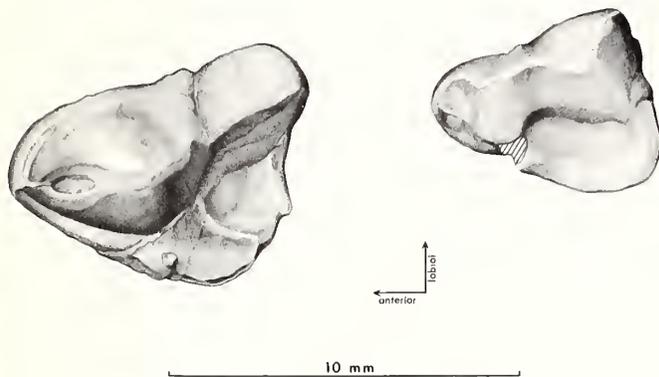


FIGURE 12. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, left P⁴ and M¹, occlusal view, slightly smaller than 5 x natural size.

zygomatic arch attaches to the rostrum spanning between the anterior root of P⁴ and the space between M¹ and M² (see Fig. 9a). The zygomatic arch of *E. mitchelli* attaches in essentially the same location. In *E. mealsi*, however, the zygomatic arch attaches to the skull relatively farther anteriorly so that its posterior margin is opposite the middle of M¹ (see Fig. 20a).

The dentition of *P. bishopi* is incompletely known. On the holotype, the crowns of P⁴ and M¹ and the roots of P³ and M² are preserved. P³ has a round anterior root which is separated by 3 mm of bone from a bilobed posterior root. The posterior root is bilobed presumably because it was formed by the union of two roots that were once separate. P⁴ apparently has three roots, but they have suffered damage. These three roots are more tightly clustered into an equilateral triangle than in either *E. mealsi* or *E. mitchelli*. The crown of P⁴ (Figs. 11, 12) is a nearly equilateral triangle with a lingual protocone shelf that is slightly posterior to the middle of the tooth. By homology with the cusps on the P⁴ of *E. mealsi* (Mitchell and Tedford 1973:241–242), the paracone is the main labial cusp. It is broad and low, and therefore, unlike the paracone of the P⁴ of *E. mealsi*. There is a wear facet on its anterior edge. The metacone is short and broad and apparently had little shearing capability. It has a lingual wear facet. There is a broad basin lingual to the metacone. A cingulum extends from the anterolingual side of the tooth to the anterolabial side. There

is a small cingular cusp in the middle of the lingual side of the tooth. There is a minimum space of 4.7 mm between the crowns of P⁴ and M¹. This contrasts with *E. mealsi*, in which these two teeth touch (compare Figs. 20a and 21a).

The crown of M¹ is triangular, and shaped somewhat like that of *E. mealsi*, but has lower cusps (Figs. 11, 12). The paracone is lower than the metacone. It is situated on an anterior lobe of the tooth. Compared with the M¹ of *E. mealsi*, the cingulum is less developed, absent labially, and the paracone and metacone are closer to the labial margin of the tooth. As in *E. mealsi* there is a broad posterolingually positioned protocone shelf with a shallow basin, a single anterior root, and a bilobed posterior root with its lingual lobe above the protocone shelf. The anterior alveolus for the M² is 4 mm posterior to the posterior root of M¹, and contains a fragment of a bilobed root. There is another very small posterior root for M². This condition is different from that in *Enaliarctos* spp. in which the M² has one bilobed root.

Each optic foramen is circular and nearly 4 mm in diameter; proportionally and actually larger than in *E. mealsi*. The openings of the optic foramina are located much more ventrally and posteriorly within the interorbital region than in *E. mealsi*. In *E. mealsi*, the external openings of the foramina are just below the mid-part of the brain case. In *P. bishopi* they are recessed beneath the anterior end of the brain case in virtually the same position as in *Allodesmus packardii*. In the past, I have discussed (Barnes 1972:19, 50–51, 62) the unique posteroventral position of the optic foramina (and other nearby structures) in species of *Allodesmus*. In those species and in *P. bishopi*, the internal narial passage is broad and low, and passes through the interorbital part of the skull in a ventral position. In *E. mealsi* and in modern Otariinae, the internal narial passage is narrower and more highly arched through the interorbital region. The optic foramen in these animals is none-the-less, just above the dorsal wall of the narial passage, but is therefore in a more dorsal location.

The optic foramina of *P. bishopi* emerge from the brain case at the narrowest part of the interorbital septum, and are separated by about 6 mm of bone. The optic chiasm is well within the brain case, and the two nerve canals do not merge near the external openings of the optic foramina as they do in *Allodesmus kernensis* and in Recent Otariinae. The anterior lacerate foramina (= orbital fissures) of *P. bishopi* pierce the brain case lateral to and slightly posterior to each optic foramen (see Fig. 7b).

The foramen rotundum of *P. bishopi* lies within the anterior aperture of the alisphenoid canal. This relationship is typical of ursids and canids, but differs from modern Otariinae and Odobeninae in which the foramen rotundum is combined with the anterior lacerate foramen. The greatly enlarged common aperture of the alisphenoid canal and the foramen rotundum in *P. bishopi* is located within a lateral eminence of the pterygoid, and is separated medially from the anterior lacerate foramen by a vertical septum. In *E. mealsi*, the lateral part of the pterygoid is thicker and constricts the anterior aperture of the alisphenoid canal, and the foramen rotundum is merged with the anterior lacerate foramen approaching the condition in modern Otariinae and Odobeninae.

The glenoid fossa of the squamosal in anteroposterior cross section forms a semicircle of approximately 180°. There are both a preglenoid and postglenoid process, but neither is as large as in *E. mealsi*. The preglenoid process is widest toward the lateral margin of the glenoid fossa. The postglenoid process is largest at a more medial location in front of the auditory bulla. The

posterolateral corner of the glenoid fossa is rounded as in *E. mealsi*, and is very different from the prominent corner that is present in *Allodesmus kernensis*. The posteromedial corner of the glenoid fossa is separated by approximately 6 mm from the lateral edge of the Eustachian canal. This proportionally wide separation also exists in *E. mealsi*, in *Allodesmus packardii*, and in some fissiped carnivores, and is unlike what I interpret to be the derived condition in modern Otariinae and in *Allodesmus kernensis* in which the Eustachian canal is much closer to the glenoid fossa (see also Barnes 1972:51–52). Unlike the condition in *E. mealsi*, the posteromedial corner of the glenoid fossa of *P. bishopi* bears a small transverse groove. Both *Allodesmus packardii* and *A. kernensis* have a larger groove in the same location (Barnes 1972:51). The groove leads to a small foramen in the squamosal which may be the canal for the chorda tympani nerve. Medial to this, and separated from it by an eminence in the squamosal as in *Allodesmus packardii*, is the relatively large foramen ovale. It measures 5 mm by 3 mm.

The opening of the posterior nares is ventral to the anterior edge of the brain case (Fig. 9a), and in shape is wide and low, differing greatly from the narrow but high opening in *E. mealsi*. In *P. bishopi* the opening is 23 mm wide and 8 mm high, compared with 24 mm wide and 15 mm high for the holotype of *E. mealsi* (Mitchell and Tedford 1973:223). The roof of the choanal region is nearly flat in *P. bishopi* and this flat surface continues posteriorly beneath the cranium to the basisphenoid surface as one plane. This same surface in *E. mealsi* is much more vaulted both from side to side and from anterior to posterior. At either side of the roof of the choanal region in *P. bishopi* is a pterygoid groove for the palatine (= Vidian) nerve. This groove is absent on the holotype of *E. mealsi* (Mitchell and Tedford 1973:fig. 5a), but is present on the holotype of *Allodesmus packardii* (Barnes 1972:50, figs. 18–19, pl. 1c). The basisphenoid lateral to this groove extends laterally, and in ventral view partly obscures the posterior foramen of the alisphenoid canal and the foramen ovale. In *E. mealsi* these foramina are not so obscured in this view by the basisphenoid. In *P. bishopi*, the entire choanal region, including the bones bordering it, and the posterior narial opening are nearly identical to *Allodesmus packardii*.

The strut formed by the palatine, pterygoid, and alisphenoid bones spanning between the palate and the braincase in *P. bishopi* differs from that of *E. mealsi*. In *E. mealsi*, the strut has a rounded or convex lateral margin extending the total distance from the posterior palatine process to the alisphenoid canal. In its posterior one-half, it bends dorsally toward the brain case. In *P. bishopi* the strut is more slender, and not convex laterally, but has a crest-like lateral margin extending from the palate to the alisphenoid canal (see Fig. 7b, 9a). Lateral to the alisphenoid canal the bone projects laterally in a rugose eminence. A thin ventral crest is continuous with the slender, posteriorly projecting pterygoid hamulus. Between the pterygoid hamulus and the alisphenoid canal, the lateral surface of the bone is excavated into a large fossa. The whole structure in this area in *P. bishopi* is closest to that of *Allodesmus packardii* among the known skulls of fossil and Recent otariids.

In *P. bishopi* the basicranial region between the tympanic bullae is relatively wider than in *E. mealsi*. The pharyngeal tubercle in the center of the basioccipital is nearly as prominent as in *E. mealsi*, but narrower. The posterior lacerate foramen is relatively large. Unlike the shape of this foramen in *E. mealsi*, its transverse dimension (7.3 mm) is greater than its anteroposterior

dimension (6 mm). The shape of this foramen in *P. bishopi* is similar to that in *Allodesmus packardii* and *A. kernensis* (compare Figs. 20a, 21a, and 21b). The openings of the relatively widely spaced hypoglossal foramina face laterally, and they are located directly posterior to the medial edges of the posterior lacerate foramina.

The tympanic bulla (Fig. 13) is relatively more inflated than in *E. mealsi*. The relationship of the bulla to the surrounding bones and structures is similar in *E. mealsi* and other otariid pinnipeds. Judging by a slight ridge and some foramina traversing the surface of the bulla from the area of the anterior carotid foramen to a point lateral to the posterior carotid foramen, the entotympanic forms only a small part of the bulla as in *E. mealsi* and other otariids (see Mitchell and Tedford 1973:254–255; Tedford 1976:fig. 2). As in *E. mealsi*, therefore, the ectotympanic comprises the inflated part of the bulla.

The bulla is fused to the mastoid process and to the postglenoid process. It forms the ventral lip of the external auditory meatus, is notched posteriorly at the posterior lacerate foramen, and is not sutured or fused to the basioccipital. The carotid canal passes almost straight through its medial wall. Compared with *E. mealsi*, the bulla is slightly deeper dorsoventrally in its middle part, and is more inflated in its medial and anterolateral parts. It is not separated from the postglenoid process by as wide a sulcus as in *E. mealsi*, and spreads more extensively over the posterior side of the process. Any remnant of a postglenoid foramen is obscured somewhere within a small transverse crease that marks the contact between the anterior margin of the bulla and the postglenoid process. A postglenoid foramen is present in *E. mealsi* (Mitchell and Tedford 1973:227, with possibly multiple openings on each side), but is characteristically lost in later otariid pinnipeds.

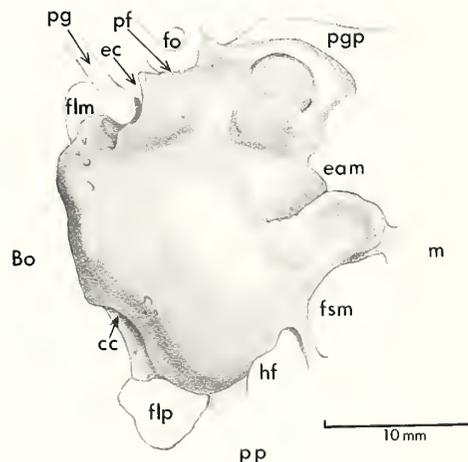


FIGURE 13. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, left tympanic bulla and adjacent structures, ventral view, 2 x natural size. Abbreviations: Bo — basioccipital; cc — posterior carotid foramen; eam — external acoustic meatus; ec — bony Eustachian canal; flm — median lacerate foramen; flp — posterior lacerate foramen; fo — foramen ovale; fsm — stylomastoid foramen; hf — hyoid fossa; m — mastoid process; pf — petrotympanic fissure; pg — pterygoid groove for palatine (=Vidian) nerve; pgp — postglenoid process of squamosal; pp — paroccipital process.

In previous text I have noted the probable existence in *E. mealsi* of an embayment in the lateral edge of the basioccipital by an inferior petrosal venous sinus. Hunt (1974a, b; 1977) has reviewed the literature and data on the occurrences of such embayments in the lateral edges of the basioccipital in bears and in fossil amphicyonids. In bears the embayment holds an elongate loop of the median branch of the internal carotid artery, and Hunt (1974a:47-48) has suggested that the loop functions as a countercurrent heat exchange mechanism to cool arterial blood in the absence of an orbital rete such as is present in various other carnivores. Hunt (1974b, 1977) has suggested that the embayment in the basioccipital of amphicyonids carried a similar carotid loop.

The evidence for the existence of an embayment in the lateral edge of the basioccipital in *P. bishopi* is as follows: On the holotype of *P. bishopi*, there are small, paired, hemispherical basioccipital tuberosities as in *E. mealsi*. These tuberosities are the probable areas of insertion of the paired rectus capitis ventralis muscles (Miller, Christensen, and Evans 1964:173, 175, fig. 3-29; Howell, 1928:50-51, fig. 4 uses slightly different terminology). As in *E. mealsi*, the tuberosities are ventral to part of the inferior petrosal venous sinuses. On the holotype of *P. bishopi*, the left tuberosity is larger than the right. Where the right petrosal was removed from the skull, an embayment filled with matrix may be seen in the lateral margin of the basioccipital bone. This same matrix-filled embayment in the right side of the

basioccipital may also be seen in the reproduction of the natural matrix endocranial cast of the holotype (see Fig. 15b). On the matrix endocranial cast (LACM [CIT] 5302) referred to the species, the bulla and part of the petrosal had been broken away on the left side and the embayment in the basioccipital is exposed (see Mitchell and Tedford 1973:fig. 13c). Part of the thin ventral wall of the lateral basioccipital tuberosity had broken through, further exposing this embayment. It was partly covered dorsally, within the brain case, by a thin, laterally projecting shelf of the basioccipital that extends to within 3 mm of the medial edge of the petrosal. The embayment widens anteriorly and extends posteriorly as far as the anteromedial edge of the posterior lacerate foramen. This embayment may be homologous with the embayment of the inferior petrosal venous sinus of ursids and amphicyonids and is a character suggesting relationships between them and the Enaliarctinae.

The medial side of the tympanic bulla is nearly vertical and bulges slightly ventral to the lateral margin of the basioccipital. By contrast, in *E. mealsi*, the medial part of the bulla slopes ventrolaterally as a continuation of the plane of the adjacent basioccipital surface. The carotid canal in *P. bishopi* passes nearly straight through the medial side of the bulla. Its posterior foramen encloses a smaller, medially located foramen. The posterior carotid foramen is exposed ventrally because the bulla is retracted anterior to the posterior lacerate foramen. A wide and prominent crest of bone spans between the posterolateral corner of the bulla

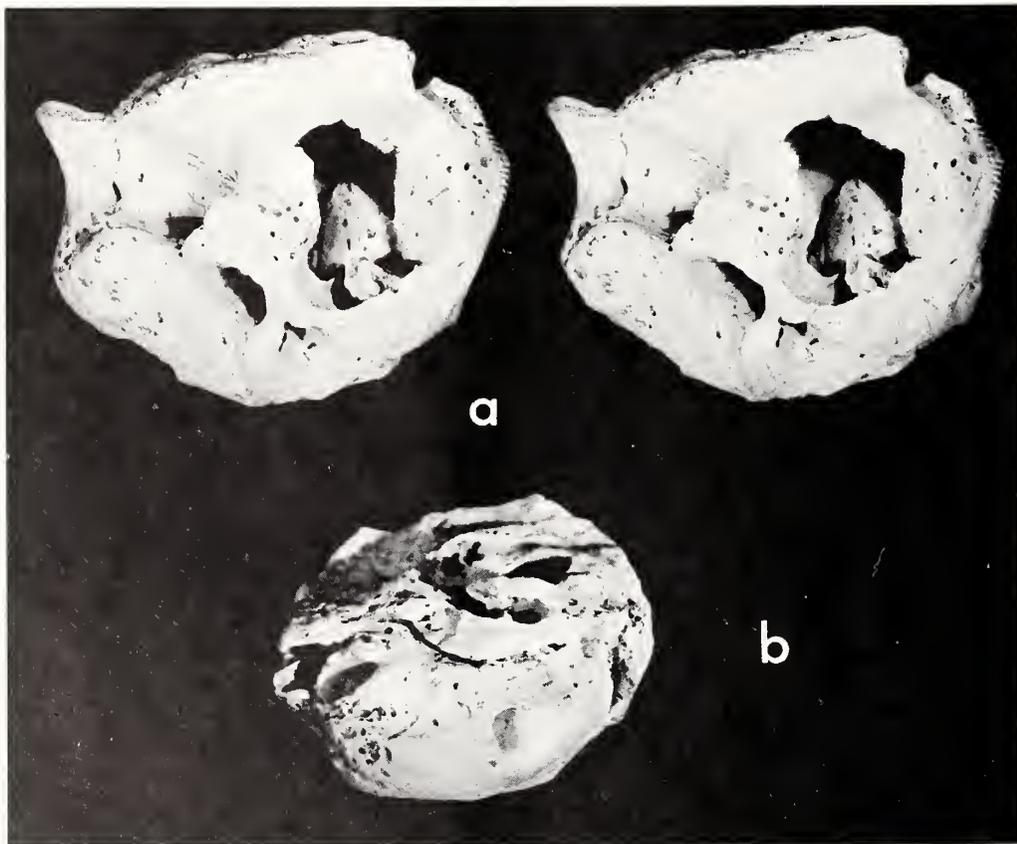


FIGURE 14. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, right ear region separated from skull, 2 x natural size; a, stereophotographs of ventral view into open middle ear cavity; b, medial side of petrosal and tympanic bulla.

and the ventral side of the paroccipital process. Anterolateral to this crest is the large tympanohyal pit (see Barnes 1972:52, and Mitchell and Tedford 1973:227; the vagina processus styloidei of Mitchell 1968; and Mitchell and Tedford 1973:227, fig. 9). The tympanohyal pit is not obscured by any large projection from the bulla, and faces posterolaterally into a large fossa in the ventral surface of the paroccipital-mastoid crest. This latter fossa is similarly shaped in such Recent Otariinae as *Zalophus californianus* and *Arctocephalus* spp.

A narrow, vertical ridge of bone separates the tympanohyal pit from the stylomastoid foramen. This foramen is directed antero-ventrolaterally, and is compressed between the bulla and the medial side of the mastoid process. Anteromedial to the stylomastoid foramen, the ventral surface of the bulla is flat, and extends toward the anteromedial corner of the mastoid process as a horizontal lip that underlies the posterior part of the external auditory meatus. The meatus is nearly circular, approximately 4 mm in diameter, and opens externally in an anterolateral direction. A crest projects laterally from the squamosal above the meatus. A flattened styloid process of the bulla projects anteromedially beneath the anterior opening of the Eustachian canal. Medial to this, however, the bulla is notched ventral to the median lacerate foramen and the anterior carotid foramen.

The tympanic cavity within the bulla is larger than in *E. mealsi*, both relatively and quantitatively. The tympanic cavity is expanded in *P. bishopi* in the same places as in *Allodesmus packardii*. The epitympanic recess is greatly enlarged, being at least twice the size of that in *E. mealsi*, and is expanded anterolaterally. The tympanic crest is relatively large (5 mm in diameter) and projects approximately 4 mm into the tympanic cavity, but is smaller than that of *E. mealsi*. As in *Allodesmus* spp., the ventrolateral wall of the carotid canal creates only a very slight shelf within the cavity in contrast with *E. mealsi*. There is only a vestige of the anterior septum and process which are large in *E. mealsi*, but in the anteromedial corner of the cavity there is a prominent, nearly vertical eminence.

The promontorium of the petrosal is less covered medially by an extension of the bulla than in *E. mealsi*, but is of approximately the same absolute dimensions, making it relatively larger in *P. bishopi*. The fenestra vestibuli faces laterally and is about the same as in *E. mealsi*. There is a groove crossing the anteromedial corner of the promontorium that may have marked the course of the promontory branch of the internal carotid artery. I cannot locate a specific site either of the promontory foramen or of a foramen in the medial wall of the bulla where the promontory branch might have diverged from the median branch of the internal carotid artery. In the expected location of either structure, however, there are two or three possible small holes, one of which could be the structure in question.

There does not appear to be a distinct fossa for the tensor tympani in *P. bishopi* as was described for *E. mealsi* (Mitchell and Tedford 1973:228, fig. 9). Such a fossa is present in fissipeds. The problem in interpreting the structure in the holotype of *P. bishopi* is because the roof of the tympanic cavity lateral to the

promontorium is partly broken away. There is a faint groove leading from the Eustachian canal to this area, but there are no ridges demarcating a fossa as in *E. mealsi*.

The right petrosal and tympanic bulla were found broken from the remainder of the holotype skull of *P. bishopi* when it was discovered in the field. The top of the petrosal is therefore visible. Because of the breakage, however, there are some difficulties in interpreting the relationship between the bony tentorium and the petrosal. My interpretation is that the tentorium contacted the lateral margin of the petrosal, but that this contact, unlike the condition in walrus or ursids, did not extend much toward the opening of the floccular fossa, and that the tentorium projected into the brain case in a more horizontal position than is typical of modern Otariinae. The floccular fossa is relatively very large, having an estimated inside diameter of 7 to 8 mm. The aperture is smaller (4 mm by 5 mm in diameter), and nearly circular. This fossa is much larger than in *Allodesmus kernensis*. The petrosal resembles those of both *Imagotaria downsi* (holotype, SBMNH 342; Mitchell 1968; fig. 7) and *Allodesmus kernensis* (referred specimens, UCMP 81708, 83363; Barnes 1972:6) by being broad, dorsoventrally flattened, and by having a dorsoventrally flattened, bilobed internal acoustic meatus in which the facial nerve canal and the vestibulocochlear nerve canal are separated by low septa. The petrosal apex is incomplete, but it appears from the shape of the petrosal as preserved that the apex is not significantly enlarged (Fig. 14b). In none of these structures is the petrosal of *P. bishopi* remarkably similar to those of modern Otariinae.

The isolated natural matrix endocranial cast, LACM (CIT) 5302, that Mitchell and Tedford (1973:229–232, 237–241, figs. 13, 14) referred to *E. mealsi* is nearly identical in morphology to the endocranial cast (Figs. 15a–b) of the holotype (UCMP 86334) of *P. bishopi*. I reidentify the isolated endocranial cast, LACM (CIT) 5302, as belonging to *P. bishopi* on the basis of the following characters of *P. bishopi* that differ from the holotype (LACM 4321) and the other specimen (LACM [CIT] 5303) confidently referred to *E. mealsi*: The posterior lacerate foramen is larger and expanded transversely rather than anteroposteriorly. The basisphenoid is not arched and is more in the same plane as the basioccipital. The optic foramina are larger in diameter, closer together, and positioned more ventrally and posteriorly beneath the anterior edge of the brain. The anterior lacerate foramen is broader, lower on the brain case, and at least dorsally, bilobed. The fossae on the supraoccipital dorsal to the condyles are deeper and wider. The part of the exoccipital that descends toward the paroccipital process is more expanded reflecting the larger size of that process. The endocranial cavity is proportionally and measurably wider, particularly across the anterolateral corners. Relative to its width, the endocranial cavity is flatter dorsoventrally. The coronal gyrus and the anterior ectosylvian gyrus are more vertically oriented and enlarged. The enlargement emphasizes the depth of the pseudosylvian sulcus on the endocranial cast, but the sulcus is not expressed by as profound a sulcus on the external wall of the brain case as in *E. mealsi*.



FIGURE 15. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, natural matrix endocranial cast, natural size; *a*, right lateral view of endocranial cast subsequent to removal of damaged surface bone; *b*, ventral view of reproduction of matrix endocranial cast made prior to reassembly of broken skull.

TABLE 3

Measurements (in mm) of skulls of Enaliarctinae from Pyramid Hill, California. Methods of making measurements were as defined by Sivertsen (1954:18–20, those followed by the number given by Sivertsen for the same measurement) or by Barnes (1972:fig. 1, those followed by a dot). Other measurements are explained in text under *Methods*. Parentheses indicate estimated measurements. Asterisks indicate measurements with values differing from those given by Mitchell and Tedford (1973).

	<i>Enaliarctos mealsi</i> Mitchell and Tedford 1973		<i>Enaliarctos mitchelli</i> new species		<i>Pimmarctidion bishopi</i> new genus and species	
	LACM 4321, holotype	LACM(CIT) 5303, referred	UCMP 100391, holotype	UCMP 80943, paratype	UCMP 86334, holotype	LACM(CIT) 5302, referred
Post-palatal length (palatal notch to basion).....	92.5	—	—	—	80.5	—
Basion to anterior edge of zygomatic root (18)	144.7*	124.7*	—	—	130.2	—
Length of tooth row, C to M ² (●)	—	—	63.0	69.2	—	—
Width of rostrum across canines (12)	—	(43.)	40.9	(42.)	—	—
Width of palate across ante- rior alveoli of P ⁴ (●)	55.0*	48.6*	42.4	(44.)	(44.)	—
Width between infraorbital foramina (●)	53.8	49.7	42.0	(46.)	41.0	—
Width across antorbital processes (5)	(47.0)	(42.)	41.1	—	36.8	—
Width across greatest inter- orbital constriction (6) ...	39.6	32.2	28.1	—	26.1	—
Width across supraorbital processes (7).....	37.6	30.9	26.7	—	26.3	—
Width across greatest inter- temporal constrict- ion (●)	31.0	26.0	19.8	—	21.4	—
Width of braincase at ante- rior edge of glenoid fossa (8)	58.1	(57.)*	—	—	(59.)	(60.)
Zygomatic width (17)	(136.)	—	(106.)	—	(104.)	—
Auditory width (19)	(90.)	—	—	—	82.6	—
Mastoid width (20)	(98.)	—	—	—	90.6	—
Paroccipital width	65.7	—	—	—	(78.)	—
Greatest width across occipital condyles	45.7	—	—	—	49.0	—
Greatest width of anterior nares (●)	—	30.6	30.0	—	—	—
Greatest height of anterior nares	—	(21.0)	26.0	—	—	—
Width of zygomatic root of maxilla (14)	14.3*	13.6*	13.4	15.7	16.6	—
Greatest width of foramen magnum	23.8	(24.5)	—	—	24.1	(25.)
Greatest height of foramen magnum	16.5	(18.4)	—	—	14.7	(19.)
Transverse diameter of infraorbital foramen	10.0	9.5	8.6	(8.5)	7.2	—

DISCUSSION

The present recognition of a total of three species within two genera of primitive otariid pinnipeds of late Oligocene or early Miocene age provides a new perspective on the evolutionary diversity and classification of enaliarctine pinnipeds. The new genus *Pinnarctidion* is similar to *Enaliarctos* in many characters, most of them primitive, but it shares many apparently unique derived characters with the subfamily Allodesminae, to which it is probably ancestral.

The assignment of *Pinnarctidion bishopi* to the otariid subfamily Enaliarctinae and the re-interpretation of the holotype of *Enaliarctos mealsi* eliminates or modifies some of the characters used by Repenning and Tedford (1977:11) to diagnose the family Enaliarctidae. The emended diagnosis of the subfamily presented in previous text reflects this.

The interpretation of subfamily and family level classification of fossil and modern otariid pinnipeds has varied markedly between different authors (see Mitchell 1966, 1968, 1975; Barnes 1972; Repenning 1975, 1976; Repenning and Tedford 1977; Tedford 1976). I believe that the recognition of the four families Enaliarctidae, Desmatophocidae, Odobenidae, and Otariidae (Repenning 1975, 1976; Repenning and Tedford 1977) is unwarranted. Equal consideration of the morphologic characters used by Repenning and Tedford (1977:8–12) to define these families might require the establishment of yet another family group for the new genus *Pinnarctidion*.

I recognize several distinct lineages of otariid pinnipeds and give them subfamily rank. To include *Pinnarctidion bishopi* in the subfamily Enaliarctinae may stretch the concept of that subfamily and make it a horizontal group. As such, however, I recognize the Enaliarctinae as a common ancestral group from which several other derived groups originated (see Repenning 1975:fig. 11; 1976:376–379; Repenning and Tedford 1977:fig. 6). This concept of the relationship of such a group to its derivatives is similar to that which the family Palaeoryctidae is thought to have to several mammalian orders (*sensu* Lillegraven 1969:fig. 40), or which the subfamily Hyracotheriinae is thought to have to other subfamilies of the Equidae.

I believe that some middle ground exists in which the classification of otariid pinnipeds is internally consistent and is comparable to the family level classifications of other mammals. To this end, I employ a classification that includes one family, the Otariidae, with six subfamilies. The subfamily Dusingathinae (Mitchell 1968) I include in the Odobeninae, and the subfamily Desmatophocinae, as previously used by Mitchell (1966) and myself (1972), I now divide into the Desmatophocinae and the Allodesminae following Mitchell's later (1968, 1975) papers. The broad phylogenetic relationships, I believe, are basically as shown by Repenning (1975) and Repenning and Tedford (1977), except in details of the relationships which the Allodesminae and Desmatophocinae have with the Enaliarctinae. These relationships are discussed below following the observations on enaliarctine species.

Enaliarctos remains the most primitive otariid genus yet described. Many of the characters it has that distinguish it from *Pinnarctidion* and from derived otariids are fissiped-like and are interpreted as being primitive. I have described the structure of its foramen rotundum, alisphenoid canal, and anterior lacerate foramen as intermediate between such fissipeds as the canids or ursids and the modern otariines. The zygomatic arch, palate, or-

bit, and basicranium share many characters with fissiped carnivores as noted by Mitchell and Tedford (1973). I also agree with suggestions that *Enaliarctos* is near the ancestry of the Otariinae (Mitchell and Tedford 1973; Mitchell 1975:19–20, fig. 1; Repenning and Tedford 1977:fig. 6).

Of the two currently known species of *Enaliarctos*, the more primitive one, *E. mealsi*, is known by skulls that are probably from the lower concretion-bearing bed in the basal part of the Pyramid Hill Sand Member of the Jewett Sand, and by isolated teeth from a stratigraphically correlative nearby locality. Both the holotype and paratype of the more derived species, *E. mitchelli*, are probably from the higher fossiliferous concretion-bearing bed in the Pyramid Hill Sand Member. Thus, the available evidence suggests that the morphologically more derived species of *Enaliarctos* occurs stratigraphically higher, and is, therefore, geochronologically younger than the more primitive species.

This chronologically younger species, *E. mitchelli*, differs from *E. mealsi* by possessing the following apparently derived characters: high rostrum, larger nares, fewer posterior palatine foramina, zygomatic arches that are not so greatly arched at mid-point, more horizontal ventral surface of the zygomatic arches beneath the infraorbital foramina, relatively narrower interorbital region, straighter cheek tooth row, and roots of P⁴ relatively closer together suggesting at least partial suppression of the carnassial function of this tooth. I believe that these characters are derived for *E. mitchelli* because they either depart from conditions in generalized terrestrial fissipeds, or approach aquatic adaptations in modern pinnipeds, or both. The significance of some other characters in which *E. mitchelli* differs from *E. mealsi* is uncertain. Such characters are the higher rostrum and more anterior position of the roots of M¹ relative to the origin of the zygomatic arch. The heightened rostrum is probably correlated with the enlargement of the anterior narial opening; an aquatic adaptation. The meanings of some of these differences may be understood when other species of enaliarctines are described. It is interesting to note that the high rostrum and large anterior narial opening of *E. mitchelli* resemble those of some Recent phocids, particularly the Weddell seal, *Leptonychotes weddelli* (Lesson 1826) and the Grey seal, *Halichoerus grypus* (Fabricius 1791). In contrast, the narrower rostrum and smaller narial opening of *E. mealsi* bear a closer resemblance to Recent species of the genera *Phoca* Linnaeus 1758 and *Pusa* Scopoli 1777.

Both the taxonomic diversity and some of the morphological characters of various mid-Cenozoic otariids have previously (Mitchell 1968:1887–1888, 1892; 1975; Barnes 1972:63–65) been compared with those of more recent true seals of the family Phocidae. It is becoming apparent that North Pacific otariids were previously more diversified than they are now and may have occupied some of the niches now filled by phocids. It is probably quite significant that even among the earliest fossil otariids, some species had characters that were convergent with phocids.

The third known late Oligocene or early Miocene enaliarctine, *Pinnarctidion bishopi*, differs markedly from species of *Enaliarctos*. The holotype of *P. bishopi* is known to have come from the upper fossiliferous concretion-bearing bed at Pyramid Hill, and was probably at least contemporaneous with, if not sympatric with, *E. mitchelli*. The morphology of the skull of *P. bishopi* suggests that this species had attained a greater degree of aquatic adaptation than either *E. mealsi* or *E. mitchelli*. Most of the char-

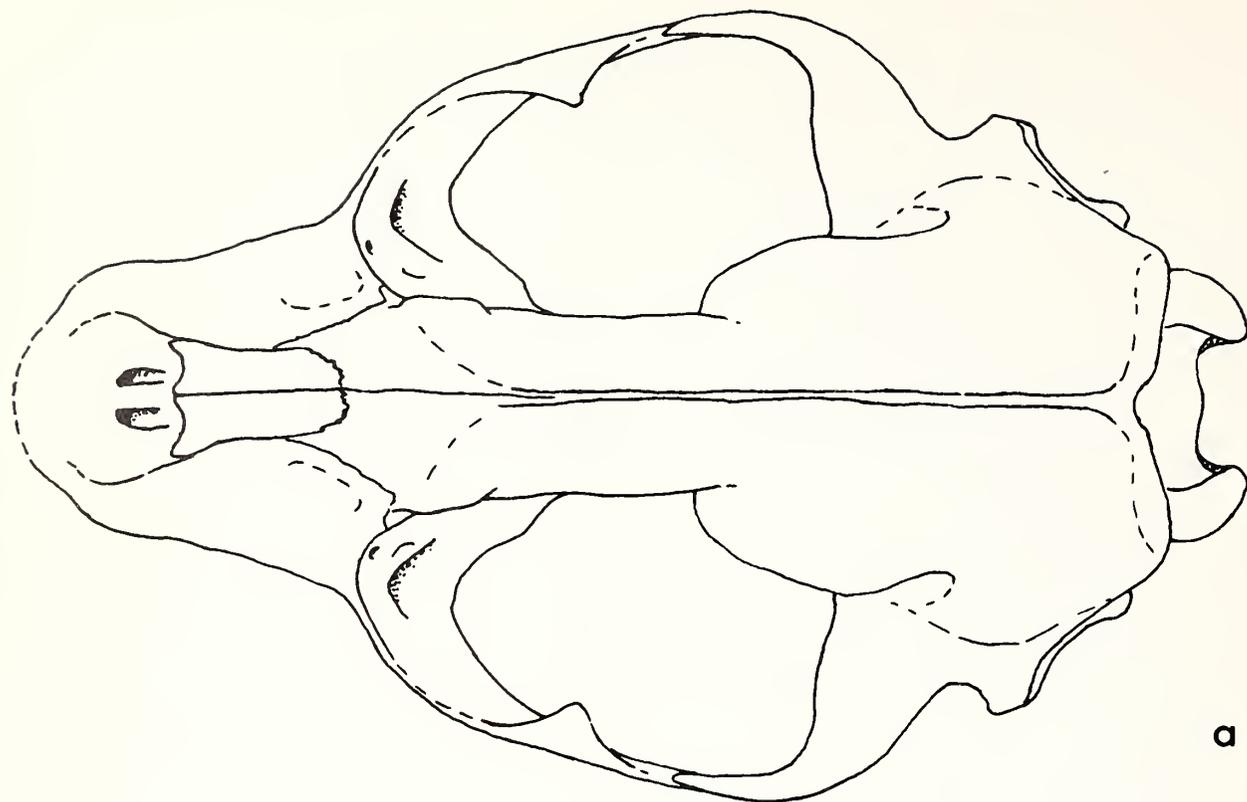
TABLE 4

Characters shared by *Pinnarctidion bishopi* new genus and species, and *Allodesmus packardi* Barnes 1972 or *A. kernensis* Kellogg 1931, that differ from *Enaliarctos* spp. An asterisk denotes characters known in *A. kernensis* and presumed to also exist in *A. packardi* although not preserved.

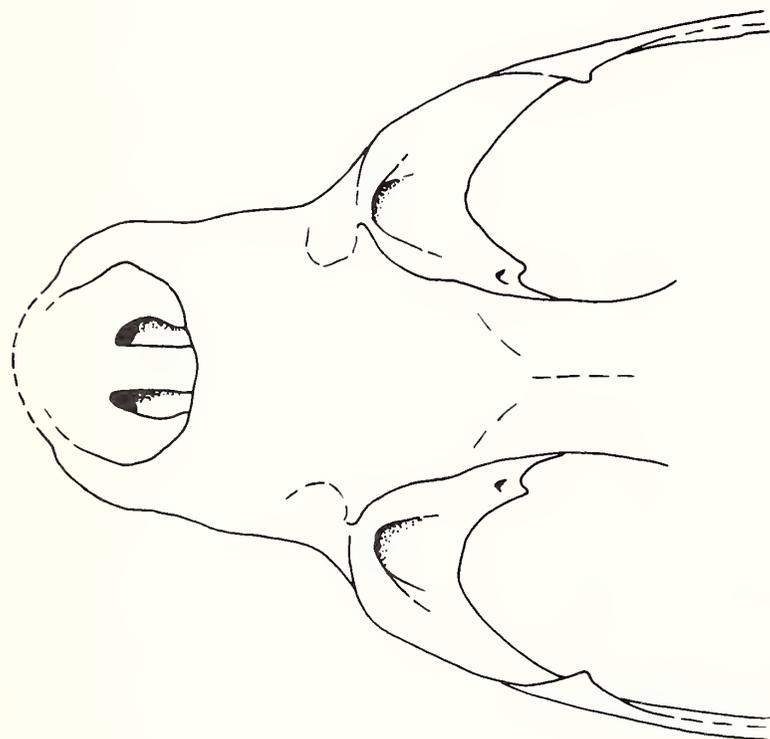
<i>Pinnarctidion bishopi</i> and <i>Allodesmus</i> spp.	<i>Enaliarctos</i> spp.
1. Palate broad and relatively flat.	1. Palate relatively narrower and arched.
2. Pterygoid strut between braincase and palate is excavated laterally.	2. Pterygoid strut is rounded and inflated on lateral surface.
3. Occipital condyles diverging dorsally.*	3. Condyles nearly parallel.
4. Paroccipital process large.*	4. Paroccipital process small.
5. Posterior nares wide and low.	5. Posterior nares relatively narrower and higher.
6. Infraorbital process of palate thin and expanded laterally.	6. Process small and spur-like.
7. Preglenoid process small.	7. Preglenoid process relatively larger.
8. Optic foramen posteroventrally located beneath anterior end of braincase.	8. Foramen anterodorsally located in front of braincase.
9. Dorsal surface of braincase equal to or higher than dorsal surface of interorbital region.	9. Braincase lower than dorsal surface of interorbital region.
10. Anterior lacerate foramen (= orbital fissure) large and bilobed.	10. Foramen relatively smaller and more circular.
11. No sagittal crest on interorbital region.	11. Sagittal crest on interorbital region.
12. Skull flattened dorsoventrally.	12. Skull arched dorsoventrally.
13. Mastoid process cubic.	13. Mastoid process more rounded.
14. Zygomatic arch low and nearly paralleling palatal-basioccipital plane.	14. Zygomatic arch more curved dorsally at midpoint.
15. Palatal margin lateral to posterior part of choanal area sharp edged laterally.	15. Margin smoothly rounded laterally.
16. Fossa in alisphenoid anteromedial to glenoid fossa.	16. Fossa medial to glenoid fossa.
17. Epitympanic recess in ear cavity large.	17. Epitympanic recess small.
18. Cheek teeth with wide spaces between them.	18. Cheek teeth closely spaced.
19. Posterior lacerate foramen elliptical transversely.	19. Foramen elliptical anteroposteriorly.
20. Zygomatic arch joins rostrum near palatal plane.	20. Zygomatic arch descends dorsolaterally from palatal plane.
21. Median lacerate foramen visible in ventral view.	21. Median lacerate foramen covered by anteromedial corner of bulla.
22. Lambdoidal crest low, rounded.	22. Crest more prominent.
23. Sagittal crest small or absent.	23. Sagittal crest prominent.
24. Apex of postorbital process of jugal is expanded anteroposteriorly.	24. Apex is narrow, pointed.
25. Anterior extremity of zygomatic process of squamosal is expanded dorsoventrally and contacts postorbital process of jugal.	25. Anterior extremity pointed, not expanded dorsoventrally, and does not contact postorbital process of jugal.

acters separating it from either species of *Enaliarctos* are derived characters, apparent aquatic adaptations, or characters shared with geochronologically younger species of *Allodesmus*, especially the middle Miocene *Allodesmus packardi*. Table 4 lists 25 characters shared by *P. bishopi* with *A. packardi* and/or *A. kernensis*, and not shared with *Enaliarctos mealsi* and *E. mitchelli*. These numerous similarities, and the fact that *P. bishopi* is chronologically older than any species of *Allodesmus*, suggest that it may be the ancestor of *Allodesmus*. Although *Allodesmus packardi* is more derived in its dental characters than *A. kernensis*,

it is more primitive in its basicranial characters. The following ten characters of *P. bishopi* separate it from *A. packardi*: cheek teeth multiple rooted, orbital vacuity small (or absent?), zygomatic process of the jugal not so greatly expanded dorsoventrally, infraorbital foramen more recessed beneath the flange-like anterior orbital margin of the zygomatic arch, interorbital region relatively wider, presence of the antorbital process, bulla more inflated, tympanic crest wider and extended more into the tympanic cavity, and presence of the nasolabialis fossa. These characters are shared with *Enaliarctos* spp., but are primitive,



a



b

FIGURE 16. Restorations of skulls: a, *Enaliarctos mealsi* Mitchell and Tedford 1973, holotype, LACM 4321, and referred specimen, LACM (CIT)5303; b, *Enaliarctos mitchelli*, new species, holotype, UCMP 100391; both dorsal views reduced to approximately the same cranium length. (a modified from Mitchell and Tedford 1973:fig. 17a, with anterior-most rostral extremity in part from *E. mitchelli*, new species.)

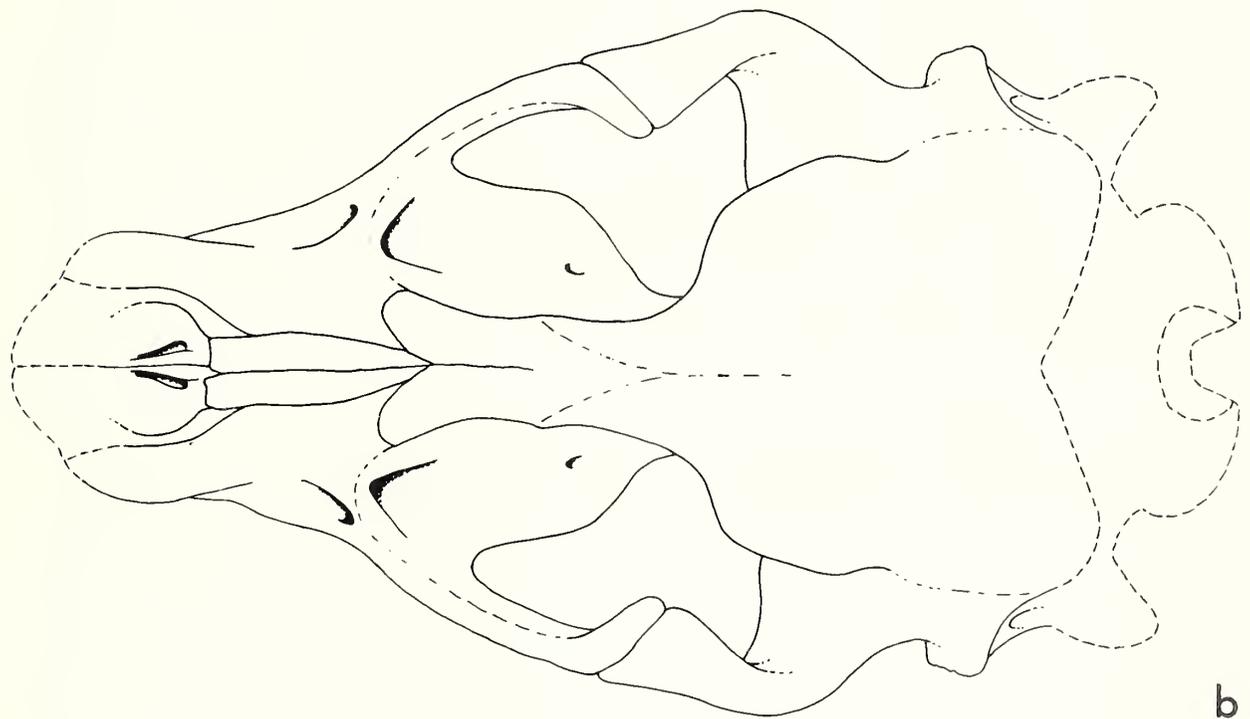
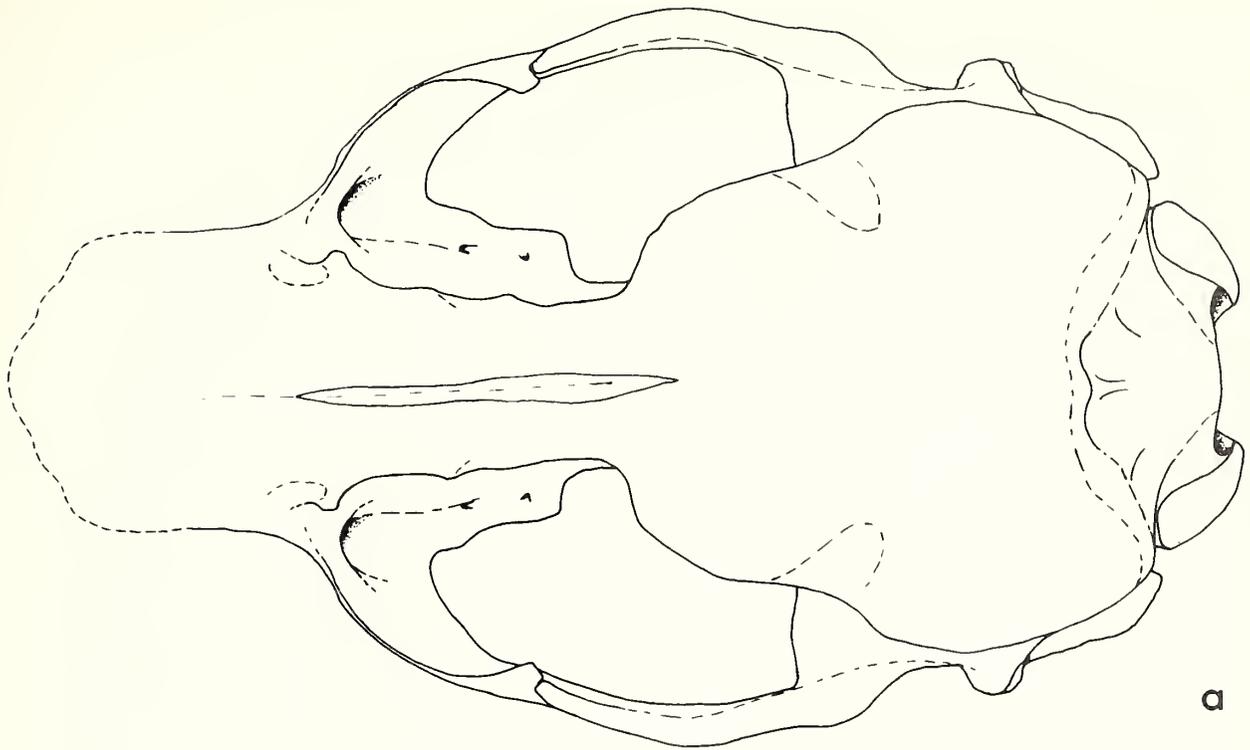


FIGURE 17. Restorations of skulls: *a*, *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334; *b*, *Allodesmus packardi* Barnes 1972, holotype, CAS 4371A; both dorsal views reduced to approximately the same cranium length. (*b* modified from Barnes 1972:fig. 21a.)

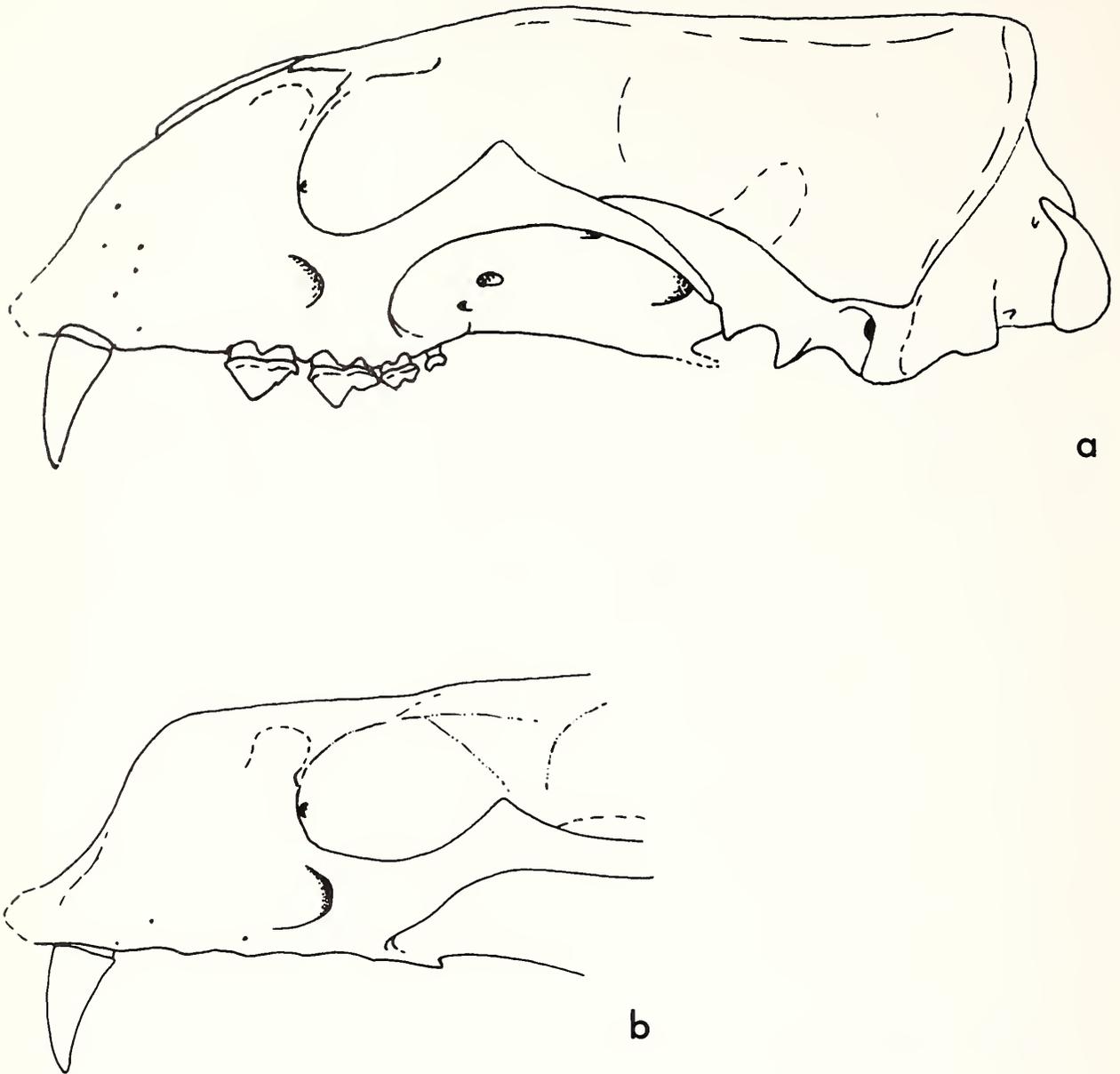


FIGURE 18. Restorations of skulls: *a*, *Enaliarctos mealsi* Mitchell and Tedford 1973, holotype, LACM 4321, and referred specimen, LACM (CIT) 5303; *b*, *Enaliarctos mitchelli*, new species, holotype, UCMP 100391, and paratype, UCMP 80943; both left lateral views reduced to approximately the same cranium length. (*a* modified and reversed from Mitchell and Tedford 1973:figs. 6b, 17b, with anterior-most part of rostrum and canine in part from *E. mitchelli*, new species.)

however, and do not preclude *P. bishopi* from being an ancestor of *A. packardi*. Further modification of some of these structures, particularly in the specializations that are considered aquatic modifications, could lead to the structures present in *A. packardi*.

All known enaliarctines share with *A. packardi* the deep vertical sulcus on the lateral wall of the cranium in the area of the pseudosylvian sulcus of the brain (see Mitchell and Tedford 1973:239). Such a sulcus is minimal to non-existent on the crania of *A. kernensis* and Recent otariids. There are profound differences in the structure of the anterior orbital margin on the zygomatic arch. I have previously described (Barnes 1972:14) the unique retracted dorsal margin of the infraorbital foramen and the

rounded anterior orbital margin in *Allodesmus* spp., and this differs from the more sharp margin in fissiped carnivores, in enaliarctines (including *P. bishopi*), and in modern otariines. This may be a diagnostic character for Allodesminae.

The morphologic similarities and suggested ancestral-descendant relationship between *Pinnarctidion bishopi* and *Allodesmus* spp. probably exclude *Desmatophoca oregonensis* from some intermediate position in the same lineage. *D. oregonensis* has usually been considered to be closely related to *Allodesmus* or to be close to the ancestry of that genus (Mitchell 1966, 1968, 1975; Barnes 1972; Repenning 1975; Repenning and Tedford 1977). Mitchell (1968:1888; 1975:13) suggested that the common ances-

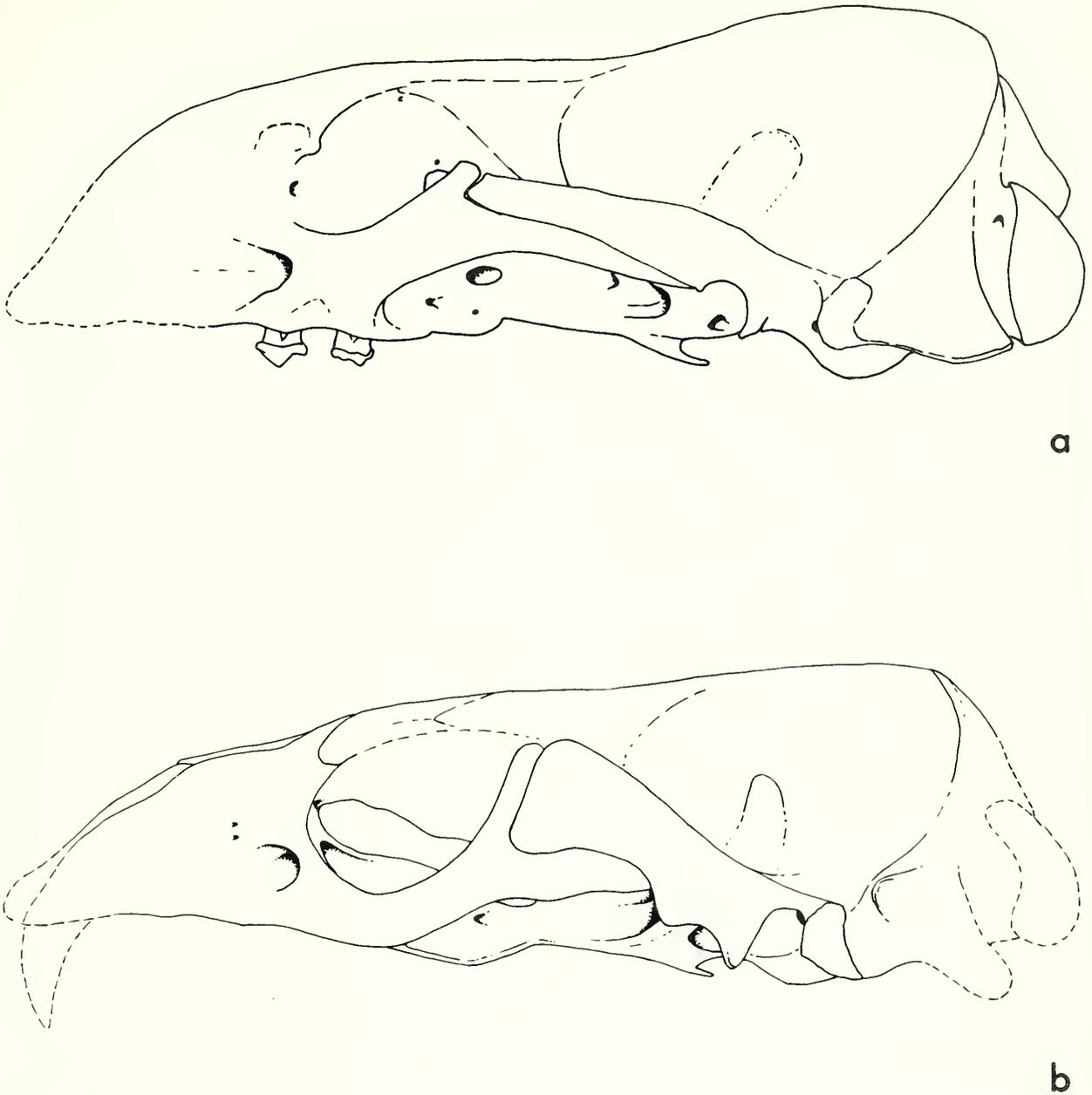


FIGURE 19. Restorations of skulls: *a*, *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334; *b*, *Allodesmus packardi* Barnes 1972, holotype, CAS 4371A; both left lateral views reduced to approximately the same cranium length. (*b* modified from Barnes 1972: figs. 21b, c.)

tor of *Desmatophoca* and *Allodesmus* was of late Oligocene or early Miocene age. I (Barnes 1972:fig. 25) once postulated a more recent common ancestry.

The cranial anatomy of *Desmatophoca oregonensis* has not been entirely described in detail, but Condon's (1906) description of the holotype has been supplemented by subsequently published information and illustrations (Mitchell 1966:36–37, pl. 29; 1968:1883, 1893–1894, table V; 1975:12–14, fig. 2; Repenning and Tedford 1977:74). By possessing three important, apparently derived characters, which it shares with *Allodesmus packardi* and/or with *A. kernensis*, *Pinnarctidion bishopi* differs from the holotype of *Desmatophoca oregonensis*. These are: the extreme

lateral excavation of the palatine-pterygoid strut between the palate and the brain case, the more dorsoventrally flattened posterior narial opening, and the more posterior and ventral position of the orbital aperture of the optic foramen. These differences suggest to me that the subfamily Allodesminae, now known mainly by species in the genus *Allodesmus*, was derived directly from the subfamily Enaliarctinae as it is defined in this report, and more specifically from species in the genus *Pinnarctidion*. Apparently *Desmatophoca oregonensis* could not have evolved from *Pinnarctidion bishopi* nor given rise to species of *Allodesmus* without there having been two reversals in the evolution of the three derived characters cited above. By this logic separate line-

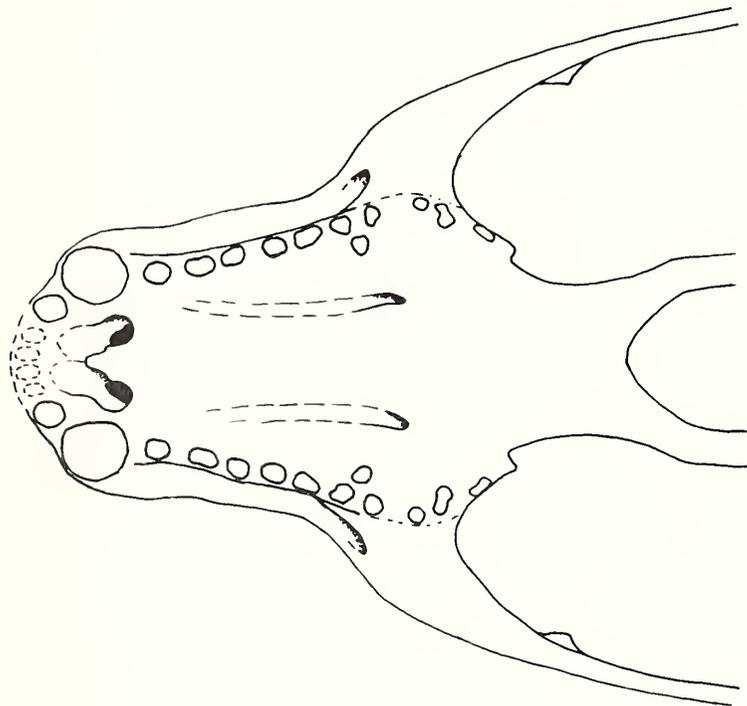
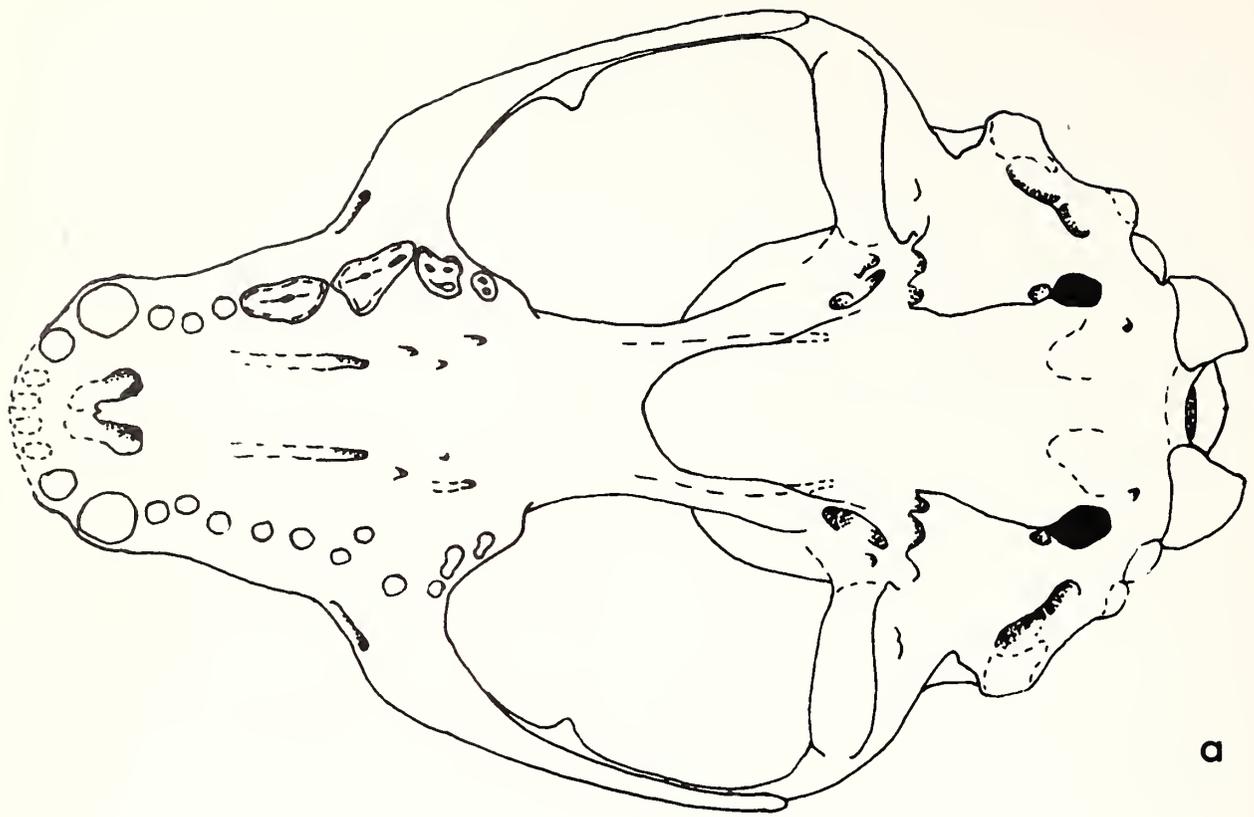


FIGURE 20. Restorations of skulls: *a*, *Enaliarctos mealsi* Mitchell and Tedford 1973, holotype, LACM 4321, and referred specimen, LACM (CIT) 5303, showing positions of cheek tooth alveoli on the right side; *b*, *Enaliarctos mitchelli*, new species, holotype, UCMP 100391, and paratype, UCMP 80943; both ventral views reduced to approximately the same cranium length. (*a* modified from Mitchell and Tedford 1973:figs. 5a, 12a, and 17c, with rostral extremity in part from *E. mitchelli*, new species.)

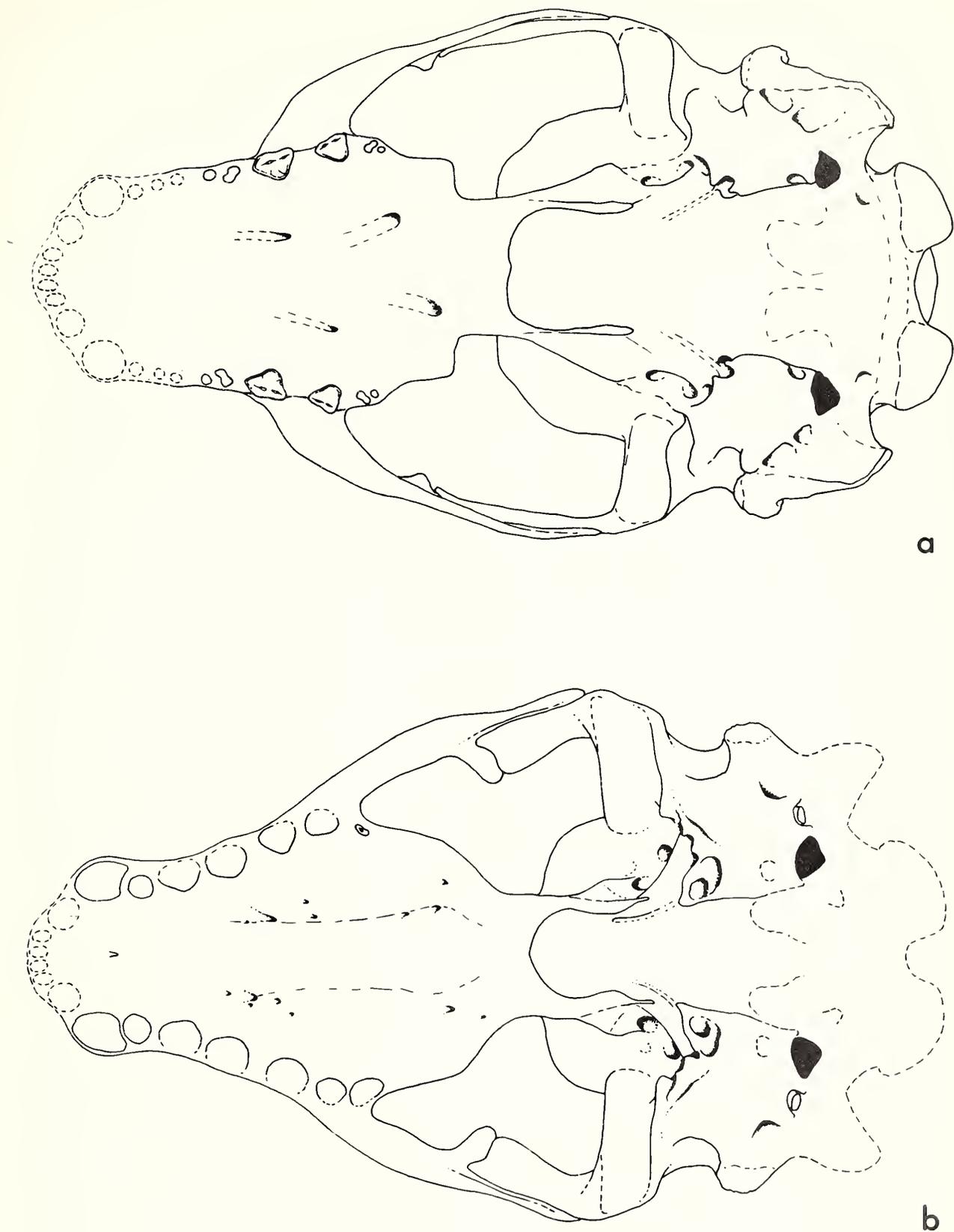


FIGURE 21. Restorations of skulls: *a*, *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334; *b*, *Allodesmus packardi* Barnes 1972, holotype, CAS 4371A; both ventral views reduced to approximately the same cranium length. (*b* modified from Barnes 1972:fig. 19.)

ages (see Fig. 22) leading to the Allodesminae and the Desmatophocinae would extend back approximately 7 million years earlier than indicated by Repenning and Tedford (1977:fig. 6), at least to a time contemporaneous with *Pinnarctidion bishopi* between about 22 and 24 million years ago, if not before. The actual evolutionary divergence between the subfamilies Allodesminae and Desmatophocine would therefore be prior to about 22 to 24 million years ago as theorized by Mitchell (1968:1888).

Repenning and Tedford (1977:fig. 6) proposed a phylogeny in which *Enaliarctos mealsi*, at about 22 million years ago, was near the basal enaliarctine stock. From this basal stock they showed the subsequent evolution of three main derived groups. These are: 1) Otariinae (their Otariidae), 2) Desmatophocinae and Allodesminae (their Desmatophocidae), and 3) Imagotariinae and Odobeninae (their Odobenidae) (see also Repenning 1975:fig. 11). As partial evidence for this early diversification, Repenning and Tedford indicated that at least four unnamed species of enaliarctines lived between about 16 and 19 million years ago.

The phylogeny I present here (Fig. 22) suggests that the subfamilies Otariinae, Desmatophocinae, and Allodesminae were each independently derived from different species within the Enaliarctinae. I have accepted the arbitrary division between the Enaliarctinae and the derived groups as being the transition point between heterodont cheek teeth including carnassials and homodont cheek teeth (see Repenning 1975:fig. 11; 1976:377; Repenning and Tedford 1977). The similarities between species of Desmatophocinae and Allodesminae indicate that these subfamilies probably arose from species of enaliarctines that were more closely related than are *Enaliarctos* spp. and *Pinnarctidion bishopi*, or that they underwent convergent evolution. The origins of the Odobeninae and Imagotariinae are presently more obscure. Repenning and Tedford (1977:55) classified the middle Miocene *Neotherium mirum* Kellogg 1931 as a species of Dusignathinae. In my classification it would be a primitive species of Imagotariinae. My observations of *Neotherium mirum* (manuscript in preparation) indicate that it is not synonymous with *Enaliarctos mealsi*, *E. mitchelli*, or *Pinnarctidion bishopi*, but has some enaliarctine characters.

The present fossil sample size is small, but preliminary indications are that individuals of *Enaliarctos* spp. are more abundant than *Pinnarctidion bishopi* in the Pyramid Hill Sand Member of the Jewett Sand exposed at Pyramid Hill. *Enaliarctos mealsi*, *E. mitchelli*, and *Pinnarctidion bishopi* are each represented by two skulls and *E. mealsi* is represented by numerous additional isolated teeth.

Pinnarctidion bishopi was probably, although not undoubtedly, contemporaneous with *E. mitchelli*. Therefore, possibly at least two enaliarctine species were sympatric, but aspects of population dynamics and interspecific competition of enaliarctines cannot be dealt with at this time.

CLASSIFICATION OF THE OTARIIDAE

CLASS MAMMALIA Linnaeus 1758.

Order CARNIVORA Bowdich 1821.

Family Otariidae Gill 1866.

Subfamily Enaliarctinae Mitchell and Tedford 1973.

Enaliarctos Mitchell and Tedford 1973.

Enaliarctos mealsi Mitchell and Tedford 1973.

Enaliarctos mitchelli new species.

Pinnarctidion new genus.

Pinnarctidion bishopi new species.

Subfamily Desmatophocinae Hay 1930.

Desmatophoca Condon 1906.

"Desmatophocine A" of Barnes 1972.

Subfamily Allodesminae Kellogg 1931.

Allodesmus Kellogg 1922.

"Desmatophocine B" of Barnes 1972.

"Desmatophocine C" of Barnes 1972.

Subfamily Imagotariinae Mitchell 1968.

Neotherium Kellogg 1931.

Imagotaria Mitchell 1968.

Pontolis True 1906.

Subfamily Odobeninae Allen 1880.

Dusignathus Kellogg 1927.

Pliopedia Kellogg 1921.

Aivukus Repenning and Tedford 1977.

Prorosmarus Berry and Gregory 1906.

Alachtherium Du Bus 1867.

Trichecodon Lankester 1865.

Odobenus Brisson 1762.

Subfamily Otariinae Gill 1866.

Pithanotaria Kellogg 1925.

Thalassoleon Repenning and Tedford 1977.

Arctocephalus Geoffroy and Cuvier 1826.

Callorhinus Gray 1859.

Zalophus Gill 1866.

Eumetopias Gill 1866.

Neophoca Gray 1866.

Phocarcos Peters 1866.

Otaria Péron 1816.

Otariidae, *incertae sedis*:

Oriensarctos Mitchell 1968.

Valenictus Mitchell 1961.

CONCLUSIONS

1. The eared seals, including sea lions, fur seals, walruses, and their fossil relatives are best classified in one family, the Otariidae, in the mammalian order Carnivora. In the Otariidae, I recognize six subfamilies: Enaliarctinae, Desmatophocinae, Allodesminae, Imagotariinae, Odobeninae, and Otariinae. This

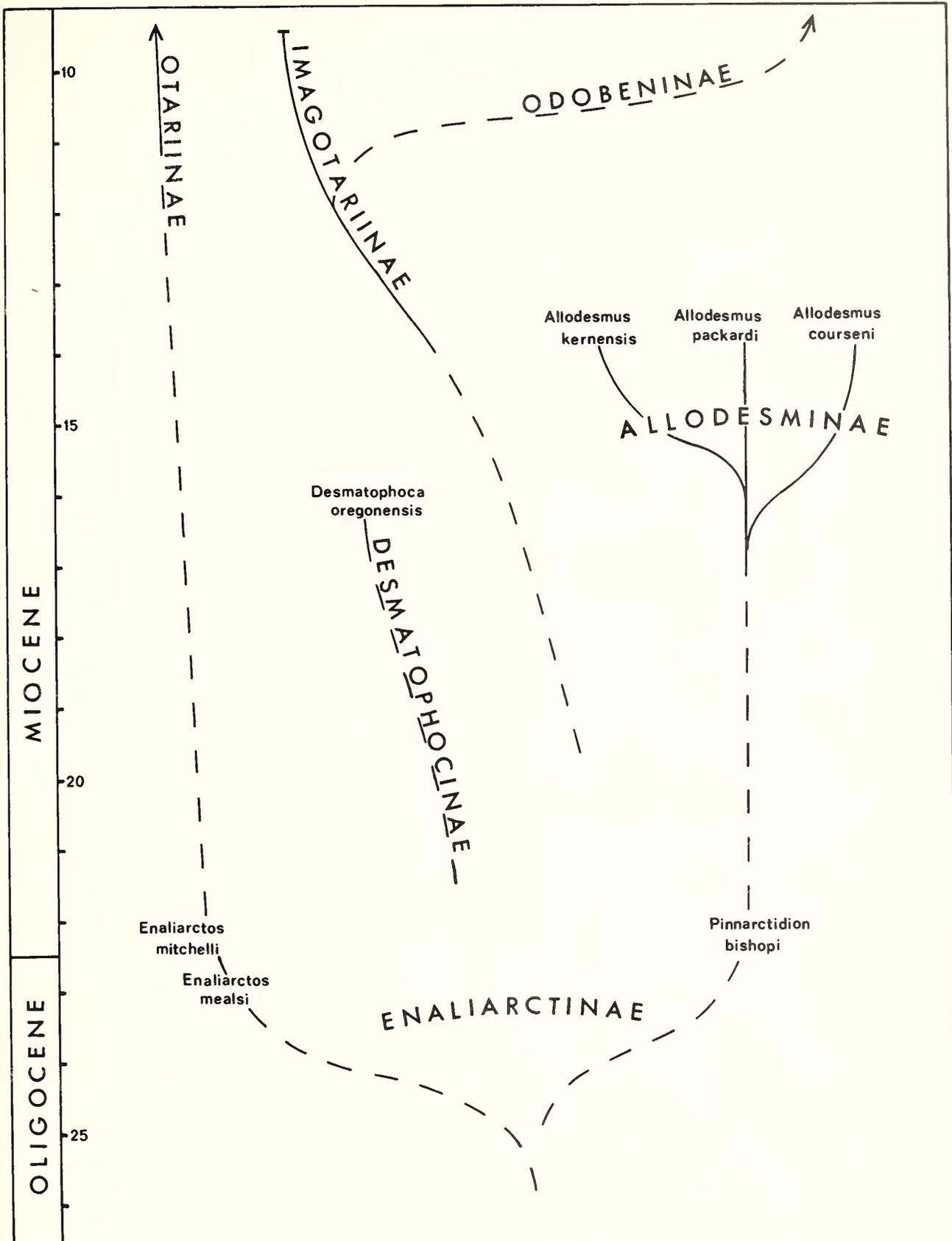


FIGURE 22. Suggested phylogeny of early enaliarctine otariids showing possible relationships to derived taxa. Dashed lines depict implied but uncertain relationships not yet documented by the known fossil record. Arrows indicate lineages that continue to present time. The positions of *Enaliarctos mealsi*, *E. mitchelli*, and *Pinnarctidion bishopi* are approximate relative to the time scale, but the positions of all indicated species are correct relative to one another based upon present stratigraphic information.

classification unites related animals into a single family having numerical and morphological diversity that is comparable with some other families of Carnivora.

2. The subfamily Enaliarctinae is the most primitive of these subfamilies and is apparently directly or indirectly ancestral to all the others. This subfamily contains three described species in two genera presently represented by fossils from the lower part of the Pyramid Hill Sand Member of the Jewett Sand which is exposed on the south face of Pyramid Hill in Kern County, California. These fossils are latest Oligocene to earliest Miocene in age, are correlated with the Arikareean North American land mammal age, the late Zemorrian or early Saucesian foraminiferal stages, and the "Vaqueros" provisional provincial marine megafaunal stage, and are, therefore, approximately 22 to 24 million years old.

3. The most primitive known genus of Enaliarctinae is *Enaliarctos* Mitchell and Tedford 1973. No new evidence contradicts previous suggestions that *Enaliarctos* may be involved in the ancestry of the derived subfamily Otariinae, which includes modern fur seals and sea lions.

4. The most primitive species of *Enaliarctos* is *E. mealsi* Mitchell and Tedford 1973. A new species, *Enaliarctos mitchelli*, is more derived than *E. mealsi*, was probably more specialized for aquatic existence, apparently had reduced carnassial function of the cheek teeth, and its source was probably from a higher stratigraphic level within the Pyramid Hill Sand Member than the beds that produced *E. mealsi*.

5. Another, very different enaliarctine is the more aquatically adapted *Pinnarctidion bishopi*, new genus and species. Its holotype is a fossil skull that was collected from rocks stratigraphically higher in the Pyramid Hill Sand Member than the probable source of specimens of *Enaliarctos mealsi*. The specimens of *Enaliarctos mitchelli* were probably derived from the same higher bed that produced *P. bishopi*, and the two species were probably contemporaries. It is not known whether these two species inhabited the same area simultaneously or whether differing migratory patterns separated their populations.

6. *Pinnarctidion bishopi* shares some primitive characters with *Enaliarctos mealsi* and *E. mitchelli*. It also shares many other characters, some of which appear to be derived, with middle Miocene species of the genus *Allodesmus*, and is therefore possibly ancestral to the subfamily Allodesminae. Some of the characters shared by *Pinnarctidion bishopi* and *Allodesmus* spp. are not present in *Desmatophoca oregonensis* of early middle Miocene age, and the latter species is therefore probably not an ancestor of *Allodesmus* spp. as has been previously suggested. This apparent dichotomy between the two lineages that led to *Desmatophoca oregonensis* and to *Allodesmus* spp. is older than has been previously suggested by some authors. This reinforces some other published arguments based on morphology that the nominal subfamilies Desmatophocinae and Allodesminae should be classified separately. Current evidence suggests, therefore, that these two subfamilies could only have shared a common ancestry prior to the existence of *Pinnarctidion bishopi* which lived between approximately 22 and 24 million years ago.

7. The anterior narial opening and other characters of *Enaliarctos mitchelli* are developed in ways indicating convergent evolution with some modern true seals of the family Phocidae. Examples of convergence between species of Phocidae and Otariidae have been pointed out by various authors, and it is significant that the phenomenon existed even among the earliest of

fossil otariids.

8. Mostly unpublished fossil evidence, including data on sharks, indicates that the two fossiliferous concretion-bearing beds at Pyramid Hill in the basal part of the Pyramid Hill Sand Member of the Jewett Sand contain different fossil vertebrate species. The existence of different pinniped species (*Enaliarctos mealsi* apparently in the lower bed, *E. mitchelli* and *Pinnarctidion bishopi* in the upper bed) in the two beds bolsters the probability that they differ substantially in age and/or environment of deposition. The Pyramid Hill Local Fauna, as defined by Mitchell and Tedford (1973), should therefore be strictly limited to the fossil assemblage from the basal "grit zone" of the Pyramid Hill Sand Member. The only specimen that Mitchell and Tedford (1973) assigned to the Pyramid Hill Local Fauna and which I would not, is the isolated matrix endocranial cast which they referred to *Enaliarctos mealsi* and which I have referred to *Pinnarctidion bishopi*, the species whose holotype is known to have been collected from the upper bed. The fossil assemblage from the upper bed, therefore, merits a separate local fauna name. I recommend that it not be named, however, until the assemblage is identified and the origin of the possibly redeposited bone-bearing concretions is investigated.

9. One other locality, at Point Arena in northern California, has produced a mandible tentatively identified as *Enaliarctos* sp. It is from the Skooner Gulch Formation of early Miocene age.

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SYSTEMATICS OF SKINKS OF THE *EUMECES*
BREVIROSTRIS SPECIES GROUP IN WESTERN MEXICO

By Michael D. Robinson



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SYSTEMATICS OF SKINKS OF THE *EUMECES* *BREVIROSTRIS* SPECIES GROUP IN WESTERN MEXICO¹

By Michael D. Robinson²

ABSTRACT: The *Eumeces brevirostris* species group as defined here contains seven species, one of which, *brevirostris*, is polytypic. Two taxa formerly allocated to the *multivirgatus* species group, *E. parviauriculatus* and *E. parvulus*, are placed in the *brevirostris* species group. The only character that distinguishes these supraspecific assemblages is the shape of the scale that medially borders the postgenial. It is wider than long in all species of the *brevirostris* group, but it is longer than wide in those of the *multivirgatus-brevilineatus* complex. Morphological variation, distribution, and ecology are summarized for the *brevirostris* group taxa in western Mexico (*E. brevirostris bilineatus*, *E. parviauriculatus*, *E. parvulus*, and *E. colimensis*).

Eumeces copei appears to have the ancestral scalation and color pattern of the *brevirostris* group, and the remaining species have character states derivable from it. The distribution of the group suggests that dispersal occurred from the Central Highlands and Trans Volcanic region of Mexico into forest and woodland habitats of the Sierra Madre Occidental and Oriental and the Sierra Madre del Sur.

In addition, scale and pattern comparisons of the syntypes of *E. humilis*, a taxon in the *multivirgatus-brevilineatus* complex, are made with *E. callicephalus* and *E. multivirgatus*; these data indicate that *E. humilis* is conspecific with and a junior synonym of *E. callicephalus*.

INTRODUCTION

In 1933 Taylor described two species of skinks, *Eumeces parviauriculatus* and *E. parvulus*, from four specimens collected in northwestern Mexico. In his monographic review of this genus (1935) and in a subsequent paper (1943), Taylor (1935:38) included these two species in the *multivirgatus* species group (although with reservations). During the next 36 years a few additional specimens were reported (Oliver 1937; Smith 1943; Peters 1954; Legler and Webb 1960; Duellman 1961; and Hardy and McDiarmid 1969), but no evaluation of interspecific and species group relationships of these skinks has been attempted. Until now, Taylor's (1935) species group arrangements have been maintained (e.g., Tanner 1957; Dixon 1969). Larger series of these and related species of montane skinks from northwestern Mexico have become available, making possible a reassessment of their relationships.

SPECIES GROUP DEFINITIONS

In the accounts below, the cephalic scale nomenclature used is that of Taylor (1935:71), but the designations for longitudinal and transverse scale rows and lateral body stripes are those outlined by Dixon (1969). Of the 27 scale and meristic characters analyzed, those most useful taxonomically are listed in Tables 1-4. A total of 151 specimens were analyzed (see Specimens Examined).

During the initial stages of this study it was apparent that Taylor's (1935) placement of *parvulus* and *parviauriculatus* with the *multivirgatus* species group was questionable. Many of the characters used by Taylor to define the *multivirgatus*, *brevilineatus*, and *brevirostris* groups are not exclusive (Table 1), and therefore

his definitions are too broad. Dixon (1969) accepted the majority of Taylor's (1935) definitions in his review of the *brevirostris* group.

When "diagnostic" characters of the species groups are compared (Table 1), two main points become obvious: first, there is no single character or combination of characters that will separate the *multivirgatus* and *brevilineatus* species groups; second, the only unequivocal character that unites skinks of the *brevirostris* group is the shape of the scale that medially borders the postgenial (not following it, *vide* Dixon 1969). This scale is wider than long in all *brevirostris* group taxa, but it is longer than wide in skinks of the *multivirgatus* and *brevilineatus* groups (Fig. 1). Three other characters are shared by members of the *brevirostris* group, but they also occur occasionally in taxa of the *multivirgatus* and *brevirostris* groups. These are the lack of a postnasal scale and median dorsal light stripe and the presence of a single postmental.

Data from this study indicate that the *brevirostris* group should be expanded to include *E. parviauriculatus* and *E. parvulus*, and that the *multivirgatus* and *brevilineatus* species groups be com-

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TABLE 1

Scale and pattern character states used to distinguish skinks in the *Eumeces brevirostris*, *multivirgatus*, and *brevilineatus* species groups.

	<i>Brevirostris</i> Group			<i>Multivirgatus</i> Group		<i>Brevilineatus</i> Group	
	Taylor (1935)	Dixon (1969)	This Report	Taylor (1935)	This Report	Taylor (1935)	This Report
Scale Medial to Postgenial ^a	W	W	W	L	L	L	L
Postmental	1	1	1	1-2	1-2	1-2	1-2
Postnasal	0	0	0	0-1	0-1	0	0-1
Med. Light Line	none	none	none	var.	var.	pres.	var.
Dorsolat. Light Line	var.	var.	var.	var.	var.	pres.	var.
Long. Scale Rows	22-28	20-28	20-28	20-26	24-28	24-28	26-30

^a W = wider than long; L = longer than wide.

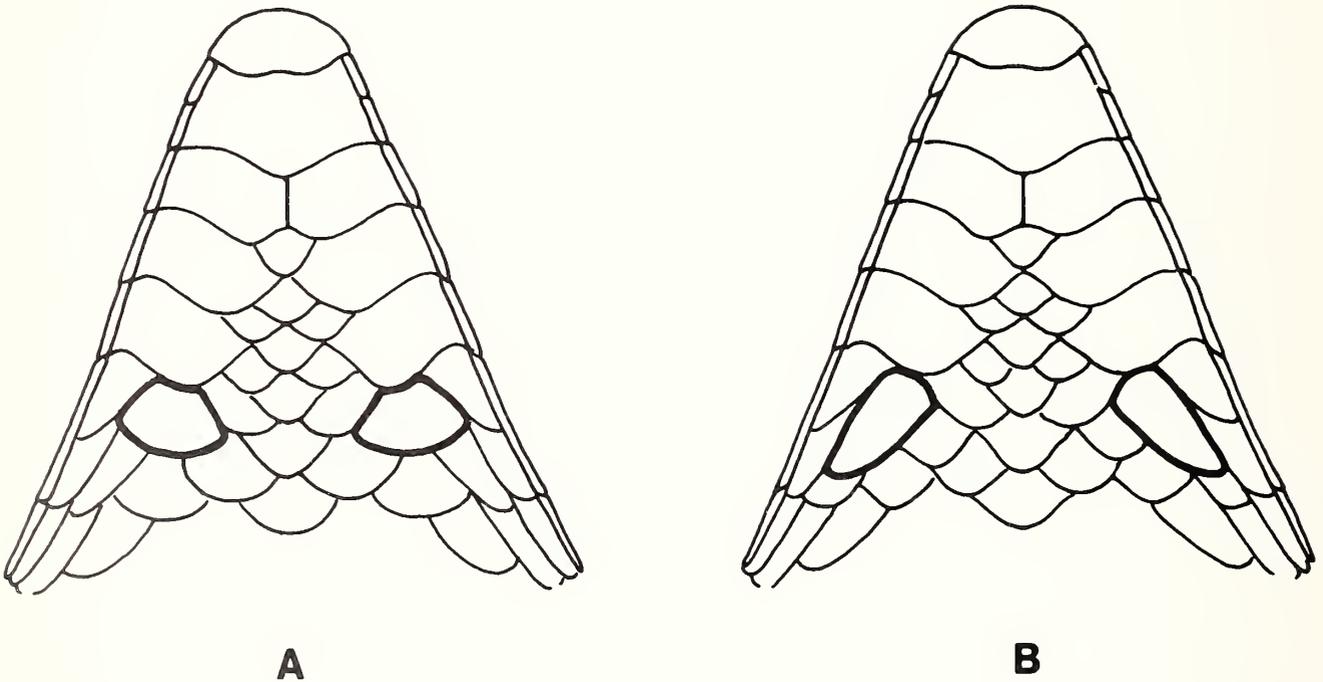


FIGURE 1. Shape of the scale medial to the postgenial in members of a) the *Eumeces brevirostris* group and b) the *multivirgatus* and *brevilineatus* groups.

bined (Table 1). Both *parviauriculatus* and *parvulus* have a scale medial to the postgenital that is wider than long, lack postnasal scales and a median dorsal stripe, and have a single postmental scale. Therefore, I have removed them from Taylor's (1935, 1943) *multivirgatus* group and include them with those species previously listed by Dixon (1969) as belonging to the *brevirostris* group. With this arrangement the *brevirostris* group contains seven species, one of which is polytypic:

E. brevirostris brevirostris (Günther)

E. b. bilineatus Tanner

E. b. dicei Ruthven and Gaige

E. b. indubitus Taylor

E. b. pineus Axtell

E. colimensis Taylor

E. copei Taylor

E. dugesii Thominot

E. ochoteranae Taylor

E. parviauriculatus Taylor

E. parvulus Taylor

The following accounts summarize and compare the scalation, color and pattern (Fig. 3, Tables 1–3), the known geographic distributions (Figs. 2, 4), and the ecological information for those taxa reaching northwestern Mexico (*b. bilineatus*, *parvulus*, and *parviauriculatus*). Holotypes were examined for *parviauriculatus*, *parvulus*, *brevirostris bilineatus*, and *humilis*. Comparisons with other taxa in the *brevirostris* group are made where existing keys and diagnoses are insufficient. In addition, the uncertain identity of a specimen of *E. colimensis* is discussed, and the taxonomic status of *E. humilis* is reviewed.

Eumeces brevirostris bilineatus Tanner

This subspecies of *brevirostris* was described by Tanner (1958) from specimens collected in montane regions of western Durango and southwestern Chihuahua. Dixon's (1969) analysis of variation in pattern and squamation of this taxon agree closely with the data presented here (Tables 2, 3) and will not be repeated. New comparisons with *parviauriculatus* and *parvulus* are made, and a zone of intergradation with *E. b. indubitus* is discussed.

COMPARISONS: A few species in the *brevirostris* group can be distinguished by the number of scales between the adpressed limbs (e.g., *parviauriculatus*, *colimensis*, and *brevirostris*). However, considerable ontogenetic variation exists in this character, and it is difficult to determine accurately on some preserved specimens. Juveniles ($s-v < 40\text{mm}$) of *bilineatus* consistently have fewer scales between adpressed limbs (0–3) than *parvulus* (8–21) or *parviauriculatus* (11–18). In adults this distinction is less clear between these species (Table 2), making identification by this character alone unreliable.

The frontonasal contacts the nasal less frequently in *bilineatus* (77%) than in *parvulus* (100%) or *parviauriculatus* (93%). Like *parvulus*, the interparietal scale of *bilineatus* is always enclosed by the parietal scales, but rarely so (3.4%) in *parviauriculatus*. In *bilineatus* the primary temporal is often absent (58.9%), and, when present, it seldom (17.4%) contacts the lower secondary temporal. All individuals of *parvulus* and *parviauriculatus* have a primary temporal scale that contacts the lower secondary temporal. The seventh supralabial contacts the upper secondary temporal in most specimens of *bilineatus* (92.8%), but never in *parvulus* or *parviauriculatus* (Table 3).

Dixon (1969) concluded that *bilineatus* differs from *indubitus*

by the lack of a longitudinal lateral light line on the neck, by the grading of the whitish color of longitudinal scale rows 5 or 6 into the white color of the belly, and by the dorsolateral light line usually extending to the tail or beyond. In contrast, *indubitus* has a longitudinal light line on the neck, the dark color below it extends laterally to the belly, and the dorsolateral light stripe becomes faint near the shoulder. One of Tanner's (1958) paratypes of *bilineatus* (USNM 64666), from the Sierra Juanacatlan, Jalisco, has these three characters of *indubitus*. Three specimens (MSU 4162, 7260, 7877) from Cueva and Pericas Summit, Durango, and from near Atenquique, Jalisco, have pattern features of both *bilineatus* and *indubitus*. They lack a longitudinal lateral line on the neck, the dark neck color extends onto the venter, and the dorsolateral line extends only to the shoulder. Two individuals (MSU 4163, 4165) collected near the type locality of *bilineatus* have patterns typical of *indubitus*. These six specimens suggest that the type locality of *bilineatus* is in a zone of intergradation with *indubitus*. The limits of this zone are unknown and must await additional material from the remote region between southern Durango and northwestern Jalisco.

DISTRIBUTION AND ECOLOGY: This race lives in the Sierra Madre Occidental from the vicinity of Mojarachic, Chihuahua to southern Durango (Fig. 2). The northern extent of the range is not established, but considerable collecting in appropriate habitats of northern Chihuahua and central Sonora have failed to produce specimens.

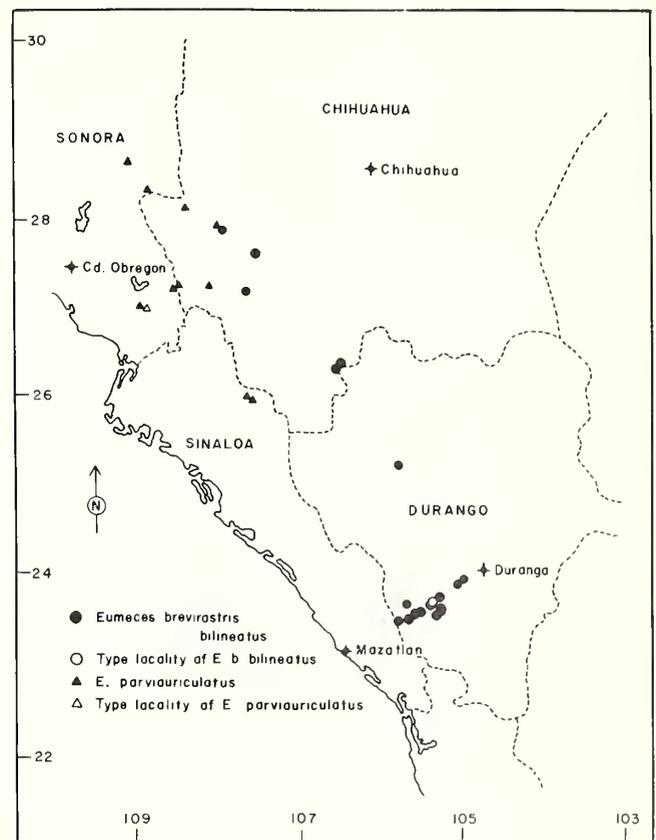


FIGURE 2. Geographic distribution of *Eumeces parviauriculatus* and *E. brevirostris bilineatus* in northwestern Mexico.

TABLE 2

Variation of four scale character states in four taxa of the *Eumeces brevirostris* species group from western Mexico. Statistics are mean, \pm standard error of mean, range, and sample size. Data for *E. b. indubitus* are from Dixon (1969; Jalisco).

	<i>E. brevilineatus indubitus</i>	<i>E. brevilineatus bilineatus</i>	<i>E. parvulus</i>	<i>E. parviauriculatus</i>
Transverse Scale Rows	60.1 \pm .36 56 – 68 51	59.6 \pm .29 55 – 63 54	60.3 \pm .59 55 – 62 12	63.5 \pm .32 61 – 66 26
Longitudinal Scale Rows	24.8 \pm .15 22 – 26 51	23.8 \pm .10 22 – 25 56	23.3 \pm .34 22 – 26 15	20.0 \pm .00 20 29
Fourth Toe Lamellae	13.4 \pm .17 11 – 16 51	10.2 \pm .11 9 – 13 56	11.1 \pm .27 10 – 12 16	10.2 \pm .12 9 – 11 29
Scales Between Adressed Limbs				
All	— — —	9.1 \pm .55 0 – 16 51	14.2 \pm 1.14 8 – 21 14	16.1 \pm .64 10 – 22 28
s-v > 40mm	— — —	9.9 \pm .44 2 – 16 45	15.6 \pm 1.21 10 – 21 9	17.2 \pm .60 10 – 22 21
s-v < 40mm	— — —	1.0 \pm .51 0 – 3 6	13.0 \pm 2.17 8 – 21 5	12.9 \pm 1.12 11 – 18 7

These skinks are commonly found under rocks, logs, and leaf litter in woodland (oak and oak-pine) and forest (pine and pine-fir) communities of 1500 to 2500 meters. At Mojarachic, Chihuahua (Fig. 2), *bilineatus* (UMMZ 117756) is sympatric with *parviauriculatus* (FMNH 106476) and *callicephalus* (Taylor and Knobloch 1940), and approximately 65 km southeast of there, near Creel, Chihuahua, both *E. multivirgatus* and *E. multilineatus* (*sensu lato*) have been collected (Legler and Webb 1960). Unfortunately, the ecological interrelationships of these five montane skinks in this area is not yet clear.

Eumeces parvulus Taylor

This species was described in 1933 by Taylor from three specimens collected in Nayarit and Sinaloa. It appears only fourteen more have been collected subsequently, but several workers have remarked on the differences between their samples and the holotype (Oliver 1937; Smith 1943; Peters 1954; Duellman 1961; Hardy and McDiarmid 1969). Variation in the scalation and pattern of the 17 specimens known to me is discussed below and summarized in Tables 2 and 3 and Fig. 3.

COMPARISONS: There are no significant differences between *bilineatus*, *parvulus* and *indubitus* in the number of longitudinal

or transverse scale rows, but *parviauriculatus* has distinctly fewer longitudinal and more transverse rows (Table 2). My counts of the number of fourth toe lamellae are one or two fewer than those reported for *indubitus* (Dixon 1969), probably from differences in our counting techniques. As juveniles (s-v < 40mm), *parvulus* has shorter limbs than *bilineatus*, but this distinction is less clear in adults (p. 5'). In cephalic scale features (Table 3), *bilineatus*, *parvulus*, and *indubitus* are similar, all having four supraoculars and an enclosed interparietal scale. Nor are there notable differences between them in the incidence of contact of the frontonasal with the frontal, or the seventh supralabial with the upper secondary temporal. The primary temporal is lacking on both sides in 58.9% of the specimens of *bilineatus*, but it is rarely absent in *indubitus* and *parvulus* (Table 3).

Eumeces parvulus is a more uniformly colored species than either *bilineatus* or *parviauriculatus*. Both the venter and dorsum of preserved specimens are uniformly pale yellow-brown (straw color), occasionally with a faint greenish cast (light olive-green). Peters (1954) described the ventral body color of a live animal as "greenish grey." The chin was yellow, while the appendages were colored similar to the body. Another live lizard had a pale blue tail, and its dorsolateral stripe was a "pale pinkish tan" (Duellman 1961).

TABLE 3

Percent of occurrence of ten cephalic scale character states in four taxa of the *Eumeces brevirostris* species group. Data for *E. b. indubitus* are from Dixon (1969; Jalisco).

	<i>E. brevirostris</i> <i>indubitus</i> (N=51)	<i>E. brevirostris</i> <i>bilineatus</i> (N=56)	<i>E. parvulus</i> (N=17)	<i>E. parviauriculatus</i> (N=27)
Frontonasal Contacts				
Frontal	37	77	100	93
Four Supraoculars (on both sides)	100	100	100	100
Three Supraoculars Border Frontal	93	99	68	96
Interparietal Enclosed	94	100	100	3
Postnasal Absent	—	100	100	100
Postmental Single	—	98	100	100
Scale Medial to Postgenial wider than long	—	100	100	100
Primary Temporal Present	99	41	100	100
Primary Temporal Contacts Lower Secondary Temporal	—	17	100	100
7th Supralabial Contacts Upper Secondary Temporal	98	93	00	00

The dorsolateral stripe arises near the rostral scale and occupies scale rows 2 and 3 posteriorly. It is short, never reaching much past the shoulder (Fig. 3). The lateral light line is seldom visible on preserved animals, but on those I examined from Michoacan it blended ventrolaterally with the color of the venter as in *bilineatus*.

Some characters of scutellation and pattern (Tables 2, 3) suggest that *parvulus* could be a geographic race of the polytypic species *brevirostris*. However, *parvulus* differs from all subspecies of *brevirostris* by lacking any contact between the seventh supralabial and the upper secondary temporal, a condition shared with *parviauriculatus* and to some extent *copei* (10% contact). Areas of sympatry between *parvulus* and other *brevirostris* group skinks are not known (Fig. 4), but the few specimens of *parvulus* from areas of potential contact have no indication of intergradation with *indubitus* or *bilineatus*. Thus, pending data to the contrary, I have retained specific status for *parvulus*.

DISTRIBUTION AND ECOLOGY: *Eumeces parvulus* appears restricted to the foothills and lowlands west of the Sierra Madre Occidental and south of the Trans Volcanic Range in the coastal states of Sinaloa, Nayarit, Colima and Michoacan (Fig. 4). The range disjunctions in coastal Jalisco and northern Nayarit probably result from lack of exploration.

The limited ecological data available for *parvulus* (Oliver

1937; Duellman 1961; Hardy and McDiarmid 1969) indicate that it occurs in lower elevation (<500 m) tropical broadleaf forests in Nayarit, Colima, and Michoacan, and in the higher elevation (ca. 1000 m) transitional communities (oak woodland and oak-pine woodland) in Sinaloa and Nayarit.

Eumeces parviauriculatus Taylor

Since the description of this species (Taylor 1933), three additional specimens, also from Chihuahua, have been reported (Taylor and Knobloch 1940; Legler and Webb 1960). McDiarmid *et al.* (1976) discussed the variation in the first specimens recorded from Sinaloa. This analysis summarizes the data from the 29 specimens now available.

COMPARISONS: The number of transverse scale rows is slightly higher in *parviauriculatus* than in *bilineatus* or *parvulus*, and the number of fourth toe lamellae is slightly lower (Table 2). The consistently low number of longitudinal scale rows (20) is characteristic of *parviauriculatus*; *copei* and *ochoterenae* occasionally have 20 scales in the longitudinal series (Dixon 1969), but they both differ from *parviauriculatus* in the length and position of the lateral and dorsolateral stripes. Members of the species have a high number of scales between adpressed limbs

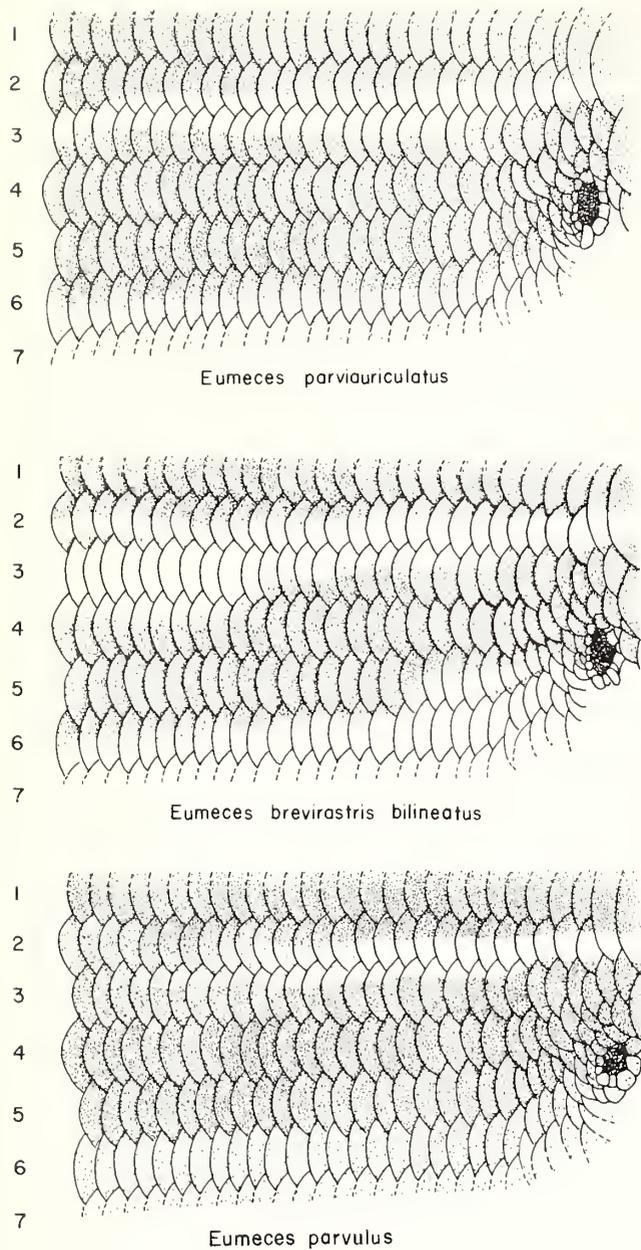


FIGURE 3. Lateral stripe patterns of three species of *Eumeces* from northwestern Mexico. View is the right lateral region of the neck and mid-body. *E. parviauriculatus*, Sonora (UAZ 28123); *E. b. bilineatus*, Durango (MSU 9375); *E. parvulus*, Michoacan (UMMZ 104447).

throughout ontogeny, and in this respect are distinctive from *bilineatus* (Table 2).

As in *parvulus*, the primary temporal is present and contacts the lower secondary temporal in all specimens; the seventh supralabial never contacts the upper secondary temporal. The frontonasal usually (93%) borders the frontal, and the interparietal is rarely enclosed (3.4%). Like other members of the *brevirostris* group, *parviauriculatus* lacks postnasals and a median white stripe, has a single postmental, and the scale medially bordering the postgenial is wider than long (Table 3). Taylor (1933) remarked that this species has a distinctly small ear opening due to

the overlapping postlabial scales. Although this condition is usually apparent, it is difficult to quantify and compare to other taxa.

The narrow dorsolateral stripe is confined to scale rows 2 and 2-3 near the nape and then to the upper half of row 3 to the rump and beyond (Fig. 3). This dorsolateral stripe formula is similar to that in *copei*, some *b. brevirostris*, and *ochoterenae* (Dixon 1969), but in these lizards this stripe does not extend onto the tail. The lateral light line extends to the shoulder on scale rows 6 and 7, and is shorter than in either *copei*, *ochoterenae*, or *b. brevirostris*. The tail is a brilliant metallic blue in young lizards but less striking in adults. Legler and Webb (1960) described the body color and pattern of a juvenile. The live adult animals that I have seen from southern Sonora differ only in having less contrast between the light stripes and the background color.

The long slender body and short legs of *parviauriculatus* are manifested in its reduced number of longitudinal scale rows, higher counts of transverse scales, and greater number of scales between adpressed limbs.

DISTRIBUTION AND ECOLOGY: This species inhabits the higher mountainous regions (1500-2300 m) of southeastern Sonora, southwestern Chihuahua, and northeastern Sinaloa (Fig. 2).

Attempts to locate this skink north of the northernmost known locality near Bamuri, Sonora, have failed, and to my knowledge appropriate habitats south of the known Sinaloan localities have not been sampled. Geographic overlap with *bilineatus* occurs at

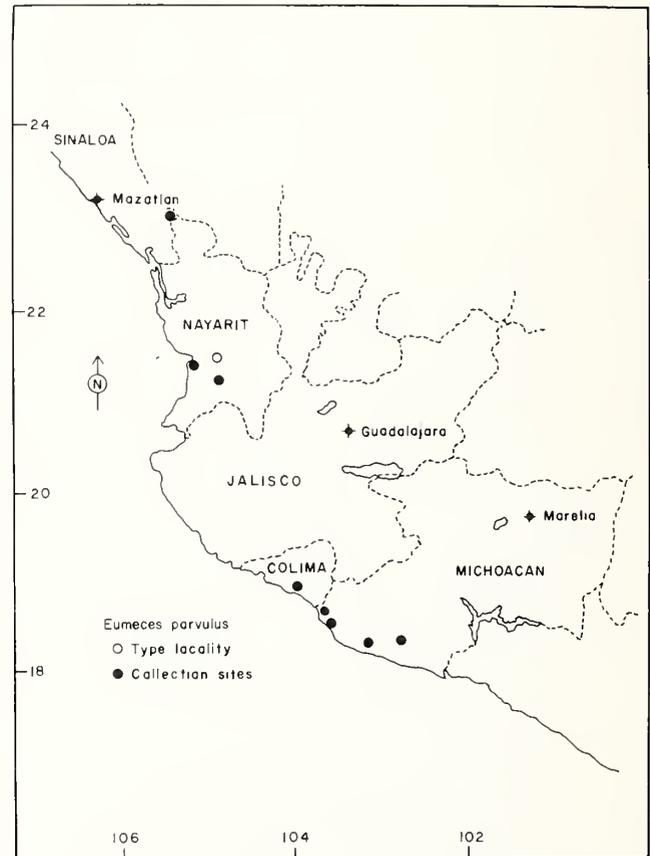


FIGURE 4. Geographic distribution of *Eumeces parvulus* in western Mexico.

TABLE 4

Scale and pattern character states of *Eumeces colimensis*, KU 44733, and *E. callicephalus*.

	<i>colimensis</i>	KU 44733	<i>callicephalus</i>
Scale Medial to Postgenial	wider than long	wider than long	longer than wide
Lower Secondary Temporal	absent	absent	absent
Postlabials	2	2	1 (.93)
Size of 6th and 7th Supralabials	7th largest (except on type)	7th largest	Approx. equal
Length of Lateral Light Line	obscure at midbody	supralabials to tail	variable
Dorsolateral Stripe Scale Row Formula	2, 3, 4, 5	2-3	2, 3, 4

Mojarachi, Chihuahua (Fig. 2), but the remaining *parviauriculatus* localities are on mountains that are western outliers from the main Sierra Madre cordillera.

Taylor (1933) designated the type locality of *parviauriculatus* as Alamos, Sonora (presumably the town), but in view of what is now known of its ecological distribution and from unsuccessful attempts to find it near the town, the holotype was most likely collected on the nearby Sierra Alamos where it lives today.

These skinks, which inhabit the semi-tropical evergreen oak woodland and pine forest, are more frequently observed at the beginning of the summer rains in late June or early July, and are found under logs, rocks, and leaf litter, especially at riparian localities.

Two additional systematic problems are considered next and involve the questioned identity of a single specimen of *E. colimensis* from Sinaloa and the uncertain status of *E. humilis*.

Eumeces colimensis Taylor

Only four specimens of this species are known, and all have considerable variation in the head scalation. Dixon (1969) questioned Webb's (1959) identification of a skink from southeastern Sinaloa (KU 44733) as *E. colimensis* because it differed from the three more southern specimens by having: 1) a well-defined lateral light line extending from the supralabials to the tail; 2) a dorsolateral light line confined to the lower half of scale row 2 and the upper two-thirds of row 3, instead of descending to rows 3, 4 and 5; and 3) a small primary temporal present, and a large seventh supralabial that contacts the upper secondary temporal. The seventh supralabial is smaller and the primary temporal is absent in the holotype. Dixon (1969) suggested that this specimen may be related to *callicephalus*.

Hardy and McDiarmid (1969) examined the same four specimens and concluded that KU 44733 was *E. colimensis*. They remarked that the type, which apparently is rather "atypical," differs from the other specimens by lacking a primary temporal

(fused with upper secondary temporal), by having a frontal-interparietal contact, and by having a greater amount of overlap of the adpressed limbs. Of the various scale and pattern characters (Table 4), the most significant is the shape of the scale that medially borders the postgenial (Fig. 1). In the KU specimen this scale is wider than long, and this precludes its assignment with *callicephalus* or any member of the *multivirgatus-brevirostris* group. The reduced size of the seventh supralabial in KU 44733 occurs occasionally in other species of *Eumeces*. The remaining deviations noted by Dixon (1969) involve the length and scale row position of the lateral lines, and these are characters known to vary intraspecifically in the *brevirostris* group. Therefore, I concur with Webb (1959) and Hardy and McDiarmid (1969) that the specimen is a *colimensis*. It may, however, represent an undescribed northern race of *colimensis*.

The nomenclatural history of *E. humilis* has been confusing. Boulenger (1883) applied the name *E. bocourtii* to two specimens collected in Mexico by Forrer from "Presidio," presumably the presidio near Mazatlan, Sinaloa (Kellogg 1932; Taylor 1935). Günther (1885) illustrated one of the syntypes. Since the name *bocourtii* was preoccupied by a New Caledonian species, Boulenger (1887) selected *E. humilis* as its replacement.

Mosauer (1932) and Taylor (1935) reported several skinks collected in southern Texas as *humilis*. Smith (1942) later demonstrated that these specimens differed from the syntypes of *humilis*, because they had a double postmental, widened subcaudals, and lacked dorsolateral light lines. He then described the Texas specimens as *E. taylori* (= *multivirgatus*) and corrected Mosauer's (1932) and Taylor's (1935) errors of considering the postmental single. The most recent reference to the name *humilis* was by Hardy and McDiarmid (1969:142) who relegated "... all specimens of *Eumeces* from the coastal lowlands ... to *E. callicephalus*."

Each syntype of *humilis* (BMNH 8.20.66-67) has a scale medial to the postgenial that is longer than wide, allying them with

the *multivirgatus-brevilineatus* complex (Table 5), not with the *brevirostris* group. The median preanal scales in both *multivirgatus* and *humilis* are of similar size and are noticeably larger than the adjacent scales overlapping them (in *callicephalus* the size is equal, or the median preanals are only slightly larger); there is no trace of a middorsal line on the head or body (it is nearly always present in *callicephalus*); the anterior median subcaudals are often 1.25 to 1.5 times wider than adjacent scales (they are approximately equal in size in *callicephalus*). I found the relative size of the anterior subcaudals to be variable within a sample and therefore a somewhat unreliable character. Similarity of *humilis* to *callicephalus* occurs in the equal size (height and width) of the sixth and seventh supralabials, whereas the seventh supralabial is wider than the sixth in *multivirgatus*.

The color pattern, which appears faded in the syntypes, is a uniform light olive-brown near the head, becoming a gray-green on the back. The throat is a pearly white. The venter has an infusion of brown from the dark-centered scales. There is no middorsal stripe, and the faint dorsolateral stripe extends from the labial region posteriorly to the front of the shoulder on scale rows 2-3, 3, 3-4, and 4. The dorsolateral light line is on these same scale rows in specimens of *callicephalus* and *multivirgatus* from Mexico (Table 5). With old or faded material it is difficult to distinguish between the few *callicephalus* that lack a middorsal stripe and the weakly striped morphs of *multivirgatus*. Thus the pattern of the syntypes could be either and offers little help toward identification of these specimens.

My first inclination was that *humilis* was most similar to *multivirgatus*, but several factors make this choice unlikely. First, the supralabials, which are less variable than either subcaudal scales or color patterns, argue for a relationship with *callicephalus*. Second, there appears to be no reason to doubt Forrer's locality (see Kellogg 1932) for *humilis*, which is very close to where *callicephalus* has been collected recently (Zweifel 1962). Moreover, although Forrer collected in Durango and probably in habitats suitable for *multivirgatus* as well as *callicephalus*, the former is not yet known from either Durango or from lowland habitats west and south of the Sierra Madre Occidental.

A good deal of the confusion with the two *humilis* specimens is no doubt due to their age and the faded condition of their patterns. In the absence of additional material, the most parsimonious decision is to regard *humilis* as a synonym of *callicephalus*. A similar conclusion was reached by Stephens and Loomis (see Hardy and McDiarmid 1969).

EVOLUTIONARY AND BIOGEOGRAPHIC RELATIONSHIPS IN THE *BREVIROSTRIS* GROUP

As defined here, the *brevirostris* group contains seven species; six are monotypic and one, *brevirostris*, is polytypic containing five subspecies. With this redefinition, the group appears to be a monophyletic assemblage whose members all share several apparently derived pattern and scale characters (p. 3) that are distinct from other phyletic lineages within the genus. The intergroup relationships of *Eumeces* have not been analyzed since Taylor's (1935) initial study, and I can only repeat his suggestion that species of the *brevirostris* group seem most closely related to those in the *skiltonianus* group. My interpretations of several evolutionary trends and biogeographic patterns, involving mainly

the species of northwestern Mexico, are given below and are compared to previous hypotheses.

Although Dixon (1969) stated that *dugesii* is intermediate to the other species in a number of scale features and is unique in having only three supraoculars, he maintained that it may be the most primitive. He also hypothesized that *copei* and *ochoterenae* are the most specialized, even though the former species is the only one with what he considered (and I agree) to be the primitive color pattern. My view is that *copei* has the ancestral pattern and cephalic scalation, and that the remaining taxa in the *brevirostris* group have features derivable from those conditions.

Both *parviauriculatus* and *parvulus* share more cephalic scale features with *copei* than do any other *brevirostris* group taxa. Like *copei*, *parviauriculatus* has the interparietal scale free, lacks contact of the seventh supralabial with the upper secondary temporal, often has the frontonasal and nasal in contact, and has a primary temporal. The single pattern difference is the shortening of the lateral white line in *parviauriculatus*, and its body is longer and slimmer. Similarity of *parvulus* to *copei* is in the lack of contact between the seventh supralabial and the upper secondary temporal, the adjacent position of the frontonasal and nasal scales, and the presence of the primary temporal. *Eumeces parvulus* differs from *E. copei* in having an enclosed interparietal scale and greatly reduced dorsolateral and lateral light lines. In cephalic scalation and pattern, *parviauriculatus* has changed little from *copei* and therefore appears closely related to it, while more divergence has occurred in *parvulus*.

Fundamental to the biogeography of these skinks is their preference for montane or plateau forest or woodland habitats; even those living near sea level (*parvulus*) occur in lowland forest extensions of the coastal mountains. The distribution of the *brevirostris* group suggests that dispersal occurred from the Central Highlands and Trans Volcanic Range region of Mexico and radiated outward through suitable habitats of the major mountain chains, such as the Sierra Madre Occidental and Oriental and the Sierra Madre del Sur. The greatest species diversity (6 of the 11 taxa) is in the mountain and plateau region of Michoacan and Guerrero, and from there it decreases in all directions.

The known range of *parviauriculatus* (Fig. 2) implies that it might be a northwestern extension of a *copei* lineage that was previously more widely distributed in the main Sierra Madre Occidental. Perhaps *parviauriculatus* has been replaced by *brevirostris bilineatus* and is now mainly confined to satellite mountains (p. 8). It is likely that *parvulus* has a more continuous distribution along the coastal mountains of western Mexico (Fig. 3). This species seems to be a western derivative of *copei* that has adapted to the semi-tropical communities of the outlying coastal ranges.

SPECIMENS EXAMINED

The specimens analyzed in this study are deposited in the following collections: American Museum of Natural History (AMNH); University of Arizona (UAZ); British Museum Natural History (BMNH); Carnegie Museum (CM); Field Museum of Natural History (FMNH); Joseph F. Copp, private collection (JFC); University of Kansas (KU); Los Angeles County Museum of Natural History (LACM); Michigan State University (MSU); Museum of Vertebrate Zoology (MVZ); Robert G. Webb, private

TABLE 5

Scale and pattern character states of *Eumeces humilis* (Sinaloa), *E. multivirgatus* (Chihuahua), and *E. callicephalus* (Nayarit, Chihuahua, Sinaloa, and Sonora). Frequencies are expressed as decimals.

	<i>E. humilis</i> (N=2)		<i>E. callicephalus</i> ^a (N=11)	<i>E. multivirgatus</i> (N=5)
	BMNH 8.20.66	BMNH 8.20.67		
Scale Medial to Postgenial	longer than wide	longer than wide	longer than wide	longer than wide
Median Preanal Scales	largest	largest	approx. equal	largest
Middorsal Line	none	none	usually present	none
Postnasals	1-1	1-1	1 (.73) 0 (.27)	0-0 (.20) 0-1 (.40) 1-1 (.40)
Anterior Subcaudals	enlarged	enlarged	approx. equal	enlarged
Postmental	1	1	1 (.45) 2 (.55)	1 (.80) 2 (.20)
Postlabials	2	1	1 (.64) 2 (.36)	2 (1.00)
6th and 7th Supraoculars	equal height width	equal height width	equal height width	7th wider than 6th
Dorsolateral Stripe Scale Row Formula	2-3, 3 3-4, 4	2-3, 3 3-4, 4	2, 2-3, 3 3-4, 4	2, 2-3 3-4, 4

^aData for a larger sample (N=34) of *callicephalus* from Mexico (Carl Lieb, pers. comm.) indicates the frequency of (1) postnasals (at least one present), .86; (2) postmental divided, .63; and (3) postlabials single, .94.

collection (RGW); University of Michigan Museum of Zoology (UMMZ); United States National Museum (USNM).

Eumeces brevirostris bilineatus: MEXICO: Chihuahua: 24 km S and 9.6 km E Creel (KU 44262-63); 3.2 km W Samachique (KU 47429, 51324-25); Mojarachic (UMMZ 117756); Rio Verde (MVZ 59139). Durango: 16 km SW El Salto (KU 44732); 14.4-24 km SW El Salto (KU 44726-31); 4 km W San Luis (UMMZ 110905); Laguna del Progreso (UMMZ 113635-38); Hacienda Coyotes (UAZ 39501, UMMZ 113639, FMNH 1506); vic. Palo Gordo (CM 57909, UAZ 39495-500); 26 km E El Salto (AMNH 96609); 16 km E Llano Grande (RGW 5649-51); 2.4 km W San Luis (RGW 5665); 9.6 km SE Llano Grande (RGW 6100, 6117); Cueva, 12.8 km S El Salto (MSU 4162-5); 28.8 km SSW Tepehuanes (MSU 9370-5); Las Adjuntas (MVZ 59141, 59143, 59145, 59147, 59149, 59151); 16 km W El Salto (UAZ 38264).

Eumeces brevirostris indubitus: MEXICO: Jalisco: N slope Nevado de Colima (UAZ 31822, 31824-27); 3 km NE Talpa (KU 73744); Sierra Juanacatlan (USNM 64666); Nevado de Colima, 11.2 km W Atenquique (RGW 3304). Durango: Cueva, 12.8 km S El Salto (MSU 4163); 1.6 km ESE Cajones (MSU 4165).

Eumeces brevirostris indubitus X *Eumeces brevirostris bilineatus*: MEXICO: Jalisco: Nevado de Colima, 11.2 km W Atenquique (MSU 7260). Durango: Cueva, 12.8 km S El Salto (MSU 4162); 2.4 km E Peracas Summit (MSU 7877).

Eumeces colimensis: MEXICO: Sinaloa: 1.6 km E Santa Lucia (KU 44733).

Eumeces callicephalus: MEXICO: Chihuahua: 12.8 km W Matachic (AMNH 68295). Jalisco: Hostotipaquillo (AMNH 17943). Nayarit: Rosamorada (AMNH 15488); NW Santiago Ixcuintla (AMNH 19305-06); 8 km NE Sentispac (AMNH

87973-77); Laguna de Santa Maria del Oro (AMNH 96608). *Sinaloa*: 8.0 km N Mazatlan (AMNH 87672); Presidio (BMNH 1946.8.20.66-67). *Sonora*: Alamos (AMNH 64219).

Eumeces multivirgatus: MEXICO: *Chihuahua*: 7.2 km SE Galeana (UAZ 36306, 35924-26). *Coahuila*: 8.0 km W Cuatro Ciénegas (UAZ 38267).

Eumeces parviauriculatus: MEXICO: *Chihuahua*: 4.8 km NE Temoris (KU 51463-64); La Pulvosa (UMMZ 114502); Mojarachic (FMNH 106476). *Sinaloa*: 1.6 km SE Los Hornos (JFC 67-17, 67-18); 0.6 km N Los Hornos (JFC 68-104); 4.3 km SE Los Hornos (JFC 69-82); 2.9 km NW Surutato (JFC 69-85, 69-86); 1.6 km E Buenas Juntas (JFC 70-15, 70-16); Rancho El Madrono (JFC 71-21). *Sonora*: Sierra de Alamos (AMNH 104462); near Alamos (USNM 47536); stream near Sonora-Chihuahua border, above Alamos (MVZ 74187-90, 74198); Yecora (UAZ 35174, 28123); Sierra Alamos (UAZ 39507); 4.6-15.5 km SE Milpillas, Chihuahua (UAZ 39502-06); 18.6 km ESE Bamuri (LACM 121432).

Eumeces parvulus: MEXICO: *Colima*: 15 km NW Periquillo (UMMZ 80108). *Michoacan*: 1.6 km NE La Placita (UMMZ 104446); 1.6 km N Pomaro (UMMZ 104447, 2 specimens); 1.6 km WNW San Pedro Damian (UMMZ 104448, 3 specimens); 4.3 km E El Ticuíz (UMMZ 115093). *Nayarit*: 1.9 km N Santa Cruz (LACM 51566-67); between Matsuchan, Santa Cruz, and Tepic (USNM 147984); "Miniman" (USNM 51395)¹; Compostela (FMNH 94825-26); Tepic (USNM 56903). *Sinaloa*: Plomosas (USNM 47667); 4.8 km SE Plomosas (KU 91415, LACM 126983).

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RESUMEN

Taylor (1935) añadió dos especies de escincidos, *Eumeces parviauriculatus* y *E. parvulus*, al grupo *multivirgatus*. El análisis del diseño de la coloración y de la escamación del material de éstos y de otros taxones recientemente coleccionados en el noroeste de México, indican que estas especies pertenecen al grupo *brevirostris*. Con esta adición, el grupo *brevirostris* consta ahora de seis especies monotípicas y de una séptima, *brevirostris*, que es politípica y que posee cinco subespecies.

El grupo *brevirostris* puede distinguirse de otras especies y grupos de escincidos mexicanos porque sus representantes tienen mas ancha que larga la escama que bordea la parte media de la postgenial. Otras características útiles para diagnosticarlos son las siguientes: ausencia de la escama postnasal, presencia de una ligera raya medial y de una sola escama postmental. En este artículo se comparan y se resumen los detalles de la escamación, el desarrollo, la distribución y la ecología de *E. parviauriculatus*, *E. parvulus*, y *E. brevirostris bilineatus*.

Se sugiere que *E. copei* es la especie mas similar al tipo ancestral del grupo, y que de ella han derivado los distintos taxones del género. *E. parviauriculatus* ha cambiado muy poco a partir

de *copei*, mientras que *parvulus* presenta varios estados de caracteres derivados. Las especies de este grupo muestran su mayor diversidad en las regiones de las mesetas y de las montañas de Michoacán y Guerrero, y a partir de allí, su número se reduce en todas las direcciones.

Se revisa la historia de la nomenclatura y el estado taxonómico de *E. humilis*, miembro del complejo *multivirgatus-brevilineatus*. Se presentan datos que indican que *humilis* es un sinónimo del *E. callicephalus*.

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¹The locality "Miniman" cannot be located on maps or gazetteers. Apparently a typographic error is involved and the locality is probably Miramar, which is near where *parvulus* has been collected recently.

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A NEW SPECIES OF ROCKFISH, GENUS *SEBASTES* (SCORPAENIDAE), FROM THE EASTERN NORTH PACIFIC OFF MEXICO AND CALIFORNIA¹

By Robert N. Lea² and John E. Fitch³

ABSTRACT: A new species of rockfish, *Sebastes melanosema*, is described from three specimens collected in the eastern North Pacific. This form is distinguished from all other Pacific species of *Sebastes* by a combination of characters: six anal soft-rays, 11 to 12 dorsal soft-rays, 34 to 37 gill rakers, black fringing of the spinous portion of the dorsal and anal fin membranes, and morphology of the lachrymal projections. The terminology of shoulder spines is corrected from previous work on this genus. The description of this rockfish brings to 69 the known number of *Sebastes* for the eastern North Pacific.

During a cruise in 1971 off Baja California, Mexico, aboard the California Department of Fish and Game research vessel *Alaska*, two small rockfish were collected which could not be identified with any known *Sebastes* from the eastern North Pacific. These specimens were taken in June from San Pablo submarine canyon in traps which had been fished at 100 fm (183 m) on the slope of the canyon.

On 16 February 1976 a single individual belonging to this same unidentified species was taken on hook-and-line by Louis N. Murphy (Costa Mesa, Calif.) while fishing in about 75 fm (137 m) off Laguna Beach, Orange County, California, over 420 miles (676 km) north of the San Pablo canyon locality.

The following description of this new rockfish is based upon these three individuals comprising the holotype and two paratypes, and brings to 69 the number of known species of *Sebastes* for the eastern North Pacific (Chen 1975). To facilitate comparison with other California species, most measurements and counts follow the format of Phillips (1957). In several instances, as noted, we have followed Chen (1971). Terminology of the shoulder spines has been modified, however.

In previous publications on the rockfishes of the eastern North Pacific, the first shoulder spine has been referred to, erroneously, as the supracleithral (Clemens and Wilby 1946, 1961; Phillips 1957; Chen 1971, 1975; Morgenroth and Morgenroth 1969; Lea and Fitch 1972; Miller and Lea 1972; Hart 1973; and others) but since it is actually a projection of the posttemporal bone (Matsubara 1943; Smith 1957; and Eschmeyer 1969), its correct terminology would be posttemporal spine. It may be either single or

double in the genus *Sebastes*. The second shoulder spine, historically noted as the cleithral in *Sebastes*, projects from the supracleithrum and thus should be the supracleithral spine. It is usually single but occasionally double. The true cleithral spine is on the cleithrum just above the pectoral fin base, and in *Sebastes* it may be buried and not visible or may appear as a slight to moderate projection. The degree of development of the cleithral spine may prove useful at the specific level (taxonomically) as have most of the cranial and other shoulder spines in this group of fishes.

The following description is based upon the three known specimens.

¹REVIEW COMMITTEE FOR THIS CONTRIBUTION.

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Sebastes melanosema NEW SPECIES

Semaphore rockfish

Figures 1 and 2

DIAGNOSIS: The following combination of characters serves to distinguish *S. melanosema* from all other known species of *Sebastes* from the eastern North Pacific. Six anal soft-rays, 11 to 12 dorsal soft-rays and 34 to 37 gill rakers will separate *S. melanosema* from the vast majority of eastern Pacific *Sebastes*. The morphology of the lachrymal projections, the anterior projection sharp and directed forward and the posterior projection distinctly bifid and directed downward, does not appear to be closely similar to any other member of the genus. Melanistic fringing of the spinous portion of the dorsal and anal fin membranes is characteristic of this new species.

DESCRIPTION: Where there is any variance in the three specimens, data concerning the paratypes are given in parentheses.

D. XIII, 12(11); A. III, 6; Pect. 18(17); Pelvics 1, 5; rakers on first gill-arch 35, 36 (34, 37); pored lateral-line scales 38, 39 (34, 40); principal caudal rays 14; vertebrae including hypural 10 + 16 = 26.

Top of head at midorbit concave, a median groove between a pair of low frontal ridges; nasal, preocular, postocular, tympanic, parietal, and nuchal spines present — on left side a spine is present between the postocular and tympanic, its position and shape indicate it is simply an extra spine (nuchal spine present only on left side in Baja California paratype, and both nuchal spines absent in California specimen); cranial spines moderately strong and sharp; parietal ridges moderately high and thin; the five preopercular spines strong and sharp, upper two directed posteriorly, lower three radially directed, these spines decreasing in size from top to bottom with lowermost spine mostly embedded; the two opercular spines strong and sharp, uppermost the longest; posttemporal and supracleithral spines present, well-developed (on right side of Baja California paratype a second spine projecting from area of supracleithrum); cleithral spine a bony projection, not a discrete spine; lachrymal projections three-pointed, first point sharp and directed anteriorly, second is bifid with points moderately sharp and directed ventroanteriorly [this terminology from Chen 1971; referred to by Phillips (1957) as sub-orbital spines], lower posterior edge of gillcover smooth.

A moderately developed, downward projecting, symphyseal knob; teeth on tip of lower jaw slightly elevated, but not a definite raised patch; end of maxillary reaches to vertical of posterior third of orbit (to mid-orbit in California paratype, under rear edge of orbit in Baja California paratype); maxillaries and branchiostegals covered with scales; mandibles finely scaled, smooth to touch; premaxillaries smooth; tips of pectorals extend beyond origin of anal fin, reach a vertical to third anal spine (extend beyond anus but not to origin of anal fin in paratypes); tips of pelvics extend beyond anus but not to origin of anal fin (not quite to anus in paratypes); second anal fin spine twice as thick as third, extends slightly past tip of third when depressed (equal in length to third in California paratype); spinous dorsal fin membranes moderately incised; caudal fin slightly indented; terminal profile of anal fin with a slight posterior slant.

Color when fresh reddish with lighter colored blotching on dorsum, blotches ventrad to D III-IV, VIII-IX, XI-1 and 12.

Lateral line in a clear, light-red zone. Dorsal and anal fin membranes red with black dotting, outer fringe of membrane between spines solid black; caudal fin membrane red; pectoral fin membrane with a black mid-section, proximal and distal portions of fin red. Mouth dusky, a dark blotch on underside of opercle. Peritoneum black.

The otoliths (sagittae) were removed from all three individuals and examined for evidence of age as well as for distinguishing characters. Those of the holotype (Fig. 3) measured 8.7 mm long by 5.3 mm high, and there were either 7 or 8 hyaline growth zones. Unfortunately, the holotype was preserved in formalin for nearly a month prior to removing its otoliths, and the acidic formalin reacted with the aragonitic otoliths in such a manner as to leave all exposed surfaces slightly chalky, which effectively masked one or two of the marginal hyaline zones. The six annuli inside these were quite distinct, however. Since the otoliths from the paratypes were removed prior to preservation, marginal annuli were crisp and readily distinguishable. The right sagitta of the Baja California specimen was 7.8 mm long by 4.7 mm high and showed six excellent annuli. The left sagitta of that fish had several freakishly-developed areas, which precluded making an age determination from it. Both sagittae of the Laguna Beach fish were in good condition and seven winter annuli (hyaline zones) could be discerned; they were of identical length and height: 9.0 by 4.8 mm.

The sagittae of *S. melanosema* (Fig. 3) are easily distinguished from those of the other five dwarf (i.e., shorter than 250 mm maximum length) species which inhabit the eastern Pacific between Magdalena Bay, Baja California, and British Columbia. Sagittae of *dalli* (Eigenmann and Beeson), *rufinanus* Lea and Fitch, and *wilsoni* (Gilbert) are less high for their lengths than those of *semicinctus* (Gilbert), *melanosema*, and most *emphaeus* (Starks). The ratio of height into length for these first three ranges from 1:1.9 to 1:2.2 as compared with 1:1.7 to 1:1.9 for *melanosema* and *semicinctus* and 1:1.8 to 1:2.0 for *emphaeus*. In *melanosema* and *emphaeus*, the anterodorsal margin of the otolith turns abruptly downward (is deeply concave) and a blunt, finger-like rostrum is present. In *semicinctus*, the anterodorsal rim slopes in a nearly straight line and results in an angular, wedge-shaped rostrum. Sagittae of *melanosema* are highest at a point anterior to midlength, whereas in *emphaeus*, greatest otolith height is almost exactly at midlength. Sagittae of the larger species of *Sebastes* need not be considered because at identical lengths these would have significantly fewer annuli (growth zones) than otoliths of the dwarf forms.

Meristic and morphometric data are presented in Table 1.

RANGE: Known only from the type locality off San Pablo Point, Baja California, Mexico and from off Laguna Beach, Orange County, California.

DERIVATION OF NAME: From the Greek *melanos*, meaning black (adj.), and *sema*, a mark or flag (noun). The combination *melanosema* when used with *Sebastes* stands as a noun in apposition. The specific name is an allusion to the black marks or "flags" on the spinous portion of the dorsal and anal fin membranes.

DISPOSITION OF TYPE MATERIAL: The holotype, an adult male 155.5 mm SL (185.5 mm TL) collected at 183 m in a submarine canyon off San Pablo Point, Baja California, Mexico (Lat. 27°12.9'N, Long. 114°30.5'W) on 21 June 1971, is de-

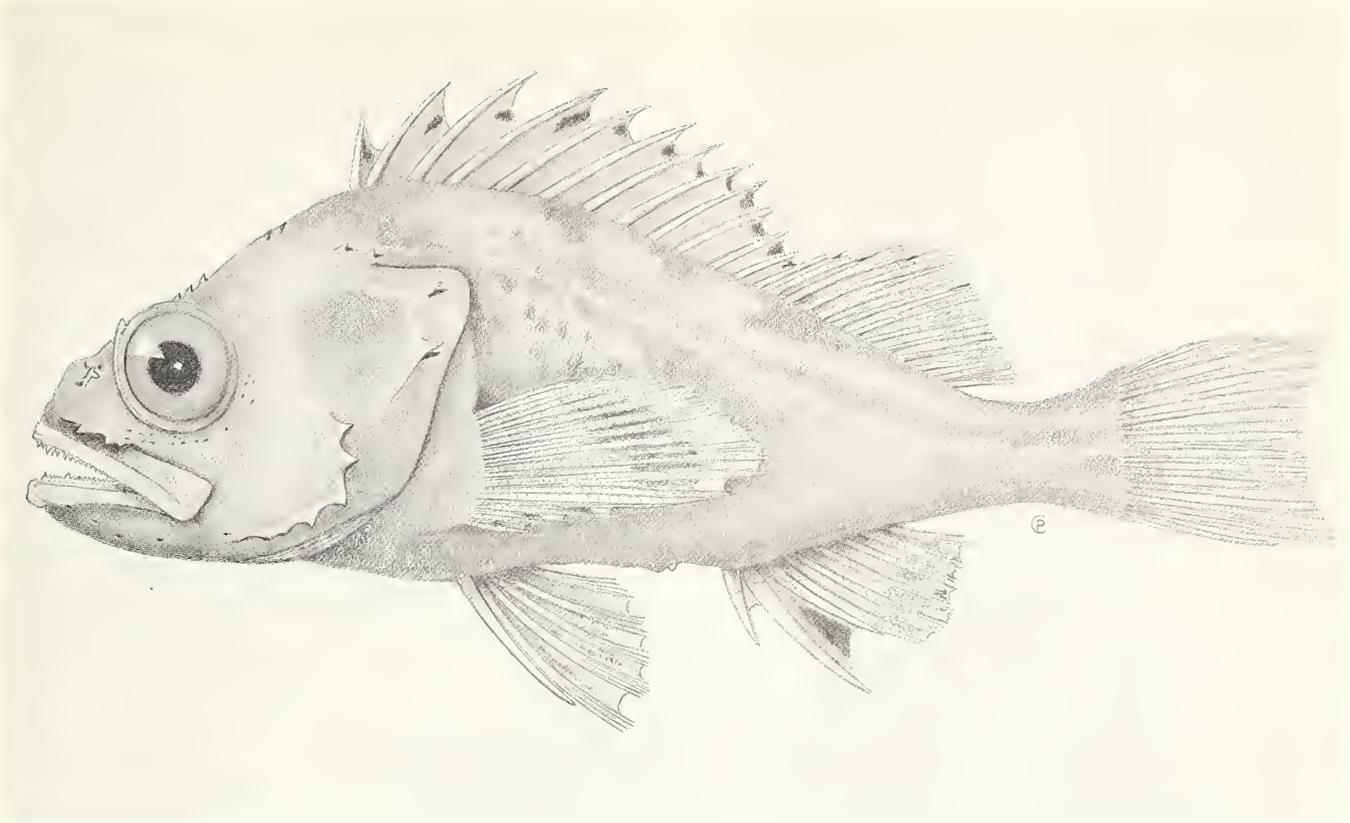


FIGURE 1. Holotype of *Sebastes melanosema*, CAS 27631, from off San Pablo Point, Baja California, Mexico.



FIGURE 2. Paratype of *Sebastes melanosema*, LACM 36965-1, from off Laguna Beach, California.

TABLE 1

Measurements (in mm, proportional measurement into SL and as percent of standard length — %SL) and Counts of Meristic Characters for *Sebastes melanosema*.

Measurement	LACM 33538-1			CAS 27631*			LACM 36965-1		
	mm	SL	%SL	mm	SL	%SL	mm	SL	%SL
Standard length	124.8	—	—	155.5	—	—	166.0	—	—
Head length	55.0	2.3	44	68.5	2.3	44	67.2	2.5	40
Body depth at pelvic origin	46.5	2.7	37	57.0	2.7	37	61.7	2.7	37
Body depth at anal origin	32.0	3.9	26	40.5	3.8	26	47.3	3.5	28
Length of anal base	17.9	7.0	14	23.5	6.6	15	24.2	6.9	15
Length of dorsal base	72.6	1.7	58	92.0	1.7	59	95.7	1.7	58
Snout length	11.6	10.8	09	16.5	9.4	11	16.2	10.2	10
Orbit width	17.0	7.3	14	18.0	8.6	12	17.7	9.4	11
Bony interorbital width	9.6	13.0	08	12.8	12.1	08	11.1	15.0	07
Bony suborbital height	3.7	33.7	03	4.5	34.6	03	2.6	63.8	02
Upper jaw length	24.5	5.1	20	30.6	5.1	20	28.8	5.8	17
Lower jaw projection	0.5	249.6	00	0.0	—	00	0.2	830.0	00
Body width	21.0	5.9	17	26.5	5.9	17	30.5	5.4	18
Pectoral base height	12.2	10.2	10	15.6	10.0	10	15.8	10.5	10
Pectoral length	36.2	3.5	29	44.3	3.5	29	47.9	3.5	29
Pelvic length	25.8	4.8	21	32.2	4.8	21	34.5	4.8	21
Pelvic spine length	18.9	6.6	15	23.6	6.6	15	26.7	6.2	16
First anal spine length	10.3	12.1	08	13.1	11.9	08	10.6	15.7	06
Second anal spine length	20.0	6.2	16	25.7	6.1	17	21.1	7.9	13
Third anal spine length	16.3	7.7	13	21.3	7.3	14	20.3	8.2	12
Anal ray length (longest)	22.2	5.6	18	25.8	6.0	17	26.9	6.2	16
Dorsal spine length (longest)	21.2	5.9	17	28.8	5.4	19	25.8	6.4	16
Dorsal ray length (longest)	21.1	5.9	17	25.1	6.2	16	25.3	6.6	15
Caudal peduncle depth (least)	10.8	11.5	09	14.7	10.6	09	14.1	11.8	08
Caudal peduncle length (ventral)	24.7	5.1	20	32.8	4.7	21	35.0	4.7	21
Caudal peduncle length (dorsal)	15.8	7.9	13	22.3	7.0	14	26.3	6.3	16
Posterior anus to anal origin	4.5	27.7	04	5.7	27.3	04	9.4	17.7	06
Gill raker length (longest)	7.5	16.6	06	9.1	17.1	06	6.2	26.8	04
Predorsal length	46.0	2.7	37	59.0	2.6	38	54.7	3.0	33
Preanal length	89.2	1.4	71	103.4	1.5	66	112.2	1.5	68
Prepectoral length	52.8	2.4	42	60.5	2.6	39	62.2	2.7	37
Prepelvic length	53.6	2.3	43	63.9	2.4	41	65.3	2.5	39
Total length	154.0	0.8	123	185.5	0.8	119	203.0	0.8	122
Dorsal soft-rays		12			12			11	
Anal soft-rays		6			6			6	
Pectoral rays (left/right)		18/18			18/18			17/17	
Unbranched lowermost pectoral rays		9/9			8/8			7/6	
Total gill rakers (left/right)		37/37			36/35			35/34	
Pored lateral-line scales (left/right)		34+1/34+1			39+2/38+2			40+1/ca.41+2	

*Holotype



FIGURE 3. Right sagitta, inner face, from holotype of *Sebastes melano-sema*.

posited in the ichthyological collection of the California Academy of Sciences (CAS 27631). One paratype, a male 124.8 mm SL (154.0 mm TL), collected at the same time and place as the holotype, has been placed in the fish collection of the Natural History Museum of Los Angeles County (LACM 33538-1). The other paratype, a male 166.0 mm SL (203.0 mm TL) collected off Laguna Beach, Orange County, California, on 16 February 1976 in about 137 m is also deposited at the Natural History Museum of Los Angeles County (LACM 36965-1).

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We would like to thank the following persons who aided in various ways during the preparation of this manuscript. Lo-chai Chen, San Diego State University, discussed with us the relationship of this species with other members of the genus *Sebastes*. Andrew Felando, Master, and the crew of the R/V *ALASKA* aided in collecting the Baja California specimens. Robert J. Lavenberg, Natural History Museum of Los Angeles County, and William N. Eschmeyer, California Academy of Sciences, made specimens and the facilities of their respective institutions readily available. Ms. Cherryl Pape illustrated the holotype and Jack W. Schott did the photographic work.

RESUMEN

Una especie nueva de la familia Scorpaenidae, *Sebastes melano-sema* es descrita basado en 3 especímenes del este del Pacífico del Norte. Esta forma se distingue de las otras especies de *Sebastes* en el Pacífico con una combinación de caracteres: 6

rayos en la aleta anal, 11 a 12 rayos en la aleta dorsal, 34 a 37 branquiaspinas, color negro bordeando la membrana en la porción espinosa de la aleta dorsal y anal, y la morfología de las espinas lacrimales. La terminología de las espinas escapulares en escritos previos sobre este género se corrige. La descripción de este especie eleva a 69 el número de *Sebastes* en el este del Pacífico del Norte.

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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

LARVAE OF SOME EUSOCIAL BEES AND WASPS

By George C. Wheeler and Jeanette Wheeler



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Edward Ostermeyer
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LARVAE OF SOME EUSOCIAL BEES AND WASPS¹

By George C. Wheeler and Jeanette Wheeler²

ABSTRACT: The larvae of 17 species of social wasps in the genera *Apoica*, *Belonogaster*, *Microstigmus*, *Mischocyttarus*, *Polistes*, *Polybia*, *Ropalidia*, *Synoeca* and *Vespa* are described and many figured; the same for eight species of social bees in the genera *Apis*, *Bombus*, *Braunsapis*, *Lasioglossum*, *Melipona* and *Trigona*. Appended are a list of published descriptions and illustrations of the larvae of eusocial wasps and bees, a list of the published characterizations of the larvae of the higher taxa and a list of published keys to larvae.

When we were invited to write the chapter on the larvae of social Hymenoptera for "Social Insects," H.R. Hermann, ed., Academic Press (1979), we had no misgivings about ant larvae, because we had just finished a monograph about them (1976), based on a leisurely half-century of the study of 692 species in 182 genera representing all 10 of the living subfamilies. But about eusocial bee and wasp larvae we knew nothing and we had less than a year to learn. We sent out appeals for specimens and references. We acknowledge the generous responses with advice and/or specimens from the following: D.R. Davis, National Museum of Natural History, Smithsonian Institution; Howard E. Evans, Colorado State University; Saul I. Frommer, University of California, Riverside; Charles D. Michener, University of Kansas; Jerome G. Rozen, American Museum of Natural History; Robert O. Schuster, University of California, Davis; Roy R. Snelling, Natural History Museum, Los Angeles County; Philip F. Torchio, Utah State University.

We processed representatives of 16 species of eusocial wasps and eight species of eusocial bees by the techniques (1960) we had used for ant larvae and prepared descriptions according to our paradigm (1976: 2–3); drawings were prepared according to the style we had developed for ant larvae. As in our ant larvae papers we used the integuments of the largest larvae which had not defecated. We follow Snodgrass (1960) in considering post-defecation larvae as pharate pupae (= semipupae). Those studies gave us a good acquaintance at first hand with these larvae, but there was no room in our chapter for this material. It seems unfortunate to us that the detailed results of so much labor should not be publicly available; hence we are publishing them herewith.

In our chapter on social Hymenoptera we did not refer to the larvae of the sphecids in the genus *Microstigmus*, because we were not certain they were eusocial. Since then Roy R. Snelling, Los Angeles County Museum, has assured us that they are indeed eusocial. We follow his advice and a description of the larvae of *Microstigmus comes* Krombein is included here. This makes a total of 17 species of eusocial wasps we have studied.

We also asked specialists if they kept (or knew of) a catalog of published figures and/or descriptions of the larvae of eusocial bees and wasps. Such a catalog would have saved us considerable time in learning what was already known. No one had (or

knew of) such a catalog; but some said that it would be extremely useful.³

We therefore append below a list of those species of eusocial wasps and bees whose larvae we have found described and/or illustrated in the literature. The list is incomplete, for we have not had the time to search the literature (as we did for the ants), but it can be used as a starting point for specialists. We hope that they will bring it up to date and keep it so, in order that future students will not be caught in our predicament.

TERMS

We follow Snodgrass in regarding the head of an insect—either larva or adult—as hypognathous. Consequently we consider the face to be anterior and the vertex dorsal, while the mouth parts are directed ventrally.

The praesaepium is a shallow depression on the ventral surface of certain anterior somites; it resembles somewhat the trophothylax of the pseudomyrmecine ant larvae and serves the same function: the workers deposit food in it and the larvae eat from it.

We use T1, T2 and T3 as symbols for the thoracic somites and A1 to AX for the abdominal somites.

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³"Discovering from the literature what species have been described as larvae is most difficult for obvious reasons. Hence I cannot but feel that a published list of social bees (and presumably other Hymenoptera) might be a significant contribution to the work of others in the future." (Dr. Jerome G. Rozen in a letter of 4 March 1976.)

VESPOIDEA

Body profile straight and fusiform; diameter greatest at A1 and AII; gradually attenuated toward posterior end and more rapidly toward anterior end; with temporary trophothylax (= praesaepium), except in *Mischocyttarus* which has a permanent shelf; transverse welts on dorsum of some somites. Hairs usually lacking or minute and simple. Mandibles highly varied.

VESPIDAE: POLISTINAE

Apoica pallens (Fabricius)

Figure 1

Length (through spiracles) about 18 mm. Body straight; dorsal profile arcuate; ventral nearly straight, except head and terminal somites curved slightly ventrally; mouth parts directed antero-ventrally. Anus terminal; with prominent lips. Leg and gonopod vestiges small knobs; wing rudiments brown lines on unstained integuments. **Spiracles** small; peritreme feebly sclerotized; atrial wall with minute spinules in encircling rows. Entire integument spinulose, the spinules large and isolated anteriorly, becoming smaller and in short rows posteriorly. **Body hairs** moderately abundant on dorsal and lateral surfaces, minute (about 0.09 mm long), fewer ventrally, very fine and flexuous. **Cranium** not sclerotized (= same color as body); large (about 2.34 mm wide and 1.9 mm long); subpentagonal in anterior view, widest immediately below antennal level; with distinct temporal sulci, the lateral portions appearing sieve-like. Antennae just below mid-length of cranium; each mounted on large slightly elevated base; small; with 4 sensilla, each bearing a minute spinule. Head hairs (and/or minute sensilla) 0.003–0.025 mm long; numerous. **Labrum** bilobed; dorsal border sinuate; each half of anterior surface with about 25 minute (about 0.013 mm long) hairs dorsally and sensilla ventrally; ventral surface with about 25 large projecting sensilla medially and 6 smaller sensilla laterally on each half; posterior surface spinulose, the spinules minute and in short rows ventrally; longer and isolated laterally; posterior surface with about 6 sensilla medially. **Mandible** small (about 0.36 mm wide and 0.64 mm long), moderately sclerotized; falcate; tapering to a very sharp apical tooth with medial blade; a narrowly rounded long tooth projecting anteromedially from blade. **Maxilla** appearing adnate; stripes with about 24 hairs (about 0.025 mm long, simple, slender) on lateral surface; medial and apical surfaces sparsely spinulose, spinules minute; palp a slender peg with 4 apical sensilla; galea stouter than palp and with bifid apex; one branch of apex with 4 sensilla, the other with 1. **Labium** small, surface with fine rugulae; palp a frustum with 4 apical sensilla; an isolated hair (about 0.03 mm long) between each palp and opening of sericteries, the latter wide and feebly projecting. Hypopharynx rugulose. (Material studied: three larvae from Costa Rica, courtesy of Roy R. Snelling.)

Belonogaster lateritius Gerstaecker

Figure 2

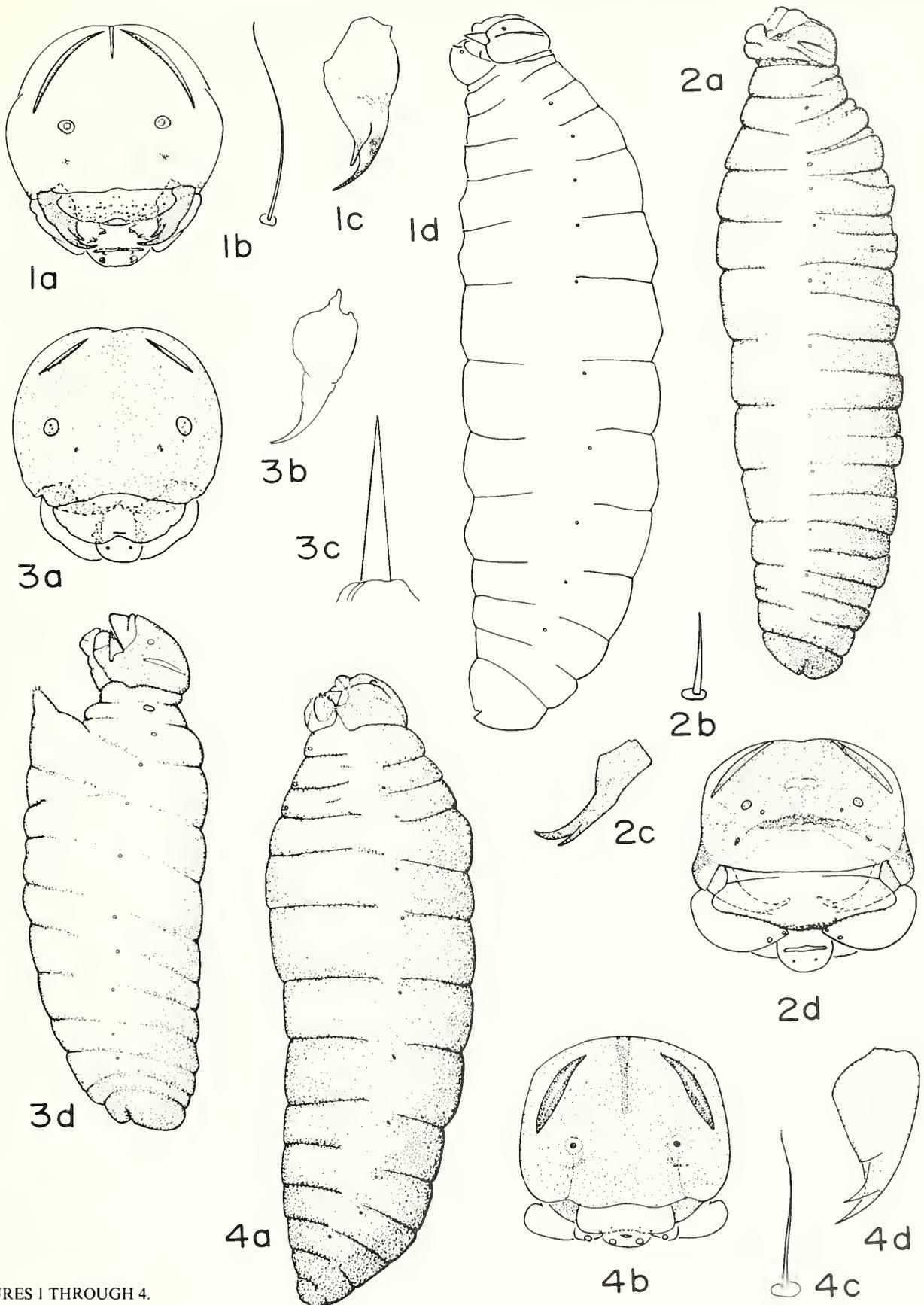
Length (through spiracles) about 22 mm. Body straight and stout; diameter greatest at AIII; a pair of transverse welts on dorsum of each A1–AV1; each lateral surface of A1 with a circular

raised area; venter of T1–T3 and A1 forming floor of praesaepium, AII swollen and forming its ventral lip. Head large and terminal. Anus terminal. Leg, wing and gonopod vestiges present. Integument around **spiracles** markedly sclerotized. **Integument** entirely spinulose, spinules long (about 0.013 mm). **Body hairs** sparse, minute (about 0.013 mm long), simple. **Cranium** heavily sclerotized (= dark brown); subquadrangular, widest at mandible level; about 2.9 mm wide and 1.76 mm long; major portion sclerotized; portion of frons and ventral portion of labrum heavily sclerotized (= dark brown); temporal sulci well developed; pleurostoma feebly sclerotized. Antennae near mid-length of cranium; each a low rounded elevation, with 3 sensilla, each of which bears a minute spinule. **Labrum** nearly as wide as head, about 2.2 mm wide and 0.76 mm long; trapezoidal, widest ventrally; ventral and dorsal borders sinuate; ventral border with about 90 sensilla, most of which are on short sclerotized pegs, some on same level as integument and bearing a minute spinule each; anterodorsal portion with about 14 hairs and/or sensilla; integument with minute spinules, isolated or in very short rows. **Mandible** long and slender (about 0.36 mm wide and 1.3 mm long); feebly sclerotized; apex forming a long slender medially curved tooth which bears an anteromedial tooth. **Maxilla** large and lobose; cardo with numerous large isolated spinules and with about 30 hairs, which are about 0.025 mm long and spike-like; stipes with minute isolated spinules; palp a short peg with 4 apical sensilla, its integument with minute spinules in short encircling rows; galea digitiform, with 2 apical sensilla. **Labium** small; integument roughened with short arcuate rows of spinules medially, spinules few and isolated laterally; palp a short peg with 4 or 5 sensilla; opening of sericteries wide and salient. **Hypopharynx** rugulose, some rugulae bearing a few minute spinules. (Material studied: four larvae from Kenya, courtesy of Roy R. Snelling.)

Mischocyttarus flavitarsis (Saussure)

Figure 3

Length (through spiracles) about 13 mm. Body with thorax narrowed anteriorly; abdomen widest at AII, decreasing to narrowly rounded posterior end, with a pair of small knobs on dorsum of each T2–AIX; praesaepium floor T1–T3; A1 projecting ventrally into 2 spinulose cones. Anus terminal. Head on anterior end; its diameter greater than that of T1 or T2. **Spiracles**: diameter of T2 spiracular atrium twice diameter of remainder; atrial walls with encircling rows of minute spinules. **Integument** of body spinulose, spinules in short rows or isolated on ridges, ridges numerous and transverse or reticulate. **Body hairs** few, stout, 0.025–0.1 mm long, only on ventral projection on A1. **Cranium** moderately sclerotized (= light brown); feebly subcordate; about 2.4 mm wide and 2.16 mm long; with numerous minute sensilla; temporal sulci present. Antennae small; just below midlength of cranium. **Labrum** bilobed, wide and short (about 1.56 mm wide and 0.48 mm long); anterior surface of each half with a small ventrolateral boss, which bears about 25 minute hairs and/or sensilla; entire anterior surface rugulose; posterior surface of each half with about 20 sensilla, each of which is mounted on a slight projection. **Mandible** falcate; long and slender (about 0.4 mm wide and 0.98 mm long), with very slender apex. **Maxilla** lobose; palp digitiform with 5 (2 apical, 2 sub-apical and 1 basal) sensilla; galea digitiform, more slender than



FIGURES 1 THROUGH 4.

FIGURE 1. *Apoica pallens*. a, Head in anterior view, X22; b, body hair, X390; c, left mandible in anterior view, X40; d, larva in side view, X7. FIGURE 2. *Belonogaster lateritius*. a, Larva in side view, X5.5; b, body hair, X600; c, left mandible in anterior view, X21; d, head in anterior view, X13. FIGURE 3. *Mischocyttarus flavitarsis*. a, Head in anterior view, X14; b, left mandible in anterior view, X94; c, body hair, X1390; d, larva in side view, X14. FIGURE 4. *Polistes exclamans lineonous*. a, Larva in side view, X7; b, head in anterior view, X15; c, body hair, X400; d, left mandible in anterior view, X38.

palp but about as long, with 2 apical sensilla. **Labium** small and rounded; sparsely spinulose, spinules minute and in short transverse rows; palp a low knob; an isolated sensillum between each palp and opening of sericteries; the latter wide and salient. **Hypopharynx** densely spinulose, spinules arranged in subtransverse rows, rows so close together that spinules overlap. (Material studied: four larvae from Arizona, courtesy of Roy R. Snelling.)

Polistes exclamans lineonotus R. Bohart

Figure 4

Length (through spiracles) about 17 mm. Body straight; dorsal profile arcuate, ventral feebly sigmoid; diameter greatest at AII, decreasing slowly to posterior end (which is narrowly round-pointed) and more rapidly to anterior end; head terminal and slightly smaller than diameter of T1. Anus ventral. A small boss posterior to anus on AX; lateral longitudinal welts well developed; paired bosses on T2, T3 and AI–AIX; praesaepium floor formed from depressed ventral surfaces of T1–T3 and AI, ventral wall formed from an anteroventral extension of AII. Leg vestiges rather large, each with sclerotized ring; wing rudiments present. **Spiracles** on T2 largest, remainder small and subequal. Entire **integument** spinulose, the spinules coarse and isolated ventrally, grading into minute and in short rows dorsally, on thorax and anterior abdominal somites; posterior spinules finer and less numerous. **Body hairs** sparse, simple, minute to short (0.005–0.06 mm long), most numerous on venter of T3 and AI. **Cranium** moderately sclerotized (= light brown); subtrapezoidal in anterior view, widest ventrally (about 2.45 mm wide and 1.68 mm long); temporal sulci long and wide. Antennae just below midlength of cranium; each a low knob with 3 or 4 sensilla. Head hairs numerous (about 200) and minute (about 0.008 mm long). **Labrum** short and trapezoidal; narrowed ventrally (about 1.27 mm wide and 0.42 mm long); entire anterior surface with about 120 minute hairs (0.005–0.03 mm long) and/or sensilla (each bearing a spinule); ventral border with about 30 sensilla (some heavily sclerotized and elevated) and with numerous minute spinules; posterior surface with about 24 sensilla and with a few minute spinules in short rows. **Mandible** falcate; about 0.44 mm wide and 0.84 mm long; with a rather long tooth arising from the anterior surface and with a very small tooth between it and apical tooth; anterior surface with a few transverse rugulae; posterior surface with longitudinal rugulae. **Maxilla** appearing adnate; swollen and lobose laterally; with about 45 minute to short (0.005–0.03 mm long) hairs; with minute isolated spinules medially, in short arcuate rows laterally and posteriorly, palp a tall peg with 5 or 6 apical sensilla; galea an irregular peg with 5 apical sensilla. **Labium** small and globose, with about 50 minute to short (0.005–0.03 mm long) hairs between palps and opening of sericteries; hairs continued onto posterior surface; each palp a small boss with 5 apical sensilla; opening of sericteries as wide as labium and slightly salient. **Hypopharynx** with a few minute ridges (rows of spinules?). (Material studied: five larvae from Mexico, courtesy of Roy R. Snelling.)

Polistes erythrocephalus Latreille

Length (through spiracles) about 25 mm. Similar to *P. exclamans lineonotus* except as follows. Body with a small mid-

dorsal boss on AIX; anus terminal; ventral profile feebly J-shaped. **Integument** with spinules all rather coarse and isolated. **Cranium** about 3.1 mm wide and 2.6 mm long; integument minutely reticulogrose and with numerous sensilla. Each antenna with 3–7 sensilla. No head hairs seen. **Labrum** about 1.6 mm wide and 0.6 mm long; subrectangular, with a slight median impression; about 130 hairs and/or sensilla (each bearing a spinule) on anterior surface. **Mandible** about 0.42 mm wide and 1.2 mm long; with subapical tooth slightly smaller than apical. **Maxilla** with about 30 minute hairs and/or sensilla; palp a paxilla with 6 or 7 apical sensilla; galea an irregular cluster of about 7 irregularly elevated sensilla. **Labium** with hairs 0.025–0.05 mm long, simple and slender; palp a low knob with 5 or 6 sensilla. **Hypopharynx** with short arcuate rows of minute spinules. (Material studied: three larvae from Costa Rica, courtesy of Roy R. Snelling.)

Polistes fuscatus (Fabricius)

Length (through spiracles) about 13 mm. Similar to *P. exclamans lineonotus* except as follows. Body with a chair-shaped knob terminally on AX; a small projection directed anteriorly dorsal to each spiracle of AV; AI–AVII a pair of transverse bosses meeting at middorsum, a pair per somite; AI or AII forming ventral surface of praesaepium. **Integument** of dorsal bosses without spinules. **Body hairs** 0.05–0.125 mm long; most numerous and longest on T3, AI and AX. **Cranium** and mouth parts heavily sclerotized (= dark brown); cranium about 2.8 mm wide and 1.8 mm long. Each antenna with 3–5 sensilla. About 300 head hairs 0.01–0.1 mm long, longest with flexous tip. **Labrum** about 1.4 mm wide and 0.44 mm long; feebly bilobed; each half of anterior surface with about 30 hairs (0.012–0.027 mm long) and minute sensilla; posterior surface with 7 sensilla on each half and with a few minute spinules in short arcuate rows. **Mandible** about 0.35 mm wide and 0.78 mm long; apical tooth with a small medial blade; apical and subapical teeth subequal. **Maxilla** with hairs 0.025–0.625 mm long; palp a short peg; galea taller. **Labium** with palp a short peg. **Hypopharynx** with a few minute spinules in short arcuate rows. (Material studied: three larvae from Colorado, courtesy of H.E. Evans.)

Polistes fuscatus aurifer Saussure

Length (through spiracles) about 17 mm. Similar to *P. exclamans lineonotus* except as follows: Body stout; dorsal profile J-shaped, ventral profile S-shaped; diameter greatest at AIII; with paired dorsal bosses on T3–AIX; single more prominent boss on AX. Entire **integument** with large isolated spinules. **Body hairs** longer (0.012–0.1 mm long). **Cranium** about 2.7 mm wide and 2 mm long; transversely subelliptical in anterior view; dorsal border feebly impressed. Head hairs twice as numerous (about 400) and longer (0.01–0.1 mm long). **Labrum** feebly bilobed; about 1.39 mm wide and 0.48 mm long; posterior surface with about 14 sensilla. **Mandible** about 0.38 mm wide and 0.9 mm long. **Maxilla** with palp and galea subequal in height. **Labium** with hairs about 0.05 mm long and simple or about 0.025 mm long and bifid at tip. **Hypopharynx** with sparse minute spinules. (Material studied: three larvae from California, courtesy of R.O. Schuster.)

Polistes major castaueicolor Bequaert

Length (through spiracles) about 37 mm. Similar to *P. exclamans lineonotus* except as follows. Body with a pair of welts on dorsum of each AI–AVI. **Integument** with all spinules minute. **Body hairs** 0.01–0.15 mm long, longest and most numerous on venter of AII, the longest flexuous. **Cranium** heavily sclerotized (= dark brown); about 2.9 mm wide and 1.9 mm long. Antennae above midlength of cranium. Head hairs about 400, 0.06–0.18 mm long, very slender and flexuous. **Labrum** about 1.6 mm wide and 0.6 mm long; transversely subelliptical in anterior view; anterior surface with about 90 sensilla and minute hairs (about 0.025 mm long). **Mandible** about 0.52 mm wide and 0.86 mm long. **Maxilla** with about 20 hairs, 0.01–0.05 mm long; palp stout and digitiform, with 4 apical and 2 lateral sensilla, integument with a few minute spinules; galea digitiform, with bifid apex, the larger branch with 5 or 6 apical sensilla, the smaller with 1 apical sensillum. **Labium** with palp a short peg with 7 or 8 apical and 1–3 lateral sensilla; integument with isolated spinules and about 24 short (0.012–0.025 mm long) hairs, the longer with bifid apex. **Hypopharynx** with a few minute spinules in short arcuate rows. (Material studied: two larvae from Arizona, courtesy of Roy R. Snelling.)

Polistes poeyi Lepeletier

Length (through spiracles) about 13 mm. Similar to *P. exclamans lineonotus* except as follows. Entire **integument** spinulose, the spinules numerous, isolated and large on thorax and dorsum of AI–AX and venter of AI–AIV, less abundant and smaller posteriorly. **Body hairs** simple; most numerous and longest (0.005–0.1 mm) on venter of AI, fewer and shorter anteriorly and posteriorly. **Cranium** heavily sclerotized (= dark brown), about 2.4 mm wide and 1.6 mm long. Antennae above midlength of cranium, each with a heavily sclerotized ring, elevated, with 2 or 3 sensilla. Head hairs about 130 and minute (about 0.005 mm long). **Labrum** about 1.25 mm wide and 0.4 mm long; transversely subelliptical; entire anterior surface with about 8 sensilla and a few isolated spinules; ventral border with about 12 sensilla; posterior surface with about 25 sensilla, most numerous dorsally and near midline ventrally; posterior surface with a few minute spinules in short arcuate rows. **Mandible** about 0.36 mm wide and 0.9 mm long; small medial tooth lacking. **Maxilla** less swollen laterally; anterior surface with about 35 simple, very slender hairs, 0.006–0.025 mm long; medial surface with minute spinules, spinules isolated or in short rows; palp stout, digitiform, with 4 or 5 apical sensilla; galea approximately same size as palp but with an irregular apex, with 5–7 apical sensilla. **Labium** small, transversely subelliptical, with a slightly raised, sparsely spinulose, transverse welt dorsally, with about 12 hairs (0.005–0.025 mm long) near each palp; palp a low knob with 4 apical sensilla. **Hypopharynx** with sparse isolated spinules. (Material studied: two larvae from Cuba, courtesy of Roy R. Snelling.)

Polybia occidentalis (Olivier)

Figure 5

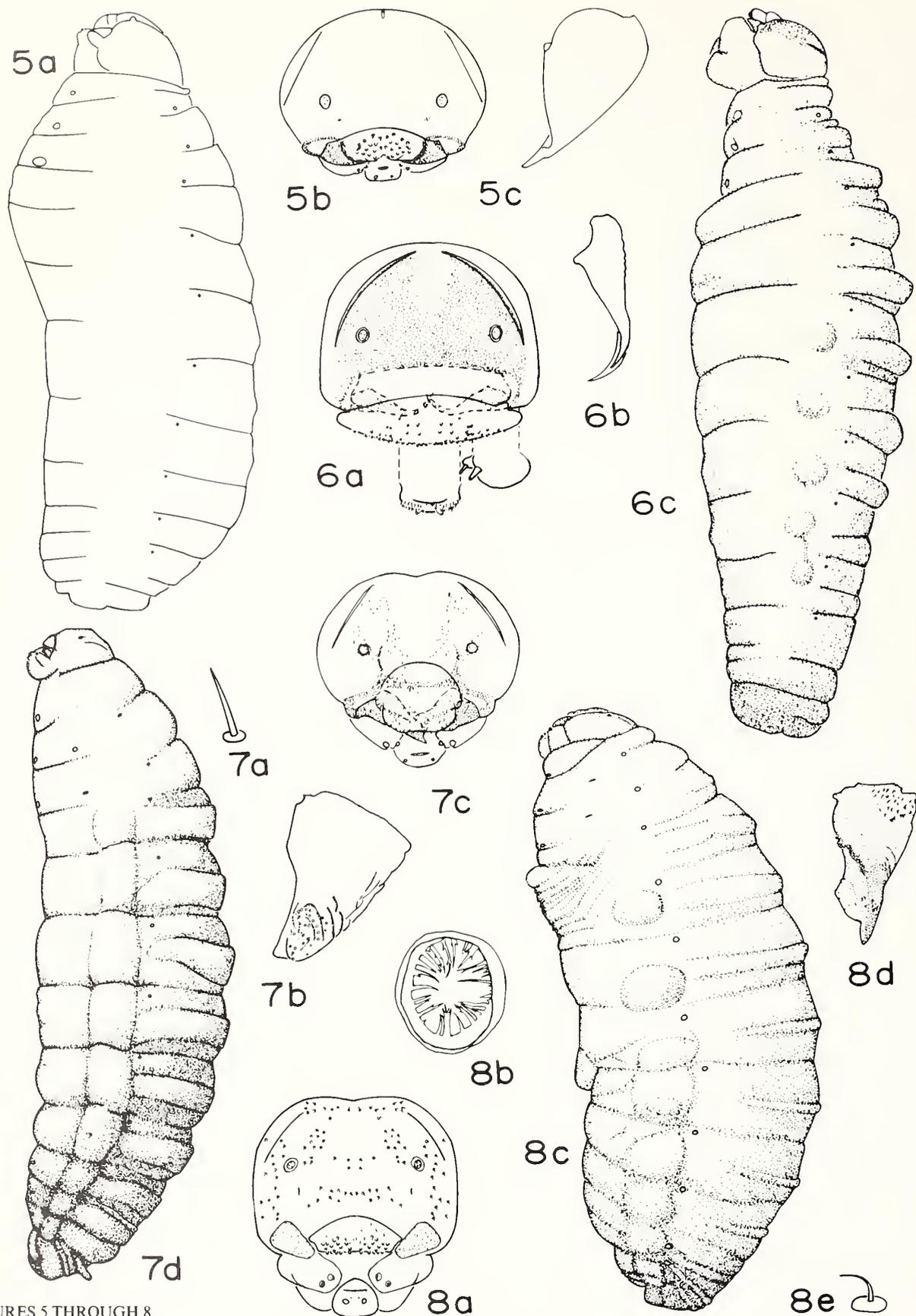
Length (through spiracles) about 6 mm. Body straight; stout; diameter greatest at AI and AII, diameter decreasing rapidly an-

teriorly and gradually posteriorly. Anus terminal. Head on anterior end, with diameter greater than that of AI; T2, T3 and AI with paired dorsolateral denticles. Leg, wing and gonopod vestiges distinct. **Spiracles** small; T2 largest, remainder subequal. **Integument** spinulose, spinules isolated and coarse, decreasing in size and number posteriorly. No **body hairs** seen. **Cranium** large, about 1.24 mm wide and 0.74 mm long; transversely subelliptical in anterior view; feebly sclerotized (= yellow); temporal sulci long. Antennae large; at lower third of cranium; each with 3 sensilla. **Labrum** short (about 0.45 mm wide and 0.1 mm long) and bilobed; each half of anterior surface with about 12 sensilla (each on a small peg), 5 hairs (about 0.125 mm long) and numerous papillae; ventral border with papillae and about 9 sensilla; posterior surface with an isolated sensillum near middle and with a few oblique arcuate rows of minute spinules. **Mandible** small, about 0.2 mm wide and 0.24 mm long, falcate, with irregular apex; a subapical lateral tooth, a crooked apical tooth and a short medial blade; basal portion with short arcuate ridges, apical portion with a few longitudinal ridges. **Maxilla** appearing adnate; basal surface with numerous rather coarse spinules, apical with about 10 hairs about 0.13 mm long, and numerous short ridges; palp a short rugose irregular peg with 5 apical sensilla; galea an irregular rugose boss with 2 sensilla, each on a slight elevation. **Labium** transversely subelliptical; with short transverse ridges; palp a cluster of 4–6 slightly elevated sensilla; an isolated sensillum between each palp and opening of sericteries; the latter a transverse slit with lips as wide as labium. **Hypopharynx** sparsely spinulose, the spinules minute and in short transverse rows. (Material studied: five larvae from Costa Rica, courtesy of Roy R. Snelling.)

Ropalidia cincta (Lepeletier)

Figure 6

Length (through spiracles) about 18 mm. Body fusiform; head and anus terminal; thorax slender; abdomen abruptly enlarged; venter of T1–T3 forming floor of praesaeptum; AI produced ventrally to form its lip; transverse welts meeting on middorsum of T1–AVII, a pair each; diameter of head nearly equal to that of T2. Leg, wing and gonopod vestiges present. **Spiracles** on T2 about twice diameter of remainder. **Integument** entirely spinulose, the spinules rather large and isolated, largest on AI, abruptly reduced on AIX, lacking on AX. **Body hairs** 0.005–0.025 mm long, sparse, simple, very fine. **Cranium** about 2.9 mm wide and 1.6 mm long; semicircular in anterior view; heavily sclerotized (= dark brown) between sulci and to its ventral border, excluding clypeus; sclerotization heaviest along ventral border of cranium and of labrum; temporal sulci long and narrow; clypeus with about 34 sensilla. Antennae at lowest third of cranium; large; each a slightly raised circle with 3 minute sensilla. **Labrum** trapezoidal in anterior view, narrowed dorsally, very short and wide (about 0.4 mm long and 2.1 mm wide); anterior surface with about 30 sensilla and with minute hairs (about 0.012 mm long); ventral border and adjacent portions of anterior and posterior surfaces with about 66 sensilla, each on a low knob; posterior surface with numerous short rows of minute spinules. **Mandible** large (about 0.4 mm wide and 1.2 mm long); slender; falcate; apical tooth slender and sharp-pointed, with a slender sharp-pointed anterior tooth; mandible with a dark band around basal edge. **Maxilla** lobose ventrolaterally; anterior



FIGURES 5 THROUGH 8.

FIGURE 5. *Polybia occidentalis*. a, Larva in side view, X18; b, head in anterior view, X30; c, left mandible in anterior view, X50. FIGURE 6. *Ropalidia cincta*. a, Head in anterior view (left maxilla and labium normally hidden behind labrum but drawn here separately), X13; b, left mandible in anterior view, X25; c, larva in side view, X7. FIGURE 7. *Synoeca surinama*. a, Body hair, X400; b, left mandible in anterior view, X56; c, head in anterior view, X15; d, larva in side view, X5.5. FIGURE 8. *Vespula maculata*. a, Head in anterior view, X17; b, spiracle, X200; c, larva in side view, X3.5; d, left mandible in anterior view, X40; e, body hair, X508.

surface with about 20 hairs (about 0.25 mm long) and minute spinules; appearing adnate; palp digitiform, with 4 apical and 1 lateral sensilla, integument of palp with minute spinules in short transverse rows; galea slightly shorter and slenderer, with 2 apical sensilla. **Labium** short and subtrapezoidal in anterior view, slightly wider basally; with large transverse dorsal welt; palp a peg with 2 apical sensilla and 4 adjacent slightly raised sensilla; area between each palp and opening of sericteries with long slender spinules; an isolated sensillum between each palp and opening of sericteries; the latter wide and transverse, with slightly protruding lips. **Hypopharynx** with numerous minute spinules in short transverse rows. (Material studied: four larvae from Kenya, courtesy of Roy R. Snelling.)

Synoeca surinama (Fabricius)

Figure 7

Length (through spiracles) about 24 mm. Body fusiform; nearly straight; diameter greatest at AIII, attenuated gradually toward each end; lateral longitudinal welts on sides of abdomen; a pair of transverse welts meeting at midline on dorsum of each AI–AVII; AIX with digitiform middorsal projection. No suggestion of a praesaepium. Leg, wing and gonopod vestiges dark brown. **Spiracles** with minute spinules in transverse rows on atrial wall. Entire **integument** spinulose, spinules longer and isolated anteriorly, minute and in rows posteriorly. **Body hairs** 0.025–0.05 mm long; simple spikes; most numerous on venter of thorax and anterior abdominal somites, sparse elsewhere. **Cranium** feebly sclerotized (= yellow); feebly bilobed due to median impression of dorsal border; about 2.6 mm wide and 1.8 mm long; temporal sulci long and slender. Antennae at midlength of cranium; each with sclerotized border and with 3 minute sensilla. Head hairs short (0.019–0.037 mm long), spike-like and numerous (about 220). **Labrum** short (about 1.4 mm wide and 0.4 mm long), transversely subelliptical; anterior surface with about 24 hairs (about 0.03 mm long) dorsally and numerous sensilla (each mounted on a small papilla); ventral border thick and feebly sclerotized, with sensilla on small papillae; posterior surface with small papillae and with minute spinules in short arcuate rows. **Mandible** small about 0.45 mm wide and 0.55 mm long; subpentagonal in anterior view, distal end blunt; apex sclerotized, with a small boss directed anteromedially and bearing a few rows of minute spinules; subapical portion with about 36 minute sensilla; medial portion with minute spinules in short transverse rows; basal portion reticulorugose and with minute spinules in short transverse rows. **Maxilla** appearing adnate; cardo swollen ventrolaterally, with about 6 hairs (about 0.05 mm long); stipe rather slender and with about 18 hairs (about 0.25 mm long); palp sclerotized, an irregular peg with 5 sensilla, subequal to galea; galea with 2 apical sensilla. **Labium** small, transversely subelliptical in anterior view, dorsal portion densely spinulose, the spinules long and slender; palp sclerotized, a small peg with 3 apical sensilla; an isolated sensillum between each palp and opening of sericteries; the latter a transverse slit, with lips as wide as labium. **Hypopharynx** with numerous short transverse ridges bearing minute spinules. (Material studied: three larvae from Mexico, courtesy of Roy R. Snelling.)

VESPINAE

Vespula maculata (Linnaeus)

Figure 8

Length (through spiracles) about 19 mm. Body stout and slightly curved ventrally; head moderately large and anteroventral; anus terminal; AX with 2 stout posterodorsal cones; lateral longitudinal welts well developed; praesaepium floor formed by depressed venter of T1–T3 and A1; A1 strongly projecting ventrally to form lip; AII–AIV with lateral bosses; A1–AVIII with a pair of transverse welts meeting at middorsum, one pair per somite. Leg, wing and gonopod vestiges present. **Spiracles** of thorax small; abdominal large, with rather wide peritreme; atrial walls with minute spinules, varying to hair-like with minute denticles. **Integument** entirely and densely spinulose, spinules large and isolated or minute and in short rows. **Body hairs** minute (about 0.03 mm long), simple, sparse. **Cranium** feebly sclerotized (= yellow); about 2.6 mm wide and 1.7 mm long; subhexagonal or transversely subelliptical in anterior view, with feeble medial impression of occipital border; temporal sulci distinct; ventral border of clypeus straight. Antennae at midlength of cranium, each mounted on a small boss, with 3 sensilla, each bearing a small spinule. Head hairs numerous (about 170), minute (about 0.008 mm long), concentrated on clypeus. **Labrum** small (about 0.8 mm wide and 0.4 mm long), short and bilobed; anterior surface of each half with about 30 minute hairs and/or sensilla, each bearing a spinule; each half of ventral border with about 6 large projecting sensilla and numerous minute spinules; posterior surface with about 8 large sensilla on a sclerotized base. **Mandible** subquadrangular in anterior view; about 0.4 mm wide and 0.77 mm long; medioventral border sclerotized; with a thin subapical blade adjacent to thicker medial blade, both distal to swollen base; numerous papillae at junction of thicker blade and base; a few minute spinules on anterior surface. **Maxilla** with cardo and stipes feebly separated; cardo with about 7 sensilla; integument of stipes spinulose, spinules minute and isolated; palp a short peg with short transverse rugae on integument, apex with 4 sensilla and a denticle; galea a low knob with 2 apical sensilla. **Labium** small; with several lateral sensilla, each bearing a spinule; anteromedial surface with long slender spinules; palp a low boss with 4 apical sensilla and a denticle; an isolated sensillum between each palp and opening of sericteries; the latter wide, transverse and slightly protruding, with numerous minute spinules on lips. **Hypopharynx** spinulose ventrally, spinules minute and isolated; with heavy pigmented ridges dorsally. (Material studied: numerous larvae from Colorado, courtesy of H.E. Evans, and from New Hampshire, collected by G.C. Wheeler.)

Vespula atropilosa (Sladen)

Length (through spiracles) about 21 mm. Similar to *V. maculata* except as follows. Body nearly straight; T1 very short and hidden dorsally; T2 entire and swollen dorsally; T3 feebly divided into anterior and posterior annuli, A1–AIX distinctly divided by middorsal impression; AX with a pair of lateral bosses; anus terminal and with anterior and posterior lips. **Spiracles** with long isolated spinules on atrial wall; atrial opening with numer-

ous spinules bearing denticles at opening of trachea. Integument with isolated spinules. **Body hairs** 0.06–0.25 mm long. **Cranium** about 2.4 mm wide and 1.8 mm long; temporal sulci long and narrow. Head hairs about 0.004 mm long. **Labrum** about 1 mm wide and 0.36 mm long; deeply bilobed; ventral border of each half with about 12 sensilla and a few rather long spinules in arcuate rows; posterior surface of each half with a cluster of about 6 sensilla dorsally and 9 ventrally and with isolated patches of spinules laterally and medially. **Mandible** about 0.42 mm wide and 0.79 mm long; apical tooth nearly uniformly slender, subapical tooth stouter, basal stoutest; blade bearing minute denticles basally and rows of minute spinules ventrally. **Maxilla** with about 25 hairs (about 0.005 mm long); palp with 3–4 apical sensilla. **Labium** with palp a short stout peg bearing 5 apical sensilla. (Material studied: six larvae from Colorado, courtesy of H.E. Evans.)

Vespula maculifrons (Buysson)

Length (through spiracles) about 19 mm. Similar to *V. maculata* except as follows. Body with prominent ventrolateral bosses on AII–AV; AX long and turned ventrally and with a single large dorsal boss. **Spiracles** of metathorax smaller than remainder, which are subequal. Body hairs more numerous on venter of AI. **Cranium** not sclerotized (= same color as body); about 2.2 mm wide and 1.66 mm long; temporal sulci more heavily sclerotized. Antennae at lower third of cranium. Head hairs about 200 and shorter (about 0.003 mm long). **Labrum** about 0.78 mm wide and 0.24 mm long; hairs on anterior surface 0.006–0.012 mm long; ventral border with about 12 sensilla and with minute spinules in short rows medially; posterior surface with 30–36 sensilla. **Mandible** about 0.3 mm wide and 0.7 mm long; anterior surface of teeth roughened with minute isolated denticles; posterior surface roughened with numerous minute bosses near base of blade. **Maxilla** with cardo sclerotized (= pigmented); anterior surface with about 20 minute (about 0.006 mm long) hairs and/or sensilla; stipes rugulose; palp a stout peg with 5 apical sensilla; galea with 2–4 apical sensilla. **Labium** with palp a small boss bearing 3 apical sensilla. (Material studied: four larvae from Michigan, courtesy of R.O. Schuster.)

Vespula pennsylvanica (Saussure)⁴

Length (through spiracles) about 14 mm. Similar to *V. maculata* except as follows. Body with paired dorsal bosses on AI–AVII only. **Body hairs** 0.005–0.025 mm long. **Cranium** about 2 mm wide and 1.6 mm long. **Labrum** with short rows of minute spinules near entire ventral border of anterior surface; posterior surface with spinules in short arcuate rows, except those near middle sulcus coarse and isolated. **Mandible** about 0.3 mm wide and 0.69 mm long; with medial and apical teeth covered on all surfaces with small bosses; posterior surface of proximal portion with minute spinules in short transverse rows. **Maxilla** with about 24 minute hairs (about 0.005 mm long); palp with about 5 apical sensilla; galea a slender tall cone. **Labium** with short rows of minute spinules on anterior surface. **Hypopharynx** with short transverse rows of minute spinules. (Material studied: 13 larvae from California, courtesy of R.O. Schuster.)

SPHECOIDEA
SPHECIFORMES
SPHECIDAE: PEMPHREDONINAE
Microstigmus comes Krombein

Figure 16

Length (through spiracles) about 4 mm. Slender, fusiform and slightly sigmoid; widest at AI, tapering slightly toward anterior end and more toward posterior end; AX with prominent postero-dorsal cone; anus terminal; head large. [Material inadequate to show leg, wing and gonopod vestiges.] Thirteen differentiated somites. **Spiracles** simple, small and decreasing in diameter posteriorly, on T2, T3 and AI–AVII. Entire **integument** with minute isolated spinules; minutely rugose, rugulae closely spaced and longitudinal on ventral surface, irregular elsewhere—but always fine. **Body hairs** very few, widely scattered, minute (about 0.012 mm long) and simple. **Cranium** transversely subelliptical (about 0.45 mm wide and 0.038 mm long); no temporal sulci; clypeus projecting anteriorly and overhanging labrum. Each antenna a slender peg with 2 or 3 sensilla, mounted on a large circular disc, at lower third of cranium. No head hairs. **Labrum** crescentic; anterior surface with a few scattered sensilla, each bearing a spinule; spinules few and isolated anteriorly, minute and in short rows laterally and posteriorly. **Mandible** subtriangular in anterior view; with an apical and 2 subapical teeth, all heavily sclerotized; width increasing abruptly dorsal to basal tooth, wider portion bearing about 6 slender sharp-pointed spinules which are directed ventrally. **Maxilla** large and swollen; entire integument sparsely spinulose, spinules all minute, some isolated and others in short rows, rows longitudinal medially and transverse anteriorly; palp a small slender frustum with 2 apical and 2 subapical sensilla; galea represented by an isolated sensillum. **Labium** with minute isolated spinules; palp similar to maxillary palp in size, shape and sensilla; an isolated sensillum between each palp and opening of sericteries; the latter a narrow transverse slit on anterior surface of labium. **Hypopharynx** with numerous subparallel transverse fine ridges (rows of spinules?). [Material studied: two torn integuments and a slightly shriveled semipupa (?) from Costa Rica (see Evans and Matthews, *Psyche* 75:132–134); material loaned by National Museum of Natural History, Smithsonian Institution, courtesy of Dr. D.R. Davis.]

It does not seem worth while revising our Key to the Larvae of Social Hymenoptera to accommodate one species. If one wishes to add it before more social sphecoids are known, we suggest:

- 1c. Larvae reared in separate cells; hairs few and minute; temporal sulci absent; antennae at lower third of cranium *Microstigmus comes*

⁴We cannot understand why entomologists persist in using the misspelling *pennsylvanica* for the name of this species. Obviously it is the Latinized adjective for the name of the state of Pennsylvania. We have found the names of 15 other species of Hymenoptera that were correctly spelled *pennsylvanicus* (–a, –um). Why embalm an error in the literature?

APIFORMES

(exclusive of allodapoids)

Body profile stout and crescentic; diameter greatest at AIV and AV, gradually attenuated toward either end. Hairs none or sparse and simple. Mandibles small and usually bearing small denticles.

HALICTIDAE: HALICTINAE

Lasioglossum imitatum (Smith)

Figure 9

Length (through spiracles) about 7.5 mm. Body subcrescentic; diameter greatest at AI; anterior and posterior ends almost meeting; head and anus terminal; anus without lips; head large; lateral longitudinal welts well developed; T2–AVIII each with a pair of transverse welts extending from the longitudinal welts to mid-dorsum, smaller on AIX and AX, reduced to low bosses on dorsum of T1. Wing and leg vestiges present. **Spiracles** rather large; peritreme very narrow and feebly sclerotized; atrium with rows of encircling spinules. **Integument** on dorsal and ventral surfaces with minute spinules isolated or in short rows. No **body hairs** seen. **Cranium** feebly sclerotized (= light yellow); feebly cordate in anterior view; about 0.86 mm wide and 0.63 mm long; temporal sulci short. Each antenna a small boss with 2 or 3 sensilla, each sensillum mounted on an elevated disc. No head hairs seen. **Labrum** small; about 0.28 mm wide and 0.13 mm long; feebly bilobed; anterior surface with a few short transverse rows of minute spinules; anterolateral surfaces with a few ridges; lateral and ventral surfaces spinulose; posterior surface densely spinulose, spinules long and in short rows medially, larger and isolated laterally. **Mandible** small and stout; about 0.15 mm wide and 0.24 mm long; apex heavily sclerotized; basal half subrectangular, apical half subtriangular, sharp-pointed, with a medial blade bearing a few medial denticles. **Maxilla** paraboloidal, anterior and medial surfaces of cardo with reticulate ridges and with rather large isolated spinules; apex with short transverse rows of minute spinules; palp represented by 5 isolated sensilla; galea represented by 2 apical sensilla. **Labium** small; palp represented by a few scattered sensilla; an isolated sensillum between each palp and opening of sericteries; the latter a short transverse slit. **Hypopharynx** with coarse isolated spinules. (Material studied: five larvae from Kansas, courtesy of C.D. Michener.)

Lasioglossum sp.

Figure 10

Length (through spiracles) about 14.7 mm. Similar to *L. imitatum* except as follows. Body with welts on dorsal and lateral surfaces and venter of AIX more distinct. **Integument** with numerous rugulae in varied patterns; spinulose, spinules coarse and isolated or finer and in short transverse rows. **Cranium** about 1.4 mm wide and 0.78 mm long; feebly cordate. **Labrum** about 4.9 mm wide and 0.25 mm long; subtrapezoidal in anterior view, widest dorsally; posterior surface spinulose, the spinules minute and in short arcuate rows and with about 12 sensilla. **Mandible** about 0.25 mm wide and 0.46 mm long. (Material studied: four larvae from "Wellsville res., Cache Co., Utah, June 1971," coll. P.F. Torchio, courtesy of P.F. Torchio.)

ANTHOPHORIDAE: XYLOCOPINAE

Social allodapoids. Body profile usually J-shaped; anterior end (thorax and first 3 or 4 abdominal somites) stout and strongly curved ventrally; remainder straight and elongate-subconical; tapering to a pointed posterior end; with one or a pair of projections on dorsum of thorax and a few abdominal somites. Body hairs short to long and sparse to abundant; head hairs, when present, sparse but remarkably long. Mandibles small.

Braunsapis facialis (Gerstaecker)

Figure 11

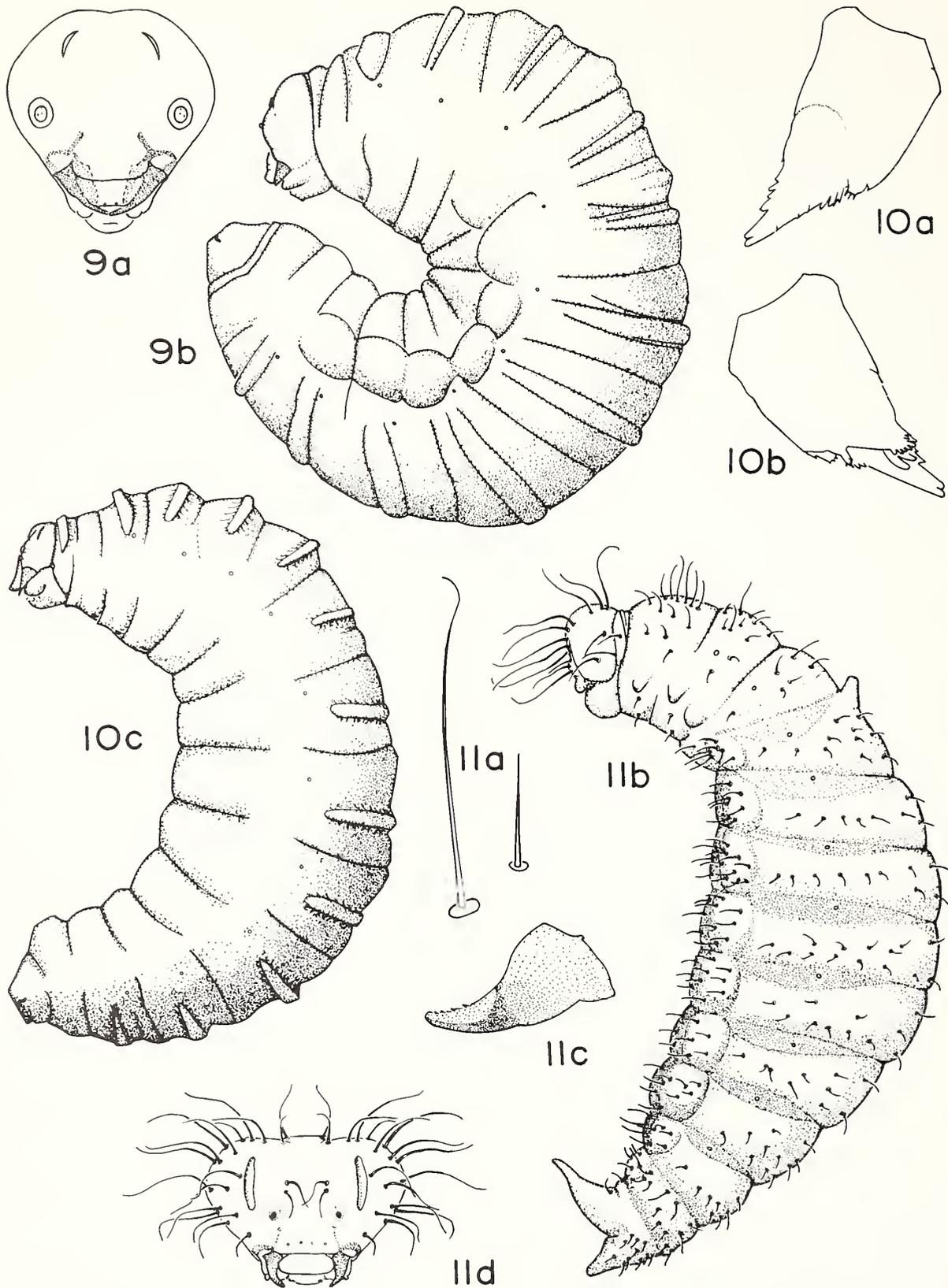
Length (through spiracles) about 5.4 mm. Body subcrescentic; diameter greatest at AIV, attenuating toward either end; dorsal profile long and C-shaped, ventral profile angulate; ventral surface flat to concave; lateral longitudinal welts well developed, forming small cones on T2, T3 and AI; a middorsal boss on AI; praesaepium with permanent bosses projecting ventrally from each lateral surface of T2, T3, and AI; AII forming ventral wall. Anus terminal, with a long subconical ventral lip and a short conical dorsal lip. Leg and gonopod vestiges present. **Spiracles** with peritreme narrow and lightly sclerotized, atrial wall with a few encircling rugulae. Entire **integument** rugulose and with papillae or spinules; rugulae on venter of thorax transverse and bearing minute spinules; integument around spiracles with numerous large granules. **Body hairs** few, simple, 0.025–0.15 mm long, short and spike-like to long with flexuous tip. **Cranium** not sclerotized (= same color as body); about 0.96 mm wide and 0.54 mm long; subcordate, sharply narrowed ventrally; temporal sulci conspicuous, rather wide and vertical. Antennae at lower third of cranium; each mounted on a small base, a slight elevation with 3 sensilla. Head hairs few (about 40), about 0.008 mm long on clypeus near labrum, long (0.125–0.6 mm) elsewhere and with fine flexuous tip. **Labrum** transversely subelliptical, about 0.35 mm wide and 0.12 mm long; with raised transversely elliptical and feebly sclerotized (= yellow) portion ventrally; anterior surface with about 20 hairs and with minute spinules dorsally; ventral surface with minute spinules in short transverse rows; posterior surface with about 4 sensilla and rows of minute spinules. **Mandible** small (about 0.1 mm wide and 0.18 mm long); feebly sclerotized; subtriangular in anterior view; apex narrowly round-pointed and directed medially; apical half with medial blade bearing a few minute denticles near apex. **Maxilla** small and appearing adnate, apex broadly round-pointed; with a few transverse rows of minute spinules on medial and posterior surfaces; palp represented by a cluster of 5 or 6 sensilla; galea apparently lacking. **Labium** small; with a basal transverse spinulose welt; anterior surface with a few transverse rows of minute spinules; palp represented by a cluster of 5 sensilla; an isolated sensillum between each palp and opening of sericteries; the latter an inconspicuous transverse slit. (Material studied: five larvae from Natal, courtesy of C.D. Michener.)

APIDAE: BOMBINAE

Bombus bimaculatus Cresson

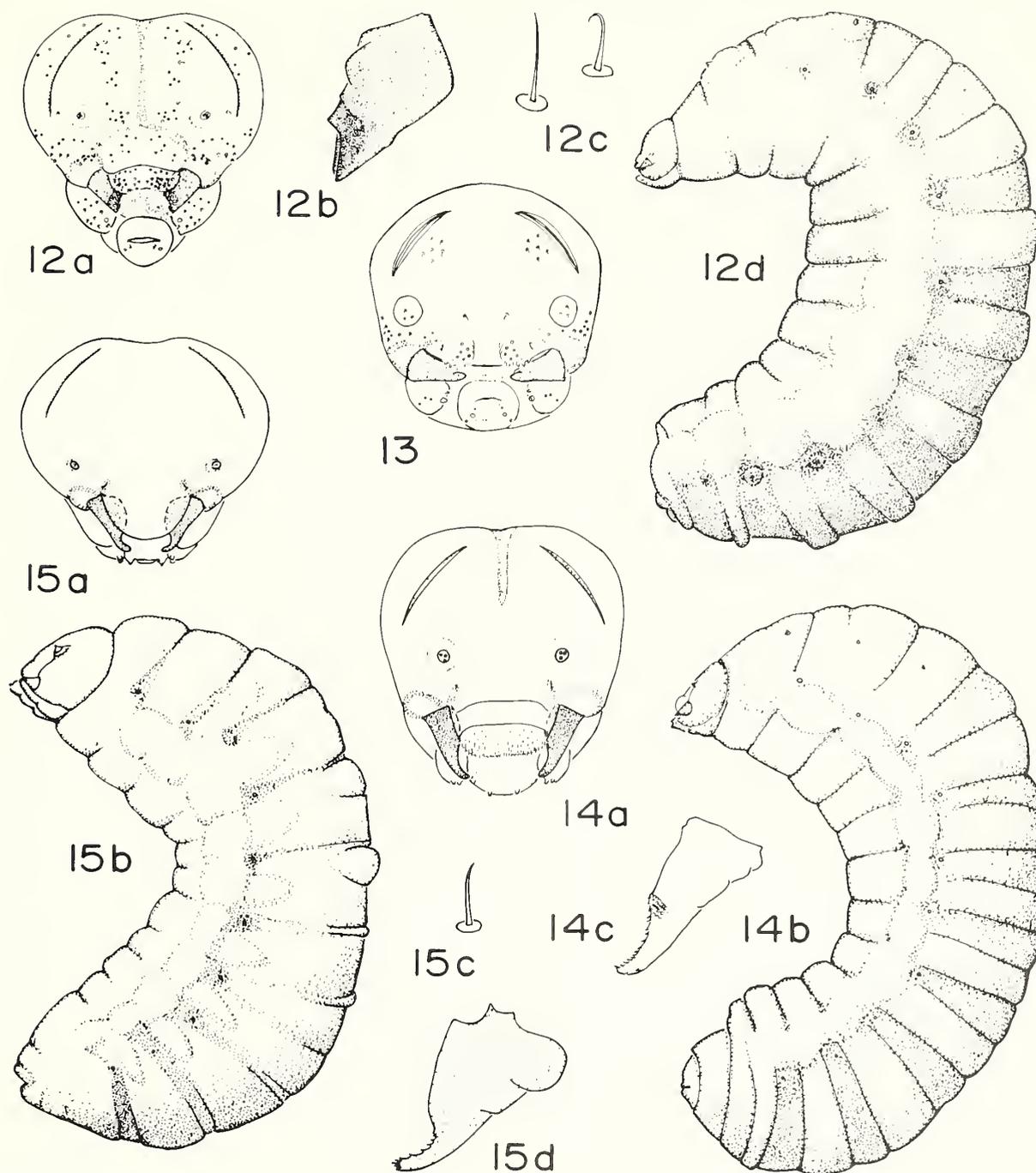
Figure 12

Length (through spiracles) about 19 mm. Body subcrescentic;



FIGURES 9 THROUGH 11.

FIGURE 9. *Lasioglossum imitatum*. a, Head in anterior view, X42; b, larva in side view, X24. FIGURE 10. *Lasioglossum* sp. a, Left mandible in anterior view, X98; b, left mandible in posterior view, X98; c, larva in side view, X10. FIGURE 11. *Braunsapis facialis*. a, Two body hairs, X135; b, larva in side view, X25; c, left mandible in anterior view, X88; d, head in anterior view, X35.



FIGURES 12 THROUGH 15.

FIGURE 12. *Bombus bimaculatus*. a. Head in anterior view, X24; b. left mandible in anterior view, X76; c. two body hairs, X400; d. larva in side view, X7. FIGURE 13. *Apis mellifera*. Head in anterior view, X30. FIGURE 14. *Melipona fasciata trinitatis*. a. Head in anterior view, X78; b. larva in side view, X9; c. left mandible in anterior view, X76. FIGURE 15. *Trigona jaty*. a. Head in anterior view, X49; b. larva in side view, X22; c. body hair, X834; d. left mandible in anterior view, X150.

dorsal profile long and C-shaped; ventral profile shorter and J-shaped; lateral longitudinal welts well developed; thoracic somites each with a pair of mammiform bosses on the dorsum, their tips acute and sclerotized; posterior portion of each abdominal somite with a transverse welt from spiracle to middorsum. Transitory praesaepium floor formed from the ventral depression of thoracic somites and AI; venter of AII forms cover. Leg and gonopod vestiges present. Area around each spiracle depressed;

peritreme narrow and feebly sclerotized; atrial wall lined with rings of long spinules, some simple and some denticulate. Entire integument with large isolated spinules grading into minute spinules posteriorly; integument roughened with numerous rugulae. **Body hairs** sparse, about 0.038 mm long, varying from slender and slightly curved to stout and hooked. **Cranium** not sclerotized (= same color as body); subcordate in anterior view, about 1.68 mm wide and 1.13 mm long; temporal sulci conspic-

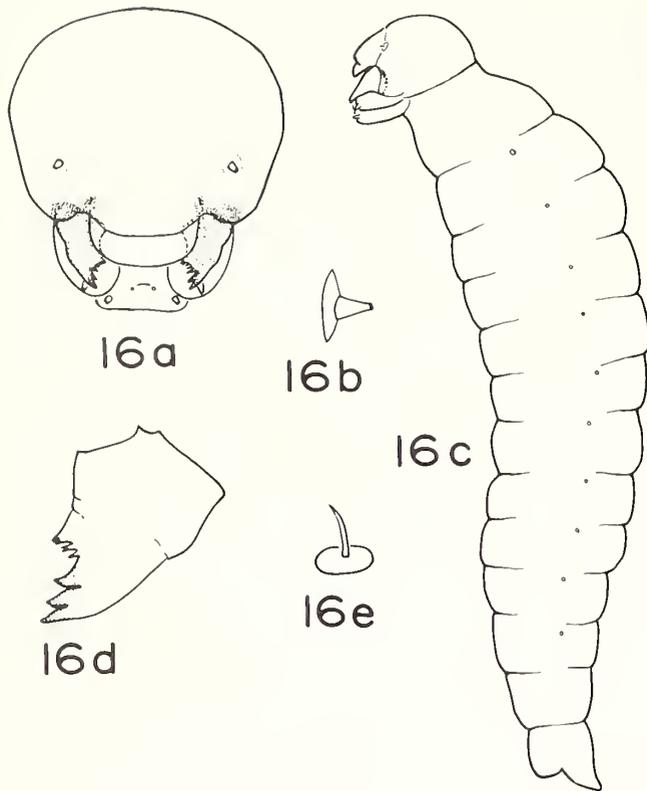
Bombus occidentalis nigroscutatus Franklin

FIGURE 16. *Microstigmus comes*. a, Head in anterior view (reconstruction), X76; b, right antenna in lateral view, X200; c, larva in side view (reconstruction), X30; d, left mandible in anterior view, X200; e, body hair, X625.

uous. Each antenna mounted on a large circular base; a small slightly sclerotized peg with 3 apical sensilla. Head hairs numerous (about 150), short (about 0.013 mm long), simple, slender and slightly curved. **Labrum** small (about 0.44 mm wide and 0.2 mm long), bilobed; each half of anterior surface with about 40 hairs (up to 0.013 mm long) and with sensilla, each of which bears a minute spinule; each half of ventral surface with minute spinules in short rows medially and dorsally, large and isolated ventrally and laterally. **Mandible** small (about 0.2 mm wide and 0.4 mm long); apex the most heavily sclerotized portion of entire larva; subtrapezoidal in anterior view; apex blunt; ventromedial border concave and furnished with both an anterior and a posterior blade; anterior blade with papillae on border and with a few rugae on surface. **Maxilla** with apex narrowly round-pointed; cardo with numerous minute spinules, isolated or in short rows; stipes with about 30 simple hairs, 0.013–0.025 mm long; with rows of minute spinules basally and laterally, spinules longer and isolated medially and apically; palp a small frustum with 3 apical sensilla; galea apparently lacking. **Labium** small and rounded; with rugae on anterior surface, short and numerous basally, longer and more widely spaced ventrally; palp a slender frustum with 3 apical sensilla; an isolated hair about 0.02 mm long between each palp and opening of sericteries; the latter wide and salient. **Hypopharynx** spinulose, spinules minute and in short rows basally, long and isolated ventrally. (Material studied: 4 larvae from New Jersey, courtesy of J.G. Rozen.)

Length (through spiracles) about 15.4 mm. Similar to *B. bimaculatus* except as follows. Body forming a nearly complete circle; dorsal profile very long and C-shaped, ventral V-shaped; middle portion of T1–T3 with a pair of transverse welts meeting at middorsum, one pair per somite. Integument of dorsal and lateral surfaces with numerous large isolated spinules, ventral with numerous subparallel ridges bearing minute spinules; no spinules around spiracles. **Body hairs** shorter (about 0.005 mm long). **Cranium** feebly sclerotized (= yellow) and transversely sub-elliptical; about 1.68 mm wide and 1.2 mm long. **Labrum** about 0.45 mm wide and 0.115 mm long; each half of anterior surface with about 30 hairs about 0.006 mm long. **Mandible** about 0.3 mm wide and 0.45 mm long; apex broadly and heavily sclerotized; no blade seen. **Maxilla** with basal portion ventral and apex directed dorsomedially; hairs all about 0.013 mm long; palp with 5 apical sensilla; galea represented by a single hair about 0.19 mm long. **Labium** with minute spinules in short arcuate rows on anterior surface, rows transverse; palp with 5 apical sensilla; 2 hairs about 0.013 mm long medial to each palp. **Hypopharynx** with minute spinules in transverse rows dorsally, laterally with ends curved ventrally. (Material studied: two larvae from California, courtesy of R.O. Schuster.)

APIDAE: APINAE

Apis mellifera Linnaeus

Figure 13

Length (through spiracles) about 14 mm. Body subcrescentic; diameter greatest at AVIII; posterior end narrowly round-pointed; anterior end nearly sharp-pointed; lateral longitudinal welts on T2–AX and a pair of transverse welts on each somite T2–AVI, meeting at middorsum, one pair per somite. Leg, wing and gonopod vestiges present. Somites indistinct. **Spiracles** with narrow peritreme and a simple atrial wall. **Integument** densely spinulose, spinules minute and in short rows or large and isolated. **Body hairs** few, about 0.013 mm long, simple. **Cranium** sub-pentagonal; about 1.6 mm wide and 1.2 mm long; no portion sclerotized (= same color as body); temporal sulci conspicuous (wide); integument with numerous denticles or papillae. Antennae very large; on lower third of cranium; each with 3 sensilla. Head hairs few (about 24); 0.006–0.013 mm long; simple. **Labrum** about 0.49 mm wide and 0.24 mm long; integument roughened as on cranium; each half of anterior surface with about 12 sensilla, each with a minute spinule; with spinules on and near ventral and lateral surfaces, spinules long and slender; posterior surface spinulose, spinules longer and in rows ventrally and laterally. **Mandible** about 0.19 mm wide and 0.9 mm long; elongate-lobose and slightly curved medially in anterior view; apex with blunt denticles directed medially. **Maxilla** with apex narrowly round-pointed; entire integument with short transverse rows of minute spinules and a few sensilla each with a long spinule; palp a short subcone with 5 (2 apical, 2 subapical and 1 lateral) sensilla; galea a rounded knob with 2 sensilla, each bearing a spinule. **Labium** subcircular; anterior surface sparsely spinulose, spinules in rows, rows longer ventrally; palp a short peg with 2 apical sensilla, each with a small rounded medial protuberance; an isolated sensillum between each palp and opening of sericteries, the latter wide and salient, lips with ridges radiat-

ing to free border. **Hypopharynx** with a few minute spinules in short arcuate rows, rows arranged into longer transverse subparallel rows. (Material studied: numerous larvae from California, courtesy of S.I. Frommer.)

APIDAE: MELIPONINAE
Melipona fasciata trinitatis Cockerell

Figure 14

Length (through spiracles) about 13 mm. Body subrescenscentic; posterior end more rounded than anterior; lateral longitudinal welts well developed; ventral swellings on AI–AIX; a pair of transverse welts from spiracle to middorsum on T1–AVIII, one pair per somite; AIX with welt across dorsum. Anus terminal and with ventral lip. No praesaepium. **Spiracles** with minute spinules on free edge of peritreme; walls of atrium with minute spinules in transverse rows. **Integument** largely spinulose, spinules isolated and rather large or in short rows and smaller. **Body hairs** minute (about 0.006 mm long), simple and very slender. **Cranium** feebly sclerotized (= yellow); about 1.44 mm wide and 0.88 mm long; feebly subcordate; temporal sulci distinct; integument rugulose; some rugae with minute spinules; clypeus with about 18 hairs near labrum. Antennae small; at lower third of cranium; each on a slightly raised boss; each with 3–5 sensilla, each of which bears a minute spinule. **Labrum** about 0.34 mm wide and 0.29 mm long; feebly bilobed; anterior surface of each half with numerous long isolated spinules and 12 sensilla; ventral and lateral surfaces with numerous spinules in short rows, more numerous ventrally; middle of ventral border of each half with prominent projecting sensilla; entire posterior surface spinulose, spinules minute and in transverse arcuate rows; posterior surface with sensilla. **Mandible** small, about 0.2 mm wide and 0.4 mm long; feebly sclerotized; subtriangular in anterior view, with apex round-pointed and curved medially; apical half with medial blade and numerous denticles; base with minute isolated spinules on anterior surface. **Maxilla** with numerous rather large isolated spinules on cardo; stipes narrowly round-pointed and spinulose, spinules rather long and in arcuate rows arranged longitudinally; palp and galea subequal; palp a low knob with 4 apical sensilla, each bearing a spinule; galea a low knob with 2 apical sensilla. **Labium** with long subparallel transverse ridges bearing spinules;

palp a low knob with 4 or 5 sensilla; an isolated sensillum between each palp and opening of sericteries; the latter wide and salient. (Material studied: one larvae and three semipupae from Trinidad, courtesy of J.G. Rozen.)

Trigona jaty Smith

Figure 15

Length (through spiracles) about 5.5 mm. Body subrescenscentic; head and anus terminal; lateral longitudinal welts well developed; AII and AIII with a pair of bosses each, which meet at mid-dorsum; smaller structures on AIV and AV. Venter flattened. Head large. Leg, wing and gonopod vestiges present. **Spiracles** with wide, feebly sclerotized peritreme; atrial wall with a few simple ridges. **Integument** entirely spinulose, spinules large and isolated on dorsal ridges above spiracles, elsewhere minute and in rows. **Body hairs** few, simple and minute (about 0.12 mm long). **Cranium** not sclerotized (= same color as body); about 0.9 mm wide and 0.6 mm long; subcordate in anterior view; temporal sulci short and narrow. Antennae at lower third of cranium; each set on a raised base; a small elevation with 3 sensilla, each bearing a minute spinule. Head hairs few (about 10), about 0.012 mm long, simple and slender. **Labrum** semicircular in anterior view, about 0.29 mm wide and 0.15 mm long; entire anterior surface spinulose, spinules short and in transverse rows; anterior surface with about 25 raised sensilla; rather long isolated spinules on ventral and lateral surfaces; posterior surface with minute spinules in short transverse rows. **Mandible** small and stout (about 0.14 mm wide and 0.2 mm long); feebly sclerotized; subtriangular in anterior view; apex round-pointed and curved medially, with spinulose margin; a few minute spinules on anterior surface near base. **Maxilla** slightly inflated; apex bluntly rounded; spinulose, spinules longer and isolated apically, shorter and in rows basally; palp a short knob with 3 apical sensilla; galea represented by 2 sensilla, each bearing a rather long spinule. **Labium** small; sparsely spinulose, spinules minute and isolated; palp a short knob; an isolated sensillum between each palp and opening of sericteries, the latter wide and salient. **Hypopharynx** with minute spinules in long subparallel transverse rows. (Material studied: numerous larvae from Panamá, courtesy of P.F. Torchio.)

LIST OF SPECIES WHOSE LARVAE ARE DESCRIBED
AND/OR ILLUSTRATED IN THE LITERATURE⁵

SUPERFAMILY VESPOIDEA
FAMILY VESPIDAE
SUBFAMILY POLISTINAE

Apoica

- flavissima* van der Vecht. Dias 1975: 3, fig. 16–23.
pallens (Fabricius). Dias 1975: 3, fig. 9–15; this paper.

Belonogaster

- lateritius* Gerstaecker. Wheeler and Wheeler 1979: 313, fig. 13h;
this paper.

Brachygastra

- augusti* (Saussure). Dias 1975: 9, fig. 175–180.
lecheguana (Latreille). Dias 1975: 9, fig. 165–174.
scutellaris (Fabricius). Reid 1942: 314, fig. 99–103.

Metapolybia

- cingulata* (Fabricius). Reid 1942: 317, fig. 109–113.

Mischocyttarus

- araujoi* Zikán. Dias 1975: 6, fig. 68–73, 85.
carbonarius (Saussure). Reid 1942: 323, fig. 118–119.
cassununga (von Ihering). Dias 1975: 5, fig. 51, 58–67.
cerebrus acheron Richards. Reid 1942: 322, fig. 124–126, 129.
c. styx Richards. Dias 1975: 5, fig. 45–50, 52–54, 57.
collarellus Richards. Reid 1942: 324, fig. 131.
drawseni Saussure. Dias 1975: 4, fig. 24–33, 55, 56.
flavitaris (Saussure). This paper.
injudundus (Saussure). Reid 1942: 326, fig. 133, 134.
laticus (Fox). Dias 1975: 6, fig. 74–84.
lecointei (Ducke). Reid 1942: 320, fig. 115, 123, 128.
metoecus Richards. Reid 1942: 321, fig. 117, 122.
oecothrix Richards. Reid 1942: 323, fig. 114, 121.
roundicollis (Cameron). Dias 1975: 4, fig. 34–44.
superus Richards. Reid 1942: 325, fig. 132.
surinamensis (Saussure). Reid 1942: 325, fig. 127.
synoecus Richards. Reid 1942: 323.
sp. Reid 1942: 325, fig. 135–137.

Parachartergus

- fraternus* (Gribodo). Dias 1975: 7, fig. 98–104.
pseudoapicalis (Fabricius). Dias 1975: 6, fig. 90–97.

Polistes

- annularis* (Linnaeus). Nelson 1969: 31.
apachus Saussure. Nelson 1969: 37.
biglumis (Linnaeus). Yamane 1976: 10, fig. 8–11.
canadensis (Linnaeus). Dias 1975: 11, fig. 228–238.
carnifex (Fabricius). Reid 1942: 300, fig. 43–51; Nelson 1969: 88.
cinctus (Lepeletier). Packard 1897: 77–79, fig. 6; Reid 1942: 304.
cinerascens Saussure. Dias 1975: 11, fig. 239–247.
comanchus Saussure. Nelson 1969: 42.
crinitus multicolor (Olivier). Reid 1942: 303, fig. 52–62.
dorsalis (Fabricius) (= *lunteri* Bequaert). Nelson 1969: 69.
erythrocephalus Latreille. Nelson 1969: 92; this paper.
exclamans Viereck. Nelson 1969: 47; this paper.

- e. lineonotus* R. Bohart. This paper.
flavus Cresson. Nelson 1969: 52.
foederatus Kohl. Grandi 1934a: 74–78, pl. 1, II; Grandi 1934b: 9–16, fig. V–X; Reid 1942: 304–305, fig. 63–66.
fuscatus (Fabricius). This paper.
f. aurifer Saussure. Nelson 1969: 56; this paper.
f. centralis Hayward. Nelson 1969: 60.
f. variatus Cresson. Nelson 1969: 65.
gallicus (Linnaeus). Parker 1943: 619–620, fig. 1–5; Reid 1942: 305–306, fig. 67–68; Soika 1934: 340, 10 fig.
kohli Dalla Torre. Grandi 1934a: 74–78, pl. I.
major castaneicolor Bequaert. This paper.
metricus Say. Nelson 1969: 74.
poeyi Lepeletier. This paper.
rothnei iwatai van der Vecht. Yamane 1976: 10, fig. 12.
rubiginosus Lepeletier. Nelson 1969: 79.
simillimus Zikán. Dias 1975: 1, fig. 221–227.
versicolor (Olivier). Dias 1975: fig. 211–220; Nelson 1969: 100.
sp. Yamane 1976: fig. 13.

Polybia

- bistriata* (Fabricius). Reid 1942: 310, fig. 86–89.
catillifex Moebius. Reid 1942: 310, fig. 82–85.
clyrsothorax (Weber). Dias 1975: 8, fig. 145–151.
dimidiata (Olivier). Dias 1975: 8, fig. 152–157.
fastidiosuscula Saussure. Dias 1975: 8, fig. 131–137.
ignobilis (Haliday). Dias 1975: 8, fig. 138–144.
jurinei Saussure. Dias 1975: 7, fig. 125–130.
micans Ducke. Reid 1942: 308, fig. 69–77.
occidentalis (Olivier). Dias 1975: 7, fig. 105–112; this paper.
paulista (von Ihering). Dias 1975: 7, fig. 113–120.
rejecta (Fabricius). Reid 1942: 309, fig. 78–81.
scutellaris (White). Dias 1975: 7, fig. 121–124.

Protonectarina

- sylveirae* (Saussure). Dias 1975: 8, fig. 158–164.

Protopolybia

- exigua* (Saussure). Dias 1975: 9, fig. 181–187.
minutissima (Spinola). Reid 1942: 312, fig. 90–93.
pumila (Saussure). Dias 1975: 9, fig. 188–194.
sedula (Saussure). Reid 1942: 312, fig. 94–98.

Ropalidia

- cincta* (Lepeletier). This paper.

Stelopolybia

- infernalis* (Saussure). Reid 1942: 316, fig. 104–108.
meridionalis von Ihering. Dias 1975: 10, fig. 195–201.
pallipes (Olivier). Dias 1975: 10, fig. 202–210

Syneoca

- surinama* (Fabricius). Wheeler and Wheeler 1979: 313, fig. 13i;
this paper.
s. cyanea (Fabricius). Dias 1975: 6, fig. 86–89.

⁵ Social parasites are included.

SUBFAMILY VESPINAE

Vespa

- affinis* Linnaeus. Yamane 1976: fig. 29, 37, 41.
analis insularis Dalla Torre. Yamane 1976: fig. 28, 42, 49, 54b, 59.
a. nigrans Buysson. Yamane 1976.
basalis Smith. Yamane 1976: fig. 36, 61.
crabro Linnaeus. Reid 1942: 296, fig. 37-41.
c. flavofasciata Cameron. Yamane 1976: fig. 44, 54a, 58.
mandarina latilineata Cameron. Yamane 1976: fig. 53.
m. nobilis Sonan. Yamane 1976: fig. 14-16, 18-21, 53.
simillima Smith. Yamane 1976: fig. 45.
tropica pseudosoror van der Vecht. Yamane 1976: fig. 44, 60.
velutina flavitaris Sonan. Yamane 1976: fig. 17.
xanthoptera Cameron. Yamane 1976.

Vespula

- arenaria* (Fabricius). Packard 1897: 80.
atropilosa (Sladen). Wheeler and Wheeler 1979: 313, fig. 13g; this paper.
germanica (Fabricius). Grandi 1935: 31; Reid 1942: 296, fig. 32-35; Soika 1934: 340, 11 fig.
karenkona Sonan. Yamane 1976: fig. 63.
lewisi Cameron. Yamane 1976.
media (DeGeer). Reid 1942: fig. 30-35; Yamane 1976: fig. 25, 38, 47, 52, 57.
maculata (Linnaeus). Wheeler and Wheeler 1979: 306, fig. 10b, 313, 13f; this paper.
maculifrons (Buysson). This paper.
norvegica (Fabricius). Grandi 1934a: 74-78, pl. I-II; Grandi 1934b: 17-23, fig. XI-XVI; Reid 1942: 296, fig. 32-35.
pennsylvanica (Saussure). This paper.
rufa (Linnaeus). Grandi 1934a: 74-78, pl. I; Grandi 1935: 29-31, fig. I, II; Reid 1942: 296, fig. 29-31; Yamane 1976.
r. schrenckii Radoszkowsky. Yamane 1976: fig. 56, 64.
saxonica nipponica Sk. Yamane. Yamane 1976: fig. 24, 48, 51, 65.
silvestris Scopoli. Grandi 1934a: 74-78, pl. I.
vulgaris (Linnaeus). Reid 1942: 294, fig. 19-28, 42; Yamane 1976: fig. 22, 23, 39, 50, 55.

SUPERFAMILY SPHECOIDEA

FAMILY SPHECIDAE

SUBFAMILY PEMPHREDONINAE

Microstigmus

- comes* Krombein. Evans and Matthews 1968: 132-134; this paper.

FAMILY HALICTIDAE

SUBFAMILY HALICTINAE

TRIBE HALICTINI

Lasioglossum

- imitatum* (Smith). This paper.
 sp. This paper.

FAMILY ANTHOPHORIDAE

SUBFAMILY XYLOCOPINAE

TRIBE ALLODAPINI

Allodapula

- acutigera* Cockerell. Michener 1975: 246, fig. 2-4, 14, 15.
dichroa (Strand). Michener 1975: 248-249.
hessei Michener. Michener 1975: 248, fig. 1, 12, 13.
melanopus (Cameron). Michener 1975: 249, fig. 5, 6, 18, 19.
ornaticeps Michener. Michener 1975: 249, fig. 8, 9, 20, 21.

Braunsapis

- acuticauda* Michener. Michener 1975: 238.
albitarsis (Friese). Michener 1975: 234.
bouyssouii Vachal. Michener 1975: 232, fig. 15-19.
draconis Michener. Michener 1975: 234, fig. 45-51.
elizabethana (Strand). Michener 1975: 237, fig. 66, 82-90.
facialis (Gerstaecker). Michener 1975: 229, fig. 1-8, 27-30; Wheeler and Wheeler 1979: 299, fig. 6, 306, fig. 10c, 313, fig. 13e; this paper.
foveata (Smith). Michener 1975: 240, fig. 101-113.
ghanae Michener. Michener 1975: 236, fig. 79-81.
gorillarum (Cockerell). Michener 1975: 231, fig. 14.
leptozenia (Vachal). Michener 1975: 233, fig. 24-26, 31-44.
luapulana (Cockerell). Michener 1975: 234, fig. 52-58, 62-65.
natalica Michener. Michener 1975: 231, fig. 9-13.
pallida Michener. Michener 1975: 231.
paradoxa (Strand). Michener 1975: 238, fig. 67-68, 91-97.
rhodesi (Cockerell). Michener 1975: 236, fig. 59-61.
rolini (Vachal). Michener 1975: 232, fig. 20.
simplicipes Michener. Michener 1975: 232, fig. 21-23.
stuckenbergerorum Michener. Michener 1975: 236, fig. 72-78.
trochanterata (Gerstaecker). Michener 1975: 240, fig. 69, 70, 114-118.
vitrea (Vachal). Michener 1975: 238, fig. 98-100.

Eucondylops

- konowi* Brauns. Michener 1975: 249, fig. 10, 11, 22, 23.

Exoneura

- concinula* Cockerell. Syed 1963: 269, 271, fig. 33-37.
hamulata Cockerell. Syed 1963: 268-269, fig. 20-32.
obscuripes Michener. Syed 1963: 271-272, fig. 44-49.
subbaculifera Rayment. Syed 1963: 273, fig. 50-52.
variabilis Rayment. Syed 1963: 266-268, fig. 1-19.

Inquilina

- excavata* (Cockerell). Syed 1963: 273, 274, fig. 38-43.

Nasutapis

- strausorum* Michener. Michener 1975: 242, fig. 71, 119-123.

FAMILY APIDAE

SUBFAMILY BOMBINAE

Bombus

- agrorum pascuorum* Scopoli. Grandi 1937: 316-320, fig. XXXI-XXXIV.

americanorum Fabricius. Michener 1953: 1087, fig. 248–253; Ritcher 1933: 59, fig. 32, 33.
auricomus Robertson. Ritcher 1933: 59, fig. 1, 4, 10, 14, 15.
bimaculatus Cresson. Ritcher 1933: 59, fig. 2, 5, 7–9, 11, 18, 19; Wheeler and Wheeler 1979: 313, fig. 13d; this paper.
fervidus (Fabricius). Packard 1897: 115; Ritcher 1933: 59, fig. 28, 29.
griseocollis (DeGeer) (= *separatus*). Ritcher 1933: 59, fig. 22.
impatiens Cresson. Ritcher 1933: 59, fig. 16, 17.
melanopygus Nylander. This paper.
occidentalis nigroscutatus Franklin. This paper.
perplexus Cresson. Ritcher 1933: 59, fig. 20, 21.
silvarum (Linnaeus). Grandi 1934b: 112–117, fig. LXXXVI–LXXX.
terricola Kirby. Ritcher 1933: 59, fig. 24, 25.
vagens Smith. Packard 1897: 117; Ritcher 1933: 59, fig. 26, 27.
vosnesenskii Radoszkowski. Michener 1953: 1089, fig. 254.

Psithyrus

variabilis (Cresson). Ritcher 1933: 59, fig. 3, 6, 30, 31; Michener 1953: 1090.

SUBFAMILY APINAE

Apis

cerana Fabricius (= *indica*). Torchio and Torchio 1975: 8, 9, fig. 3, 4, 10, 14, 24–26, 35, 42, 46, 51, 55, 61, 71, 76.
dorsata Fabricius. Torchio and Torchio 1975: 10, 11, fig. 7, 8, 12, 16, 29–33, 36, 39, 40, 44, 48, 49, 53, 56, 62, 70, 74, 78.
florea Fabricius. Torchio and Torchio 1975: 9, 10, fig. 5, 6, 11,

15, 27, 28, 37, 43, 47, 52, 57, 63–65, 67, 68, 72, 75.

mellifera Linnaeus. Grandi 1934a: 78, pl. II; Grandi 1934b: 110–112, fig. LXXIV–LXXV; Michener 1953: 1094, fig. 275–280; Nelson 1924: 1167–1170, 5 fig.; Packard 1897: 120; Torchio and Torchio 1975: 4–8, fig. 1, 2, 9, 13, 17–23, 34, 38, 41, 45, 50, 54, 58–60, 66, 69, 73, 77; Wheeler and Wheeler 1979: 306, fig. 10a; 313, fig. 13a; this paper.

SUBFAMILY MELIPONINAE

Lestrimelitta

ehrharti Friese. Oliveira 1968: 9, fig. 1–3.
linao (Smith). Oliveira 1968: 2–6, fig. 1–3.

Melipona

fasciata trinitatis Cockerell. Wheeler and Wheeler 1979: 313, 13b; this paper.
marginata Lepeletier. Michener 1953: 1092, fig. 260–262.
nigra schenski Gribodo. Oliveira 1960: 4–16, 25 fig.
quadrifasciata Lepeletier. Michener 1953: 1090, 1092, fig. 255–259.
variegatipes Gribodo. Michener 1953: 1092, fig. 263–265.

Trigona

corvina Cockerell. Michener 1953: 1094, fig. 271, 272, 274.
cupira Smith. Michener 1953: 1093, 1094, fig. 266–270, 273.
droyana (Friese). Oliveira 1965 (*vide* 1968).
jaty Smith. Wheeler and Wheeler 1979: 313, 13c; this paper.
muelleri (Friese). Oliveira 1970: 235–238, fig. 1–3.

CHARACTERIZATIONS OF LARVAE OF HIGHER TAXA

VESPOIDEA

Vespoidea:—Wheeler and Wheeler 1979: 318–319.
 Vespidae:—Dias 1975: 2, fig. 1–8; Reid 1942: 287–289.
 Vespinae:—Reid 1942: 294; Yamane 1976: 4–9, fig. 1–3.
 Polistinae:—Dias 1975: 3; Reid 1942: 299, 307; Yamane 1976: 10. *Apoica* Dias 1975:3. *Brachygastra* Dias 1975: 9. *Metapolybia* Reid 1942: 317. *Mischocyttarus* Dias 1975: 3; Reid 1942: 317–318. *Parachartergnus* Dias 1975: 6. *Polistes* Dias 1975: 10; Nelson 1969: 14–28. *Polybia* Dias 1975: 7; Reid 1942: 308. *Protopolybia* Dias 1975: 9; Reid 1942: 311. *Stelopolybia* Dias 1975: 10; Reid 1942: 315–316.

SPHECOIDEA APIFORMES GROUP

Apiformes group (excluding allodipoid bees):—Wheeler and Wheeler 1979: 317–318.
 Xylocopinae:—*Allodapula* and *Eucondylops* Michener 1975: 244. *Braunsapis* and *Nasutapis* Michener 1975: 224–225. Allodipoid bees:—African allodipine bees Michener 1976: 36. Wheeler and Wheeler 1979: 316–317.
 Bombinae:—Ritcher 1933: 54–56.

KEYS TO LARVAE

Families of eusocial Hymenoptera:—Wheeler and Wheeler 1979: 315–316.

VESPOIDEA

Subfamilies of Vespidae:—Reid 1942: 289; Soika 1934: 341.
 Species of *Vespa* and *Vespnla* of Japan and Taiwan, Yamane

1976: 13, 14.

Certain species of *Polistes* Reid 1942: 299–300.
 Certain genera of Polistinae:—Reid 1942: 307.
 Certain species of *Polybia* Reid 1942: 308.
 Two species of *Protopolybia* Reid 1942: 312.
 Eleven species of *Mischocyttarus* Reid 1942: 318–319.

SPHECOIDEA
APIFORMES GROUP

- Certain species of *Nasutapis* and the African species of *Braunsapis* Michener 1975: 228–229.
 Certain species of African *Allodapula* and *Eucondylops* Michener 1975: 248.
 Certain species of *Bombus* and *Psithyrus* Ritcher 1933: 59.
 Genera of African allodapine bees Michener 1976: 36.

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⁶ It is almost impossible to determine the dates of Grandi's publications. We have tried to follow Michener 1953.

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CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

NOMINAL GENERA AND SPECIES OF LANTERNFISHES (FAMILY MYCTOPHIDAE)

By John R. Paxton



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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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Edward Ostermeyer
Editor

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NOMINAL GENERA AND SPECIES OF LANTERNFISHES (FAMILY MYCTOPHIDAE)¹

By John R. Paxton²

ABSTRACT: The 365 species of recent fishes of the family Myctophidae are listed under 35 generic and sub-generic categories; some 225 species are considered valid. The author, date, page, type locality, number and location of types and museum registration number for primary types are listed for each species. An alphabetical list of species indicates the genus in which the species is currently placed and the genus and year of original description. Of the lanternfishes described as fossils, 89 Cenozoic species are listed.

INTRODUCTION

Lanternfishes (family Myctophidae) occur in the upper 1000 metres of all oceans of the world. With some 225 currently recognized species, myctophids are the largest family of mesopelagic fishes. The first species were described in 1810 and there is now a total of 365 nominal species of Recent lanternfishes. The number of new species descriptions is not decreasing (34 since 1969) and, with at least 10 other new species waiting description by various workers, the number of recognized species will probably reach 250.

Family revisions have been published by Cuvier and Valenciennes (1849), Goode and Bean (1896), Brauer (1904), Parr (1928) and Fraser-Brunner (1949). However, Fraser-Brunner did not effectively deal with the numerous species of *Diaphus* described by Fowler (1934), and since 1949, 67 new myctophid species have been described. Parr (1929, 1934) discussed the myctophid types in the United States National Museum and the Museum of Comparative Zoology, Harvard University respectively, while Nafpaktitis (1973) redescribed the myctophid types of Tåning (1918, 1928, 1932).

The present paper attempts to bring together all of the published names of the recent genera and species in the family Myctophidae.

MATERIALS AND METHODS

Type specimens of myctophids are located in the following institutions:

- AHF — Allan Hancock Foundation, Los Angeles (specimens now at LACM)
- AMG — Albany Museum, Grahamstown (specimens now at RUSI)
- AMNH — American Museum of Natural History, New York
- AMS* — Australian Museum, Sydney
- ANSP* — Academy of Natural Sciences, Philadelphia
- BCFH — U.S. Bureau of Commercial Fisheries, Honolulu
- BMNH* — British Museum (Natural History), London
- BOC — Bingham Oceanographic Collections, Yale University, New Haven

- BPBM* — Bernice P. Bishop Museum, Honolulu
- CAS* — California Academy of Sciences, San Francisco
- CMP — Carnegie Museum, Pittsburgh (specimens now at FMNH)
- DMBL — Dana Collections, Dana Marine Biological Laboratory, Charlottenlund (specimens now at ZMUC)
- FMNH — Field Museum of Natural History, Chicago
- IMC — Indian Museum, Calcutta (now ZSI)
- IOANM — Institute of Oceanology, Academy of Sciences, Moscow
- IOES — Indian Ocean Expedition Collections, Hamburg (specimens now at ZMH)
- ISH* — Institut für Seefischerei, Hamburg
- ISNB* — Institut Royal des Sciences Naturelles, Brussels
- LACM* — Natural History Museum of Los Angeles County, Los Angeles
- LV — Laboratoria de Vigo, Spain
- MCZ* — Museum of Comparative Zoology, Harvard University, Cambridge
- MMF — Museum Municipal Funchal, Madeira
- MNH* — Museum National d'Histoire Naturelle, Paris
- MOM* — Musée océanographique de Monaco, Monaco
- MPS — Museum of the Philosophical Society, University of Cambridge, London (specimens now at BMNH)
- NIO* — National Institution of Oceanography, Surrey (specimens now at BMNH)
- NMC — National Museum of Canada, Ottawa
- NMFS — National Marine Fisheries Service, Washington D.C. (specimens now at USNM)

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- NMG — Naturhistoriska Museet, Göteborg
 NMW* — Naturhistorisches Museum, Vienna
 NRMS — Naturhistoriska Riksmuseet, Stockholm
 NYZS — New York Zoological Society, New York (specimens now at CAS)
 ORI — Ocean Research Institute, University of Tokyo, Tokyo
 OSUDO — Oregon State University Department of Oceanography, Corvallis
 PM — Philippines Museum, Manila
 QM* — Queensland Museum, Brisbane
 RMNH* — Rijksmuseum van Natuurlijke Historie, Leiden
 ROM — Royal Ontario Museum, Toronto
 RUSI — Rhodes University J.L.B. Smith Institute, Grahamstown
 SAM — South African Museum, Capetown
 SIO* — Scripps Institution of Oceanography, La Jolla
 SMF* — Senckenberg Museum, Frankfurt
 SU — Stanford University Natural History Museum (specimens now at CAS)
 SMNS* — Staatliches Museum für Naturkunde in Stuttgart, Ludwigsburg
 SOSC — Smithsonian Oceanographic Sorting Center, Washington D.C. (specimens now at USNM)
 UMB — Überseemuseum, Bremen
 UMML — University of Miami Marine Laboratory, Miami
 USFC — U.S. Fish Commission (specimens now at USNM)
 USNM* — United States National Museum of Natural History, Washington D.C.
 VMM — Vanderbilt Marine Museum, Long Island
 ZIANL — Zoological Institute, Academy of Sciences, Leningrad
 ZMA* — Zoologisch Museum der Universiteit van Amsterdam, Amsterdam
 ZMB* — Zoological Museum, Berlin
 ZMH* — Zoologisches Institut und Museum, Universität Hamburg, Hamburg
 ZMO — Zoological Museum, University of Oslo, Oslo
 ZMUC* — Zoological Museum, University of Copenhagen, Copenhagen
 ZSI* — Zoological Survey of India, Calcutta
 ZUMT — Department of Zoology, University Museum, University of Tokyo, Tokyo.

The abbreviations are used in the body of the species list. Registration numbers were checked and most type specimens examined in those institutions asterisked. Most other placements were confirmed by correspondence with the relevant curators, while a few are taken as stated in the original description.

The species are listed under the currently recognized genera. Because agreement has not been reached on generic relationships within the family (see Moser and Ahlstrom 1970, 1972, 1974; Paxton 1972), the genera are arranged alphabetically. When subgenera are recognized, the nominal subgenus is listed first. Within each genus or subgenus, the currently recognized species are arranged chronologically by year of description; junior synonyms are indented and listed chronologically under their respective senior synonyms. Included for each species is the original combination and spelling, author, date, page number of the original description, type locality, kind and number of types, and institutional location (with registration numbers for primary types

only) as given in the original description. Additional data on the types or locality as given by subsequent authors are placed in parentheses; further information not followed by an author's name is the result of the present study.

The alphabetical index of all recent species names includes the genus in which the species is currently placed, the genus in which it was originally described and the year of description. To find more easily junior synonyms in the main list, particularly in the genus *Diaphus* with 112 nominal species, the year of description of the senior synonym is placed in parentheses after all junior synonyms in the alphabetical list.

More than 90 species of fossils have been described in the family Myctophidae; most are based on Cenozoic otoliths. The vast majority of these fossil species were originally described in, or have subsequently been assigned to, recent myctophid genera. Because of the problems of potential homonymy, an alphabetical list of fossil myctophid species is added. Each species is followed by the genus in which it is currently placed, the original genus if different, the author and year of original description, and a reference to the current generic allocation, if applicable. This list was compiled mostly from Weiler (1968) and the Zoological Record. J. Fitch kindly provided a number of recent reprints. The list is probably incomplete and should be used with some caution.

A number of species based on otoliths have been described as *Otolithus (Myctophidarum)* sp., indicating only placement in the family Myctophidae. In such cases, only the subgeneric name has been included in the list. The taxonomy of the fossil species is not stable and a number of species have changed generic allocation more than once (see Nolf 1977 and Weiler 1971). The fossil species are not included in the list of recent species and the references for the fossil species are in a separate section. A number of Cretaceous fossils have been attributed to the family Myctophidae; the genera are listed in Romer (1966). Goody (1969) and Rosen (1973) have shown that most of these genera do not belong with the myctophoids. Some species of *Sardinoides* and *Acrognathus* are most similar to the Neoscopelidae (Rosen 1973). None of the Cretaceous species is included in the list of fossil Myctophidae.

DISCUSSION

The most contentious aspect of this compilation is the listing of valid species with junior synonyms. Revisionary work is required for many genera and for some, particularly the genus *Diaphus*, the listing of valid species is admittedly premature. It is stressed that this is not a family revision and the vast majority of types were examined only to confirm the listed registration numbers. Decisions about junior synonyms have been taken mostly from the literature, using the most recent revision of the genus in question. Much advice has been given by other workers on myctophids, particularly B.G. Nafpaktitis on *Diaphus*, although none will agree with all of the decisions made herein. Where the status of a species is questioned, the name is preceded by a '?'.
 A few differences at the generic level are evident between this compilation and Paxton (1972). Subgenera have been recognized (i.e. *Metelctrona* and *Parvilux*) primarily on the larval evidence of Moser and Ahlstrom (1974).

In my opinion the designation of lectotypes should be a conservative process. Many myctophid species are represented by a series of syntypes. If the syntypic series is currently considered

conspecific, I think it more reasonable not to choose a lectotype. If in the future the syntypes are found to represent more than one species, a more valuable lectotype designation can be made at that time, in an attempt to match the known name with the more appropriate species. While some syntypic series were found to represent more than one species (*Myctophum nanfragus*, *Diaphus malayanus*, *D. splendidus*, *Triphoturus micropterus*), the designation of lectotypes has been deferred until more comprehensive descriptions and discussion could be included. In those cases the currently recognized name, usually based on the figured specimen, has been utilized in choosing senior synonyms.

A number of lectotype designations have been made in the past. Goode and Bean (1896) described 13 species and in only a few cases designated a holotype. Jordan and Evermann (1896) listed 'type' catalogue numbers for all these species and, where correct, these have been accepted herein as lectotype designations.

For those considering placement of future type specimens, USNM with primary types representing 88 species and secondary types of an additional 30 species has the largest myctophid type holdings, followed by ZMUC (65), BMNH (42) and CAS (54). The rest of the first 10 institutions, MCZ, ZIANL, ZMB, SIO, LACM and BOC, all have between 10 and 30 species represented whereas none of the other institutions have types of more than eight species. Tåning (41), Fowler (38) and Gilbert (34) have described the largest number of myctophids.

A few species require separate comment.

Scopelus pyrsobolus Alcock (1890; = *Bolinichthys pyrsobolus*) has caused some previous problems. Nafpaktitis and Nafpaktitis (1969) pointed out that on the basis of Alcock's original description the species is unidentifiable. As a result Nafpaktitis and Nafpaktitis (1969) and Johnson (1975) did not utilize the name in their respective treatments of the two species groups of the genus, while Bolin (1959) used the name for the wrong species. In a paper apparently overlooked by later workers, Misra (1949) redescribed and figured Alcock's holotype. Examination of the 76 mm SL holotype has revealed some differences from Misra's redescription. A VLO is present on the right side, slightly closer to the lateral line than the ventral base. The VO₂ is elevated to the level of the SAO₁ and PO₄. Three luminous organs are present at the base of the anal fin. No photophores are visible behind the eye. Gill rakers number 5+1+11-12. While the absence of secondary photophores and a luminous organ at the pelvic base cannot be certain due to the condition of the holotype, the position of the VLO far below the lateral line places it in the species group treated by Johnson (1975). The highly elevated VO₂ indicates that *B. pyrsobolus* is a senior synonym of *Serpa blacki* Fowler (1934).

The holotype of *Bolinichthys stilbius* (Gilbert 1908) is in poor condition, lacking almost all photophores and luminous patches. However from the figure of Gilbert (1908), the species appears to be the same as *B. photothorax* (Parr 1928). I prefer to wait a revision of the Pacific specimens of this species group before placing Parr's widely utilized name in synonymy.

The holotype of *Scopelus* (= *Myctophum indicus*) Day (1878) was found to be totally disintegrated in the bottle. Day's original description is inadequate to place the species, which must remain a nomen dubium. In a valuable contribution Whitehead and Talwar (1977) have listed the possible type specimens of Day's species in the numerous institutions that now hold his specimens. Three specimens in London (BMNH 1889.2.1.2232-4) from the

Andaman Islands are listed as possible syntypes of *Scopelus indicus*. However, the original description is clearly based on a single specimen from Vizagapatam. Day's figure is of a *Myctophum* unidentifiable to species; the three BMNH specimens represent two species of *Centrobranchus* and are not types of *Scopelus indicus*.

Scopelus tenuicauda Steindachner (1867a), *S. cuvieri* Castelnau (1873), *S. langerhansi* Johnson (1890) and *S. novaeseelandiae* Steindachner (1901) are all nomina dubia, for no types could be found and the original descriptions are inadequate.

Serpa turneri Fowler (1934) was placed in the subgenus (now genus) *Triphoturus* by Fraser-Brunner (1949). However, the holotype has only four VO, which places the species in the genus *Lampanyctus*. It is identical to, and a senior synonym of, *Lampanyctus basili* Wisner (1974).

The type locality of *Myctophum* (= *Symbolophorus*) *boops* Richardson (1845) is in error (Whitley 1953). Until the south Pacific species in this difficult complex are adequately defined, no synonymy is possible.

Three specimens of *Lampadena speculigera* (USNM 43796, 43797 and 39479) were apparently available to Goode and Bean (1896) at the time of original description. Only 43796 is mentioned in the original description, as a 50 mm specimen from 39°48'N, 70°38'W, which is an 'Albatross' locality. The specimen is now 45 mm TL. However, the counts of dorsal 15 and gill rakers 6+1+12 do not match those of the original description, nor is this specimen labelled type in the catalogue. Jordan and Evermann (1896) list 43797 as the type of the species, and it is so labelled in the catalogue. The counts of this specimen come close to those of the original description (see Bolin 1959). However, the specimen is about 130 mm TL and was collected by the schooner "Alice J. Wonson" in the Gulf Stream. Specimen 39479, now almost disintegrated but certainly closer to 130 mm TL than 50 mm TL, has the same locality data as 43796, is also labelled type in the catalogue and has a label stating "drawn" in the bottle. However, in the list of figures (Goode and Bean 1896), specimen 43797 is given with the apparently erroneous ship "Fish Hawk." The figure has no scale, is approximately 130 mm TL, and is presumably natural size. As at least two of the three specimens were apparently utilized in the original description and figure, the type listing of USNM 43797 by Jordan and Evermann (1896) is accepted as a lectotype designation, and the other two specimens are considered paralectotypes.

Fowler (1934) described 33 species of myctophids, mostly in the genus *Diaphus*. The holotypes were deposited in USNM, and in a number of cases it was stated that paratypes were deposited at ANSP. Apparently none of these were ever deposited at ANSP and all that could be found are at USNM.

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BENTHOSEMA Goode and Bean 1896

BENTHOSEMA Goode and Bean 1896:75 (type species *Scopelus mulleri* Gill 1861 (Gmelin 1788) by original designation; = *Scopelus glacialis* Reinhardt 1837).

Scopelus glacialis Reinhardt 1837:44, Greenland. (Holotype ZMUC 62, Krefft and Bekker 1973).

Scopelus mulleri Gill 1861:53 (NOMEN NUDUM).

Scopelus parvimanus Günther 1864:406, south Pacific; Holotype BMNH. (New Zealand; Holotype BMNH 1863.8.10.4; type locality probably in error).

Scopelus scoticus Günther 1889:31, Faeroe Channel, England; many Syntypes BMNH. (6 Syntypes BMNH 1889.7.22.67, 1889.7.22.8.12, Krefft and Bekker 1973; 8 Syntypes BMNH 1889.7.22.6–12).

Myctophum glaciale var. *thori* Tåning 1918:33, Mediterranean. (40°48'N, 27°59'E, Sea of Marmora; Syntype ZMUC P2329225, Nielsen 1974).

Myctophum glaciale knipovitschi Soldatov 1939:152, 164, 72°44'N, 22°47'E, Barents Sea; Holotype. (No type material, Krefft and Bekker 1973).

Scopelus (Myctophum) pterotus Alcock 1891:217, 18°30'N, 86°46'E, off Madras coast, Bay of Bengal; about 60 Syntypes. (4 Syntypes MNHN, Estève 1947; 24 Syntypes ZSI F.12737–9, Menon and Yazdani 1968; Syntypes: ZSI (58) F.12737–9, MNHN (4) 90.348–51, BMNH (7) 1890.II.28.31–36, 1947.12.17.1).

Myctophum gilberti Evermann and Seale 1907:55, Bulan, Philippines; Holotype USNM 55900, 3 paratypes: PMM (1), SU (1), USBCF (1). (Paratypes: PMM lost, SU now CAS, USBCF now USNM).

Myctophum fibulatum Gilbert and Cramer 1897:411, Kaiwi Channel, Hawaii; Holotype USNM 47711.

Myctophum hollandi Jordan and Jordan 1922:11, Honolulu Market, Hawaii; Holotype CMP 3897. (Holotype FMNH 55191).

Myctophum renschi Ahl 1929:195, breakwater at Sabang (Sumatra); Holotype. (Holotype ZMB 20724).

Benthoosema pinchoti Fowler 1932:4, Nukuhiva, Marquesas Islands; Holotype USNM 91823.

Myctophum suborbitale Gilbert 1913:82, 35°02'N, 138°38'E, Suruga Bay, Japan; Holotype USNM, paratypes. (Holotype USNM 74473, Parr 1929; 2 paratypes SU, Böhlke 1953; paratypes: USNM (4), CAS (2)).

Myctophum simile Tåning 1928:56, north Atlantic. (31°47'N, 41°41'W; Lectotype ZMUC P2329235, Nafpaktitis 1973).

Myctophum initator Parr 1928:60 (replacement name for *Myctophum suborbitale* Gilbert 1913; not preoccupied by *Diaphus suborbitalis* Weber 1913).

Myctophum fibulatum proximum Parr 1929:8, Tongue of the Ocean, Bahamas; Holotype BOC 2184, 1 paratype USNM. (21 paratypes BOC, Parr 1928; 22 paratypes BOC, Krefft and Bekker 1973).

Myctophum pterotum panamense Tåning 1932:129, Gulf of Panama. (7°30'N, 79°19'W; Lectotype ZMUC P2329233, Nafpaktitis 1973).

BOLINICHTHYS Paxton 1972

BOLINICHTHYS Paxton 1972:46 (type species *Myctophum longipes* Brauer 1906 by original designation).

Scopelus pyrsobolus Alcock 1891:218, 15°38'N, 82°30'E, off Madras coast, Bay of Bengal; Holotype. (Holotype ZSI F.12839, Menon and Yazdani 1968).

Serpa blacki Fowler 1934:284, Iligan Bay, Mindanao, Philippines; Holotype USNM 92312, 2 paratypes: USNM (1), ANSP (1). (2 paratypes USNM).

Myctophum (Lampanyctus) longipes Brauer 1906:236, 10 localities in tropical Indian and north Atlantic Oceans; 14 Syntypes. (4 Syntypes ZMB 17612–3, Krefft and Bekker 1973).

?*Lampanyctus joubini* Angel and Verrier 1931:127, 1°16'S, 138°55'E, north of New Guinea; Holotype. (Holotype not found at MOM or MNHN, 1975).

?*Macrostoma grayi* Fowler 1938:190, 40 miles south of Christmas Island, Pacific Ocean; Holotype ANSP 68366.

Lampanyctus fraserbrunneri Bolin 1946:150, 5°56'N, 76°22'E, off Cape Cormorin, India; Holotype IMC, 1 paratype SU. (Holotype ZSI, lost, Menon and Rao 1971; Holotype ZSI F7336/2, found; 1 paratype CAS).

Lampanyctus supralateralis Parr 1928:94, 23°42'N, 76°43'W, Bahamas; Holotype BOC 2229, 3 paratypes BOC. (1 paratype MCZ).

Lampanyctus photothorax Parr 1928:95, 23°55'N, 77°09'W, Bahamas; Holotype BOC 2263, 53 paratypes BOC. (2 paratypes BMNH).

?*Lampanyctus stilbius* Gilbert 1908:235, near Nukuhiva Island, Marquesas; Holotype. (Holotype USNM 757768, Parr 1929; Holotype USNM 75768).

Lepidophanes indicus Nafpaktitis and Nafpaktitis 1969:61,

22°34'S, 64°55'E, Indian Ocean; Holotype MCZ 46314, 17 paratypes: MCZ (16), LACM (1).

Bolinichthys distofax Johnson 1975:54, Hawaii; Holotype CAS 15998, 89 paratypes: CAS (74), SIO (15). (Paratypes: BMNH (2), CAS (66), FMNH (2), LACM (2), SIO (15), USNM (2)).

Bolinichthys nikolayi Bekker 1978:260, 19°39'S, 175°10'W, southwest Pacific; Holotype ZIANL 43780, 1 paratype IOANM.

CENTROBRANCHUS Fowler 1904

CENTROBRANCHUS Fowler 1904:754 (type species *Centrobranchus choerocephalus* Fowler 1904 by original designation).

Scopelus nigroocellatus Günther 1873:91, south Atlantic; Holotype. (Holotype BMNH 1873.8.1.40, Krefft and Bekker 1973).

Myctophum coccoi f. *regularis* Brauer 1904:390, no type locality given. (Specimens in NMH (=ZMH) Brauer 1906).

Scopelus (Rhinoscopelus) andreae Lütken 1892a:209, Jacobshavn Greenland; Holotype. (Holotype ZMUC 94, lost, Nielsen 1974; not found ZMUC 1975).

Centrobranchus gracilicaudus Gilbert 1905:595, west of Niihau Island, Hawaii; Holotype USNM 51518, 10 paratypes. (6 paratypes SU, Böhlke 1953; paratypes: CAS (6), USNM (1)).

Centrobranchus choerocephalus Fowler 1904:754, near Hawaiian Islands; Holotype ANSP 7972, 3 paratypes. (1 paratype SU, Böhlke 1953; possible paratypes: ANSP (5), CAS (1)).

?*Centrobranchus brevirostris* Bekker 1964:52, 33°19'N, 151°08'E; Holotype ZIANL 34344, 9 paratypes.

CERATOSCOPELUS Günther 1864

SCOPELUS (CERATOSCOPELUS) Günther 1864:405 (as subgenus; type species *Scopelus maderensis* Lowe 1839 by monotypy).

Scopelus maderensis Lowe 1839:87, Madeira; Holotype. (Holotype BMNH, Günther 1864; Holotype BMNH 1865.1.19.2, status uncertain, Krefft and Bekker 1973; I can find no reason to question the type status of this specimen, which was purchased from Lowe in Madeira).

Scopelus aonanthurus Facciola 1882a:166, Straits of Messina. (Emmended to *Scopelus acanthurus*, Facciola 1882b; no type material available, Krefft and Bekker 1973).

Scopelus doderleini Facciola 1882b:193, Sea of Messina; new name for *Scopelus acanthurus* Facciola 1882a.

Myctophum townsendi Eigenmann and Eigenmann 1889:125, Cortez Banks off southern California; several Syntypes. (Types USNM 41921, Parr 1929; Syntypes: BMNH (2) 1891.5.19.172-3, CAS (1) SU 20173, MCZ (1) 35970, USNM (3) 41921).

Scopelus (Nyctophus) warmingii Lütken 1892b:259, 32°06'N, 39°28'W, Holotype. (Holotype ZMUC 39, Krefft and Bekker 1973).

Lampanyctus polyphotis Beebe 1932:67, 5 miles south of Nonsuch Island, Bermuda; Holotype NYZS 10151. (Holotype now USNM 171200, Mead 1958).

DIAPHUS Eigenmann and Eigenmann 1890

DIAPHUS Eigenmann and Eigenmann 1890:3 (type species *Diaphus theta* Eigenmann and Eigenmann 1890 by original designation).

AETHOPRORA Goode and Bean 1896:86 (type species *Myctophum metopoclampum* Cocco 1829 by subsequent designation of Jordan 1920).

COLLETTIA Goode and Bean 1896:88 (type species *Nyctophus rafinesquii* Cocco 1838 by original designation).

PANTOPHOS Jordan and Hubbs 1925:156 (type species *Diaphus glandulifer* Gilbert 1913 by original designation; = *Diaphus suborbitalis* Weber 1913).

LAMPROSSA Jordan and Hubbs 1925:156 (type species *Diaphus anteorbitalis* Gilbert 1913 by original designation; = *Diaphus adenomus* Gilbert 1905).

COLLETTIA (CAVELAMPUS) Whitley 1933:62 (as subgenus; type species *Aethoprora perspicillata* Ogilby 1898 by original designation).

Myctophum metopoclampum Cocco 1829:144, Messina. (No type material available, Krefft and Bekker 1973).

Nyctophus rafinesquii Cocco 1838:20, Messina. (No type material available, Krefft and Bekker 1973).

Diaphus intermedius Borodin 1930:89, 33°N, 64°W, north Atlantic; 2 Syntypes. (Holotype MCZ 32289, 1 paratype MCZ, Borodin 1931; paratype not found at MCZ 1975).

Scopelus dumerili Bleeker 1856:66, Manado, Makassar, Celebes; 3 Syntypes. (2 Syntypes RMNH 6931, Krefft and Bekker 1973).

Myctophum nocturnum Poey 1861:426, Cuba. (Holotype MCZ 6871, Gilbert 1906).

?*Scopelus schmitzi* Johnson 1890:456, Madeira; 2 Syntypes. (1 Syntype BMNH 1890.5.31.4, Krefft and Bekker 1973).

Lampanyctus lacerta Goode and Bean 1896:81, 28°38'N, 85°52'W (north Atlantic); 3 Syntypes USNM 43778. (Holotype USNM 43778, Parr 1929; 3 Syntypes USNM 43778).

Scopelus (Lampanyctus) coeruleus Klunzinger 1871:592, Red Sea; Holotype. (Kosseir, Red Sea; Holotype SNMS 1775, topotype from Klunzinger at ZMB).

?*Scopelus engraulis* Günther 1887:197, Philippines; Holotype. (Holotype BMNH 1887.12.7.217).

Diaphus theta Eigenmann and Eigenmann 1890:4, off Point Loma, California; 11 Syntypes. (2 Syntypes USNM 41914, Parr 1929; 1 Syntype MCZ 27392, Parr 1934; Lectotype USNM 41914, Nafpaktitis 1978; paralectotypes: BMNH (2), MCZ (1), USNM (5)).

Myctophum protoculus Gilbert 1891:52, off Oregon-Washington; 3 Syntypes. (Type USNM 41922, Jordan and Evermann 1896; Type USNM 44290, Parr 1929; Lectotype USNM 44290, 1 paralectotype SU, Böhlke 1953; Jordan and Evermann's indication cannot be a valid lectotype

- designation, as USNM 41922 is not part of the original type series; Parr's indication is merely in a list of material examined).
- Aethoprora lucida* Goode and Bean 1896:87, 19°45'N, 75°04'W; Holotype USNM 44084.
- Diaphus monodi* Fowler 1934:306, Tanon Strait off Negros, Philippines; Holotype USNM 92315.
- Diaphus reidi* Fowler 1934:309, near Marinduque Island, Philippines; Holotype USNM 93154.
- Diaphus altifrons* Kulikova 1961:11, 10°06'S, 187°(sic)23'W; Holotype ZIANL 36107, 5 paratypes.
- Aethoprora effulgens* Goode and Bean 1896:87, Brown's Bank and 19°45'N, 75°W, north Atlantic; 2 Syntypes, 1 USNM 43770. (Lectotype USNM 43770, Jordan and Evermann 1896; Brown's Bank).
- Myctophum (Diaphus) aeolochrus* Barnard 1927:1021, 60 miles WSW Table Bay, South Africa; Holotype SAM. (Holotype BMNH 1935.7.6.3).
- Diaphus macrophus* Parr 1928:136, 24°11'N, 75°35'W, Bahamas; Holotype BOC 2172.
- Diaphus antelucens* Kulikova 1961:13, 12°55'N, 154°04'E; Holotype ZIANL 36105, 1 paratype.
- Diaphus chrysorhynchus* Gilbert and Cramer 1897:409, 21°16'N, 157°44'W, Kaiwi Channel, Hawaii; Holotype USNM 47710, 11 paratypes. (6 Syntypes USNM 47710, Parr 1929; 2 paratypes SU, Böhlke 1953; Syntypes: USNM 47710 (6, none labelled holotype), CAS SU 4927 (1), SU 5068 (1)).
- Diaphus sagamiensis* Gilbert 1913:96, Sagami Bay, Japan; Holotype CMP 4608, 6 paratypes. (2 paratypes SU, Böhlke 1953; Holotype FMNH 55831, paratypes: CAS (2), FMNH (3), USNM (1)).
- ?*Diaphus astridae* Giltay 1929:29, off New Guinea; Holotype ISNB 2548.
- Aethoprora perspicillata* Ogilby 1898:36, Lord Howe Island; Holotype. (Holotype QM I.794).
- Myctophum (Nyctophus) elucens* Brauer 1904:401, Indian Ocean. (0°27'S, 42°47'E, northeast Africa; Holotype, Brauer 1906; Holotype ZMB 17602).
- ?*Diaphus gigas* Gilbert 1913:93, Sagami Bay, Japan; Holotype CMP 4601, 2 paratypes. (1 paratype SU, Böhlke 1953; Holotype FMNH 55825, paratypes: FMNH (1), CAS (1)).
- Diaphus watasei* Jordan and Starks 1904:580, off Atami, Sagami Bay, Japan; Holotype USNM 51443, 4 paratypes SU. (SU paratypes now CAS).
- Myctophum (Nyctophus) splendidum* Brauer 1904:399, Atlantic and Indian Oceans. (11 localities in Atlantic and Indian Oceans; 13 Syntypes, Brauer 1906; Syntypes: ZMH H5676(1), Wilkens 1977; SMF 2081 (1), ZMB (3) 17600, 17601, 20773).
- Diaphus steadi* Fowler 1934:310, Macassar Strait; Holotype USNM 93164.
- Diaphus scapulofulgens* Fowler 1934:316, Buton Strait, Philippines; Holotype USNM 93155.
- Diaphus vitiazi* Kulikova 1961:36, 6°15'S, 153°44'E; Holotype ZIANL 36104, 10 paratypes.
- ?*Myctophum (Nyctophus) microps* Brauer 1904:400, Indian Ocean. (4°05'S, 70°01'E, Holotype, Brauer 1906; Holotype ZMB 17596).
- Myctophum (Nyctophus) luetkeni* Brauer 1904:400, Indian Ocean. (4 localities in Indian Ocean; 4 Syntypes, Brauer 1906; 3 Syntypes ZMB 17603, 17604, 22376).
- Diaphus luetkeni pacificus* Kulikova 1961:24, 31°02'N, 146°05'E; Holotype ZIANL 36109, 19 paratypes. (Preoccupied by *Diaphus pacificus* Parr 1931).
- Myctophum (Nyctophus) fulgens* Brauer 1904:402, 4 localities in Indian Ocean. (4 Syntypes, Brauer 1906; Lectotype ZMB 17605, 4°06'S, 70°02'E, 1 paralectotype ZMB, Nafpaktitis 1978).
- Diaphus nanus* Gilbert 1908:224, near Nukuhiva, Marquesas; Holotype, 4 paratypes. (Holotype USNM 75765, Parr 1929; 3 paratypes SU, Böhlke 1953; paratypes: USNM (2), CAS (3)).
- Diaphus adenomus* Gilbert 1905:592, between Oahu and Molokai, Hawaii; Holotype USNM 51588, at least 2 paratypes. (1 paratype SU, Böhlke 1953; paratypes: CAS (1), USNM (1)).
- Diaphus anteorbitalis* Gilbert 1913:92, 33°25'N, 135°39'E, Japan; Holotype USNM, 3 paratypes. (Holotype USNM 74471, Parr 1929; 1 paratype SU, Böhlke 1953; paratypes: CAS (1), USNM (2)).
- Diaphus garmani* Gilbert 1906:258, Cuba; Holotype MCZ 6873, 3 paratypes MCZ. (Holotype MCZ 29070, Parr 1934).
- ?*Diaphus ashmeadi* Fowler 1934:311, China Sea (13°30'N, 121°01'E, Nafpaktitis 1968); Holotype USNM 93161.
- Myctophum (Diaphus) vanhoeffeni* Brauer 1906:222, no type locality given; 2 Syntypes. (Lectotype ZMB and 1 paralectotype ZMB, Nafpaktitis 1968; Lectotype ZMB 19367, tropical Atlantic Ocean).
- Diaphus lewisi* Nafpaktitis 1966:410, 13°31'N, 18°03'W, north Atlantic; Holotype DMBL, 106 paratypes: DMBL (2), MCZ (84), USNM (20). (Holotype ZMUC P2329207, 2 paratypes ZMUC, Nielsen 1974).
- ?*Diaphus agassizii* Gilbert 1908:226, near Nukahiva Island, Marquesas; Holotype, 1 paratype. (Holotype USNM 75764, Parr 1929; 1 paratype SU, Böhlke 1953; 5 specimens in SU paratype bottle, now at CAS).
- Diaphus signatus* Gilbert 1908:228, near Nukahiva Island, Marquesas; Holotype, 1 paratype. (Holotype USNM 75767, Parr 1929; 2 paratypes SU, Böhlke 1953; 1 paratype CAS; CAS SU 20193 is 22 mm TL and cannot be a paratype).
- Diaphus malayanus* Weber 1913:89, Halmahera and Banda Seas; 9 Syntypes. (Syntypes: RMNH 9941 (1), ZMA 109.186-7, 109.193 (8)).
- Diaphus meyeri* Fowler 1934:314, off west Luzon, Philippines; Holotype USNM 93152.
- Diaphus suborbitalis* Weber 1913:90, Bali, Banda and Arufura Seas; 4 Syntypes. (Lectotype ZMA 109.968, 1 paralectotype RMNH, Wisner 1974; 1 paralectotype ZMA).
- Diaphus glandulifer* Gilbert 1913:90, Suruga Gulf, Japan; Holotype USNM, paratypes. (Holotype USNM 74472, Parr

- 1929; 3 paratypes SU, Böhlke 1953; paratypes: CAS (6), FMNH (3), USNM (17)).
- Diaphus streetsi* Fowler 1934:291, China Sea, Sombrero Island off Luzon, Philippines (13°45'N, 120°46'E, Nafpaktitis 1968); Holotype USNM 93162.
- ?*Diaphus tanakae* Gilbert 1913:88, 31°10'N, 131°58'E, Japan; Holotype USNM, 3 paratypes. (Holotype USNM 74470, Parr 1929; 1 paratype SU, Böhlke 1953; paratypes: CAS (1), USNM (2)).
- Diaphus latus* Gilbert 1913:95, Sagami Bay, Japan; Holotype CMP 4604, paratypes. (3 paratypes SU, Böhlke 1953; Holotype FMNH 56208, paratypes: CAS (3), FMNH (6)).
- Myctophum (Diaphus) holti* Tåning 1918:88, Mediterranean Sea. (36°53'N, 03°09'E; Lectotype ZMUC P2329204, 1 paralectotype ZMUC, Nafpaktitis 1973).
- Diaphus brachycephalus* Tåning 1928:59, north Atlantic. (19°22'N, 24°06'W; Lectotype ZMUC P2329197, Nafpaktitis 1973).
- Diaphus termophilus* Tåning 1928:59, north Atlantic. (14°38'N, 61°16'W; Lectotype ZMUC P2329218, Nafpaktitis 1973).
- Diaphus hypolucens* Parr 1928:130, 23°58'N, 77°26'W; Holotype BOC 2197.
- Diaphus mollis* Tåning 1928:60, north Atlantic. (19°22'N, 24°06'W; Lectotype ZMUC 2329211, Nafpaktitis 1973).
- Diaphus fragilis* Tåning 1928:61, north Atlantic. (12°11'N, 35°49'W; Lectotype ZMUC P2329202, Nafpaktitis 1973).
- Diaphus problematicus* Parr 1928:143, 24°29'N, 77°29'E, Bahamas; Holotype BOC 2195, 1 paratype BOC.
- Diaphus weberi* Tåning 1932:138, 7°23'N, 121°22'E, Zulu Sea. (7°22'N, 121°16'E; Holotype ZMUC P2329219, Nafpaktitis 1973).
- Diaphus taaningi* Norman 1930:332, 0°36'S, 8°28'E, central Atlantic; Holotype. (Holotype BMNH 1930.1.12.835).
- Diaphus pacificus* Parr 1931:34, 16°14'N, 99°36'W, off Mexico; Holotype BOC 2690.
- Diaphus anderseni* Tåning 1932:134, 20°00'S, 174°29'E, southwest of Fiji. (Holotype ZMUC P2329194, Nafpaktitis 1973).
- Diaphus parri* Tåning 1932:135, 27°21'S, 175°11'E, southeast of New Caledonia. (Holotype ZMUC P2331765, Nafpaktitis 1973).
- Diaphus longleyi* Fowler 1934:296, between Leyte and Cebu, Philippines; Holotype USNM 92320.
- Diaphus kendalli* Fowler 1934:297, between Leyte and Mindanao, Philippines; Holotype USNM 93157.
- Diaphus rassi* Kulikova 1961:28, 6°15'S, 153°44'E, off New Britain; Holotype ZIANL 36108, 11 paratypes.
- Diaphus richardsoni* Tåning 1932:136, 2°00'N, 138°22'E, north of New Guinea. (Holotype ZMUC P2329214, Nafpaktitis 1973).
- Diaphus harveyi* Fowler 1934:294, Manila Bay, Luzon, Philippines; Holotype USNM 92317, 6 paratypes. (No paratypes found USNM or ANSP, 1975).
- Diaphus diadematus* Tåning 1932:137, 24°33'S, 38°26'E, Indian Ocean. (Lectotype ZMUC P2329199, 1 paralectotype, ZMUC, Nafpaktitis 1973).
- Diaphus regani* Tåning 1932:139, 20°53'S, 164°03'E, off New Caledonia. (Holotype ZMUC P2329213, Nafpaktitis 1973).
- Diaphus danae* Tåning 1932:140, 36°23'S, 176°26'E, north of New Zealand. (Holotype ZMUC P2329198, Nafpaktitis 1973).
- Diaphus schmidti* Tåning 1932:139, 7°46'S, 167°10'W, north of Samoa. (Holotype ZMUC P2329215, Nafpaktitis 1973).
- Diaphus crameri* Fowler 1934:314, Gulf of Tomini, Celebes; Holotype USNM 93156.
- Diaphus jensei* Tåning 1932:141, 3°18'N, 129°02'E, north of New Guinea. (Holotype ZMUC P2329205, Nafpaktitis 1973).
- Diaphus kylei* Tåning 1932:133, 7°22'N, 121°16'E, Zulu Sea. (Holotype ZMUC P2329206, Nafpaktitis 1973).
- Diaphus gudgeri* Fowler 1934:302, off north Mindanao, Philippines; Holotype USNM 92322, 4 paratypes. (11 *Albatross* specimens labeled *Diaphus gudgeri* n. sp. in USNM, which presumably include the four paratypes).
- Diaphus carlsoni* Fowler 1934:312, off east Mindoro, Philippines; Holotype USNM 93151.
- Diaphus ostfeldi* Tåning 1932:142, 35°36'S, 171°52'E, west of New Zealand. (Holotype ZMUC P2329212, Nafpaktitis 1973).
- Diaphus drachmanni* Tåning 1932:144, 4°44'N, 88°05'E, Indian Ocean. (Holotype ZMUC P2329201, Nafpaktitis 1973).
- Diaphus phillipsi* Fowler 1934:287, between Panay and Negros, Philippines; Holotype USNM 93149.
- Diaphus rolfbolini* Wisner 1971:47, 10°00'N, 116°52'W, Holotype SIO 68-536, 27 paratypes: SIO (4), USNM (23).
- Diaphus thiollierei* Fowler 1934:289, off west Bohol, Philippines; Holotype USNM 93158.
- Diaphus jouani* Fowler, 1934:301, Macassar Strait (0°29'S, 118°51'E, Nafpaktitis 1968); Holotype USNM 93153.
- Diaphus handi* Fowler 1934:290, between Cebu and Siquijor, Philippines; Holotype USNM 93163.
- Diaphus aliciae* Fowler 1934:295, between Bohol and Leyte, Philippines; Holotype USNM 92316, 2 paratypes: ANSP (1), USNM (1). (Probable paratypes USNM (2)).
- Diaphus layi* Fowler 1934:292, north of Mindanao, Philippines; Holotype USNM 93145.
- Diaphus dahlgreni* Fowler 1934:299, off Darvel Bay, Borneo; Holotype USNM 93165.
- Diaphus faustinoi* Fowler 1934:300, Tanon Strait, off Negros, Philippines; Holotype USNM 92321.
- Diaphus ehrhorni* Fowler 1934:304, between Burias and Luzon, Philippines; Holotype USNM 92319, 49 paratypes. (No paratypes found at ANSP or USNM, 1975).
- Diaphus whileyi* Fowler 1934:305, Verde Island Passage and Batangas Bay, Philippines; Holotype USNM 92318, 2 paratypes. (49 *Albatross* specimens in 3 lots in USNM; presumably the 2 paratypes are included, but none is labeled n. sp. nor come from the same station as the holotype).

- ?*Diaphus atkinsoni* Fowler 1934:321, Verde Island Passage and Batangas Bay, Philippines; Holotype USNM 93159.
- Diaphus lucifrons* Fowler 1934:307, east of Luzon, Philippines; Holotype USNM 93147.
- Diaphus burtoni* Fowler 1934:315, China Sea off south Luzon, Philippines; Holotype USNM 93146.
- Diaphus bryani* Fowler 1934:319, China Sea off south Luzon, Philippines; Holotype USNM 93150.
- Diaphus umbroculus* Fowler 1934:317, Verde Island Passage and Batangas Bay, Philippines; Holotype USNM 93148.
- Diaphus dehaveni* Fowler 1934:320, between Samar and Masbate, Philippines; Holotype USNM 93160.
- ?*Diaphus gracilis* Kulikova 1961:21, 7°19'S, 155°26'E; Holotype ZIANL 36106.
- Diaphus bertelseni* Nafpaktitis 1966:405, 0°15'S, 18°35'W, Atlantic; Holotype MCZ 43121, 3 paratypes: DMBL (2; now at ZMUC), MCZ (1).
- Diaphus minax* Nafpaktitis 1968:57, 26°34'N, 79°04'W, north Atlantic; Holotype MCZ 44952, 2 paratypes: DMBL (1; now at ZMUC), UMML (1).
- Diaphus subtilis* Nafpaktitis 1968:92, 13°47'N, 61°26'W, north Atlantic; Holotype DMBL, 3 paratypes: DMBL (1), MCZ (2). (Holotype ZMUC P2329216, 1 paratype ZMUC, Nielsen 1974).
- Diaphus trachops* Wisner 1974:5, near Oahu Hawaii; Holotype SIO 71-172, 15 paratypes: BPBM (2), CAS (2), LACM (1), SIO (4), USNM (6).
- Diaphus similis* Wisner 1974:7, central Pacific; Holotype SIO 71-177, 15 paratypes: CAS (2), SIO (9), USNM (4).
- Diaphus roei* Nafpaktitis 1974:4, 17°20'N, 62°52'W, north Atlantic; Holotype USNM 210553, 7 paratypes: LACM (3), MCZ (2), USNM (2).
- Diaphus hudsoni* Zurbrigg and Scott 1976:1538, 44°14'S, 42°43'W, south Atlantic; Holotype ROM 27569, 5 paratypes: NMC (2), ROM (3).
- Diaphus nielseni* Nafpaktitis 1978:17, 06°37'N, 122°24'E, southeast Asian seas; Holotype ZMUC P2334949, 5 paratypes: LACM (1), MNHN (1), ZMUC (3).
- Diaphus antonbruuni* Nafpaktitis 1978:25, 07°56'S, 65°14'E, Indian Ocean; Holotype LACM 31389-16, 6 paratypes: LACM (2), USNM (2), ZMUC (2).
- Diaphus diademophilus* Nafpaktitis 1978:34, 04°01'S, 65°00'E, Indian Ocean; Holotype LACM 31365-6, 8 paratypes: LACM (2), ZMUC (6).
- Diaphus knappi* Nafpaktitis 1978:45, 23°36'S, 43°31'E, southwest coast of Madagascar; Holotype MNHN 1977-306, 4 paratypes LACM.
- Diaphus meadi* Nafpaktitis 1978:63, 27°10'S, 8°59'E, south Atlantic; Holotype ZMUC P2334935, 16 paratypes: LACM (6), USNM (2), ZMUC (8).
- Diaphus megalops* Nafpaktitis 1978:65, 02°00'S, 64°54'E, Indian Ocean; Holotype LACM 31362-3, 9 paratypes: LACM (2), USNM (2), ZMUC (5).
- Diaphus arabicus* Nafpaktitis 1978:77, 17°46'N, 65°02'E,

Arabian Sea; Holotype LACM 31334-6, 15 paratypes: LACM (9), USNM (4), ZMUC (2).

Diaphus lobatus Nafpaktitis 1978:79, 06°52'N, 79°30'E, Indian Ocean; Holotype ZMUC P2334930, 8 paratypes: LACM (2), USNM (2), ZMUC (4).

Diaphus kuroshio Kawaguchi and Nafpaktitis 1978:89, 31°24'N, 136°52'E, off Japan; Holotype ZUMT 54126, 28 paratypes: ORI (24), ZUMT (4).

DIOGENICHTHYS Bolin 1939

DIOGENICHTHYS Bolin 1939:119 (type species *Myctophum laternatum* Garman 1899 by original designation).

Myctophum laternatum Garman 1899:267, 3 localities in northeast Pacific. (7 Syntypes MCZ 28492, Parr 1934; 11 Syntypes MCZ: 28492 (7), 35186 (2), 35188 (1), 41788 (1)).

Myctophum laternatum atlanticum Tåning 1928:56, north Atlantic, 20°00'N, 21°55'W; Lectotype ZMUC P2329229, 1 paralectotype ZMUC, Nafpaktitis 1973).

Diogenichthys scofieldi Bolin 1939:122, 31°33'N, 119°57'W, Cortez Banks, California; Holotype SU 33657, 6 paratypes: MCZ (1), SU (4), USNM (1). (MCZ paratype not found 1975, Holotype and SU paratypes at CAS).

Diogenichthys panurgus Bolin 1946:140, 5°56'N, 76°22'E, off Cape Cormorin, India; Holotype IMC, 7 paratypes: IMC (3), SU (4). (Holotype and IMC (= ZSI) paratypes lost, Menon and Rao 1971; Holotype ZSI F 7334/2, found; paratypes: CAS (4), ZSI (3)).

ELECTRONA (ELECTRONA) Goode and Bean 1896

ELECTRONA Goode and Bean 1896:91 (type species *Scopelus risso* Cocco 1829 by original designation).

ELECTRONA (ELAMPA) Fraser-Brunner 1949:1048 (as subgenus; type species *Scopelus subasper* Günther 1864 by original designation).

ELAMPADENA Whitley 1953:135 (type species *Scopelus subasper* Günther 1864 by original designation; replacement name for *Elampa* Fraser-Brunner 1949; not preoccupied by *Elampus* Spinola 1806, Hymenoptera).

Scopelus risso Cocco 1829:144, Messina. (No type material, Krefft and Bekker 1973).

Electrona risso salubris Whitley 1933:62, between Gabo Island and Cape Everard, Victoria, Australia; Holotype AMS E.5701.

Scopelus (Dasyscopelus) subasper Günther 1864:411, 43°30'S, 123°E, Pacific Ocean; Holotype BMNH. (Holotype BMNH 1845.8.5.45).

?*Scopelus stellatus* Bennet 1840:288, 43°S, Pacific Ocean off South America; Syntypes. (No types found, 1975).

Myctophum megalops Peters 1865:393, Cape Horn; 2 Syntypes. (2 Syntypes ZMB 199).

Scopelus antarcticus Günther 1878:184, Antarctic Ocean; Holotype BMNH. (Holotype BMNH 1887.12.7.215).

Scopelus colletti Lütken 1892b: 249, 28°16'S, 97°30'W and 600 miles west of Cape Horn; 2 Syntypes. (Lectotype ZMO J710, 1 paralectotype ZMUC, Pethon 1969).

Myctophum carlsbergi Tåning 1932:126, 44°40'S, 173°39'E, east of New Zealand. (Holotype ZMUC P2329224, Nafpaktitis 1973).

Electrona paucirastra Bolin in Andriashev 1962:280, 39°30'S, 71°16'E (southern Indian Ocean); 9 Syntypes, 5 Syntypes ZIANL 36765.

ELECTRONA (METELECTRONA) Wisner 1963

METELECTRONA Wisner 1963b:24 (type species *Metelectrona ahlstromi* Wisner 1963 by original designation; = *Electrona ventralis* Bekker 1963).

Electrona ventralis Bekker 1963:26, 42°40'S, 39°07'W, south Atlantic; Holotype ZIANL 36804, 1 paratype.

Metelectrona ahlstromi Wisner 1963b:25, 46°53'S, 179°48'W, southeast of New Zealand; Holotype SIO 61-45A-25.

GONICHTHYS Gistel 1850

ALYSIA Lowe 1839:87 (type species *Alysia loricata* Lowe 1839 by monotypy; = *Scopelus cocco* Cocco 1829; preoccupied by *Alysia* Latreille 1804, Hymenoptera).

GONICHTHYS Gistel 1850:71 (type species *Alysia loricata* Lowe 1839 by original designation; = *Scopelus cocco* Cocco 1829; replacement name for *Alysia* Lowe 1839).

SCOPELUS (RHINOSCOPELUS) Lütken 1892a:209 (as subgenus; type species *Scopelus cocco* by subsequent designation of Lütken 1892b: 232; only species listed with original description, *Scopelus (Rhinoscopelus) andreae* Lutken?, invalid as type because listed as species inquirenda).

Scopelus cocco Cocco 1829:143, Messina. (No type material, Krefft and Bekker 1973).

Alysia loricata Lowe 1839:87, Madeira; Holotype. (Holotype MPS, Günther 1864; no type material, Krefft and Bekker 1973; Holotype BMNH 1948.8.9.1).

Myctophum hians Richardson 1845:41, no type locality given. (2 Syntypes BMNH, Günther 1864; BMNH 1847.12.31.1-2, Krefft and Bekker 1973; 2 Syntypes BMNH 1947.12.31.1-2).

Scopelus jagorii Peters 1859:411, 3 localities in Atlantic Ocean. (8 Syntypes ZMHU (= ZMB) 3811, Krefft and Bekker 1973).

Scopelus gracilis Lütken 1892b:255, 5 localities in Atlantic and Indian Oceans; Syntypes. (Holotype ZMO J719, 7 paratypes ZMUC, Krefft and Bekker 1973).

Myctophum tenuiculum Garman 1899:262, 6°21'N, 80°41'W (eastern Pacific). (4 Syntypes MCZ 58499, Parr 1934; 4 Syntypes MCZ 28499).

Gonichthys barnesi Whitley 1943:174, Lord Howe Island; Holotype AMS IA.953, 40 paratypes AMS. (4 paratypes exchanged SU, 1958, now at CAS).

?*Myctophum coruscans* Richardson 1845:40, between St. Helena and Ascension Islands, and Tasman Sea. (Types lost, Günther 1864).

?*Gonichthys venetus* Bekker 1964:39, 27°40'S, 171°56'E; Holotype ZIANL 37347, 10 paratypes. (Holotype ZIANL 37343).

GYMNOSCOPELUS (GYMNOSCOPELUS) Günther 1873

GYMNOSCOPELUS Günther 1873:91 (type species *Gymnoscopelus aphyia* Günther 1873 by monotypy).

Gymnoscopelus aphyia Günther 1873:91, 55°S, 85°W, near the Straits of Magellan; Holotype. (Holotype BMNH, Andriashev 1962; Holotype BMNH 1873.8.1.42).

Lampanyctus nicholsi Gilbert 1911:17, 47°S, 60°W, north of Falkland Islands; Holotype AMNH, 3 paratypes. (1 paratype SU, Böhlke 1953; Holotype AMNH 1919, paratypes: AMNH (2), CAS (1)).

Myctophum (Lampanyctus) braueri Lonnberg 1905:764, 48°54'S, 51°40'W; Holotype. (Holotype NRMS 9022658105).

Gymnoscopelus opisthopterus Fraser-Brunner 1949:1102, 64°23'S, 106°33'E (Pacific Antarctic); Holotype BMNH Discovery Collections. (Holotype BMNH 1948.5.14.612).

Gymnoscopelus bolini Andriashev 1962:272, 53°01'S, 109°30'W (south Pacific); Holotype, 1 paratype. (Holotype ZIANL 36383, 1 paratype ZIANL).

GYMNOSCOPELUS (NASOLYCHNUS) Smith 1933

MYCTOPHUM (NASOLYCHNUS) Smith 1933:126 (as subgenus; type species *Myctophum (Nasolychnus) florenti* Smith 1933 by monotypy; = *Lampanyctus piabilis* Whitley 1931).

Lampanyctus fraseri Fraser-Brunner 1931:224, 3°18'S, 5°17'E; Holotype BMNH. (Holotype BMNH 1931.2.27.6).

Lampanyctus piabilis Whitley 1931:103, Macquarie Island; Holotype AMS IA.504, 1 paratype AMS.

Myctophum (Nasolychnus) florenti Smith 1933:126, near Port Alfred, South Africa; Holotype AMG. (Holotype RUSI 55).

HINTONIA Fraser-Brunner 1949

HINTONIA Fraser-Brunner 1949:1098 (type species *Hintonia candens* Fraser-Brunner 1949 by original designation).

Hintonia candens Fraser-Brunner 1949:1104, 41°50'-54'S, 0°02'-03'E, south Atlantic; Holotype BMNH Discovery Collections. (Holotype BMNH 1948.5.14.693).

HYGOPHUM Bolin 1939

MYCTOPHUM (HYGOPHUM) Bolin 1939:113 (as subgenus; type species *Scopelus hygomii* Lütken 1892 by original designation; original indication by Tåning 1932:133, invalid due to lack of type species designation).

Scopelus benoisti Cocco 1838:12, Sea of Messina. (Emmended

to *benoiti* by Bonaparte 1840; no type material, Krefft and Bekker 1973).

Scopelus (Myctophum) macrochir Günther 1864:408, no type locality given; 3 Syntypes. (Lectotype BMNH 1947.12.16.1, 2 paralectotypes BMNH, Bolin 1959; Lectotype not found 1975).

Scopelus hygomii Lütken 1892b:256, 4 localities in Atlantic and Indian Oceans; 4 Syntypes. (38°N, 22°20'W; Lectotype ZMUC 41, 3 paralectotypes ZMUC, Bolin 1959).

Myctophum remiger Goode and Bean 1896:74, 40°34'N, 60°09'W; 8 Syntypes USNM 43792. (9 Syntypes in bottle).

Scopelus reinhardtii Lütken 1892b:256, 2 localities in north Atlantic; 2 Syntypes. (34°22'N, 18°10'W; Lectotype Gilbert 1908; Lectotype ZMUC 24, Bolin 1959; paralectotype ZMUC Nielsen 1974).

Myctophum braueri Gilbert 1905:598, south of Oahu, Hawaii; Holotype USNM 51527, 16 paratypes. (7 paratypes SU Böhlke 1953; paratypes: CAS (7), USNM (8); preoccupied by *Myctophum (Lampanyctus) braueri* Lonnberg 1905).

Myctophum atratum Garman 1899:268, 25°26'N, 109°48'W (northeast Pacific); Holotype. (Holotype MCZ 28491, Parr 1934).

Myctophum (Hygophum) hansenii Täning 1932:132, 42°32'S, 174°50'E, east of New Zealand. (Holotype ZMUC P2329226, Nafpaktitis 1973).

Serpa peccatus Whitley and Phillips 1939:228, North Cape, New Zealand; Holotype BMNH = *Lampanyctus macrop-terus* (non Brauer) Regan 1916. (Spirits Bay, New Zealand; Holotype BMNH 1910.3.20.89).

Hygophum taaningi Bekker 1965:76, 22°47'N, 63°40'W; Holotype ZIANL 37538, 2 paratypes.

Hygophum proximum Bekker 1965:81, 0°58'S, 82°53'E; Holotype ZIANL 37537, 10 paratypes.

Hygophum bruunii Wisner 1971:41, 32°48'S, 72°02'W; Holotype SIO 65-667, 203 paratypes: CAS (3), LACM (53), SIO (143), USNM (4).

IDIOLYCHNUS Nafpaktitis and Paxton 1978

IDIOLYCHNUS Nafpaktitis and Paxton 1978:495 (type species *Diaphus urolampus* Gilbert and Cramer 1897 by original designation).

Diaphus urolampus Gilbert and Cramer 1897:408, Kaiwi Channel, Hawaii; Holotype USNM 47709, 6 paratypes. (2 paratypes USNM, Parr 1929; 3 paratypes SU, Böhlke 1953; USNM 47709 with 3 specimens, none designated holotype; 1 additional USNM type, SU types now CAS).

LAMPADENA (LAMPADENA) Goode and Bean in Gill 1893

LAMPADENA Goode and Bean in Gill 1893:113 (type species *Lampadena speculigera* Goode and Bean 1896 by subsequent monotypy, Goode and Bean 1896:85; only species listed with

original description, *Scopelus parvimanus?* Günther, invalid as type because listed as species inquiring).

LAMPADENA (LYCHNOPHORA) Fraser-Brunner 1949:1080 (as subgenus; type species *Lampadena nitida* Täning 1928 by original designation; = *Myctophum luminosum* Garman 1899).

Lampadena speculigera Goode and Bean 1896:85, 39°48'N, 70°36'W, north Atlantic; Holotype USNM 43796. (Lectotype USNM 43797, Jordan and Evermann 1896; 2 paralectotypes USNM).

Lampadena braueri Zugmayer 1914:2, no type localities given. (northeast Atlantic, southeast of Halifax; 3 Syntypes MOM 3414, 3447, Belloc 1949).

Myctophum luminosum Garman 1899:263, 0°57'S, 89°03'W (eastern Pacific); Holotype. (Holotype MCZ 28498; Parr 1934).

Lampadena luminosa nitida Täning 1928:62, north Atlantic. (17°43'N, 64°56'W; Lectotype ZMUC P2330214, 1 paralectotype ZMUC, Nafpaktitis 1973).

Lampadena chavesi Collett 1905:728, Azores; Holotype. (Holotype ZMO J693, Pethon 1969).

Lampadena anomala Parr 1928:150, 32°24'N, 64°29'W, near Bermuda; Holotype BOC 2272.

Lampadena dea Fraser-Brunner 1949:1101, 48°27'S, 22°10'-06'W; Holotype BMNH Discovery Collections, 1 paratype BMNH. (Holotype BMNH 1948.5.14.344).

Lampadena urophaos Paxton 1963:29, 33°32'N, 118°25'W, southern California; Holotype AHF 2589, 6 paratypes: AHF (2), SIO (4). (Holotype LACM 6843-6, AHF paratypes now LACM).

?*Lampadena urophaos atlantica* Maul 1969:2, Madeira; Holotype MMF 2464, 18 paratypes: LV (1), MMF (17).

Lampadena notialis Nafpaktitis and Paxton 1968:13, 42°00'-08'S, 160°11'-05'E (south Pacific); Holotype LACM 11321-1, 2 paratypes: LACM (1), MCZ (1).

Lampadena pontifex Krefft 1970:227, 14°31'N, 17°39'W, Holotype ISH 662/64a, 5 paratypes ISH. (Types now at ZMH).

LAMPADENA (DORSADENA) Coleman and Nafpaktitis 1972

DORSADENA Coleman and Nafpaktitis 1972:1 (type species *Dorsadena yaquinae* Coleman and Nafpaktitis 1972 by original designation).

Dorsadena yaquinae Coleman and Nafpaktitis 1972:2, 44°54'N, 138°32'W, off Oregon; Holotype LACM 30841-1, 4 paratypes: MCZ (1), OSUDO (2), USNM (1).

LAMPANYCTODES Fraser-Brunner 1949

LAMPANYCTODES Fraser-Brunner 1949:1080 (type species *Scopelus hectoris* Günther 1876 by original designation).

Scopelus hectoris Günther 1876:399, Cook Strait, New Zealand; Holotype BMNH. (Holotype BMNH 1876.2.12.18).

Scopelus argenteus Gilchrist 1904:15, 3 localities off South

Africa; Syntypes. (8 Syntypes: BMNH 1927.12.6.4–6 (3), 1947.12.27.1–2 (2), SAM 12671–2 (3), SAM 12671 labelled holotype).

LAMPANYCTUS (LAMPANYCTUS) Bonaparte 1840

LAMPANYCTUS Bonaparte 1840:139 (type species *Nyctophus bonapartii* Cocco 1838 by monotypy; = *Gasteropelecus crocodilus* Risso 1810).

NANNOBRACHIUM Günther 1887:199 (type species *Nannobranchium nigrum* Günther 1887 by monotypy).

PROMACHEON Weber 1913:84 (type species *Promacheon sibogae* Weber 1913 by monotypy).

NYCTIMASTER Jordan 1921:645 (type species *Lampanyctus jordani* Gilbert 1913 by original designation).

SERPA Whitley 1933:64 (type species *Gasteropelecus crocodilus* Risso 1810 by original designation).

PARALAMPANYCTUS Kotthaus 1972a:13 (type species *Nannobranchium nigrum* Günther 1887 by original designation).

Gasteropelecus crocodilus Risso 1810:357, Sea of Amplova, Mediterranean. (No type material available, Krefft and Bekker 1973).

Nyctophus bonapartii Cocco 1838:29, Sea of Messina, Mediterranean. (No type material available, Krefft and Bekker 1973).

Lampanyctus gemnifer Goode and Bean 1896:80, 39°40'N, 71°35'W (north Atlantic); Holotype USNM 35604.

Lampanyctus peculiaris Borodin 1929:111, 47°40'N, 37°20'W, north Atlantic; Holotype MCZ 31628.

Lampanyctus iselini Parr 1934:60, 41°30'N, 45°57'W, north Atlantic; Holotype MCZ 33223, 1 paratype MCZ.

Nannobranchium nigrum Günther 1887:199, south of Philippine Islands; Holotype. (Holotype BMNH 1887.12.7.219, Nafpaktitis 1973).

Scopelus pusillus Johnson 1890:457, Madeira; Holotype. (Holotype BMNH 1890.5.31.8, Krefft and Bekker 1973).

Myctophum regale Gilbert 1892:544, northeast Pacific; Holotype, 3 paratypes. (Holotype USNM 44289, Jordan and Evermann 1896; 1 paratype SU, Böhlke 1953; paratype now at CAS).

Lampanyctus micropunctatus Chapman 1939:527, 53°40'N, 134°15'W, northeast Pacific; Holotype USNM 108142, 19 paratypes. (1 paratype SU, Böhlke 1953; paratypes: CAS (11), USNM (7)).

Lampanyctus alatus Goode and Bean 1896:79, 28°43'N, 87°14'W (Gulf of Mexico); 3 Syntypes USNM 43769. (2 Syntypes USNM 43769, Parr 1929; Lectotype USNM 43769, 1 paralectotype USNM, Bolin 1959).

Lampanyctus punctatissimus Gilbert 1913:103, Suruga Bay, Japan; Holotype USNM, paratypes. (Holotype USNM 74469, Parr 1929; 1 paratype SU, Böhlke 1953; 2 paratypes USNM, Krefft and Bekker 1973; 5 paratypes USNM, SU paratype now at CAS).

Lampanyctus pseudoalatus Tåning 1918:108, 2 localities in

northeast Atlantic. (20°00'N, 21°55'W; Lectotype ZMUC P2330202, Nafpaktitis 1973; 3 paralectotypes ZMUC, Nielsen 1974).

Nannobranchium macdonaldi Goode and Bean 1896:94, 39°48'N, 70°36'W, north Atlantic; Holotype USNM 39478. (Type USNM 35545, Jordan and Evermann 1896; Holotype USNM 39478, 2 paratypes USNM).

Myctophum (Lampanyctus) macropterum Brauer 1904:404, Indian Ocean. (10 localities in Indian Ocean; 22 Syntypes, Brauer 1906; Syntypes: ZMH H 5677(1), Wilkens 1977; SMF 2078 (1), ZMB 17624–6, 22377 (4)).

Lampanyctus macropterus taningi Angel and Verrier 1931:124, 1°16'S, 138°55'E, north of New Guinea; Holotype. (Holotype not found at MOM or MNHM, 1975; preoccupied by *Lampanyctus taaningi* Parr 1929).

Serpa freta Whitley 1936:162, replacement name for *Lampanyctus macropterus taningi* Angel and Verrier 1931.

Lampanyctus macropterus novaeguineae Fowler 1958:7, replacement name for *Lampanyctus macropterus taningi* Angel and Verrier 1931.

Lampanyctus basili Kotthaus 1972b:31, 180 miles ENE of Seychelles, Indian Ocean (3°S, 58°E); Holotype IOES 154A', 6 paratypes IOES. (Holotype ZMH 5110, 6 paratypes ZMH).

Myctophum (Lampanyctus) tenuiforme Brauer 1906:243, 4°34'S, 53°42'E, Indian Ocean between Zanzibar and Seychelles; Holotype. (Holotype ZMB 17620).

Lampanyctus omostigma Gilbert 1908:232, 10°58'N, 137°35'W; Holotype, 1 paratype. (Holotype USNM 75769, Parr 1929; 1 paratype SU, Böhlke 1953; SU paratype now at CAS).

?*Promacheon sibogae* Weber 1913:85, 4°14'S, 128°52'W, Banda Sea; 2 larval Syntypes. (2 Syntypes ZMA 112.630–31).

Lampanyctus jordani Gilbert 1913:104, Nemuro Hokkaido, Japan; Holotype CMP 4617, 2 paratypes. (1 paratype SU, Böhlke 1953; Holotype FMNH 55837, paratypes: CAS (1), USNM (1)).

Lampanyctus ritteri Gilbert 1915:318, Monterey Bay, California; Holotype USNM 75807, paratypes. (2 paratypes SU, Böhlke 1953; SU paratypes now at CAS).

?*Nyctimaster reinhardti* Jordan 1921:645, southwest of Hawaii; Holotype USNM 84095, 2 paratypes. (2 Syntypes USNM 84095, Parr 1929; 1 paratype BPBM, larger specimen only).

Lampanyctus nobilis Tåning 1928:66, north Atlantic. (17°41'N, 60°58'W; Lectotype ZMUC P2330211, Nafpaktitis 1973).

Lampanyctus intricarius Tåning 1928:67, north Atlantic. (38°10'N, 9°20'W; Lectotype ZMUC P2330208, Nafpaktitis 1973).

Serpa conspicua Whitley 1936:160, Kaikoura, New Zealand; Holotype AMS IA.6500.

Lampanyctus festivus Tåning 1928:67, north Atlantic. (35°44'N, 29°33'W; Lectotype ZMUC P2330215, Nafpaktitis 1973).

- Lampanyctus septilucis* Beebe 1932:68, 7 miles southwest of Nonsuch Island, Bermuda; Holotype NYZS 14292A, 2 paratypes NYZS. (Holotype now USNM 171199, Mead 1958; 2 paratypes CAS, Krefft and Bekker 1973).
- ?*Serpa bensoni* Fowler 1934:286, Suruga Gulf, Japan; Holotype USNM 92311.
- Lampanyctus ater* Tåning 1928:68, north Atlantic. (30°17'N, 20°44'W; Lectotype ZMUC P2330209, Nafpaktitis 1973).
- Lampanyctus lineatus* Tåning 1928:68, north Atlantic. (17°54'N, 64°54'W; Lectotype ZMUC P2330212, Nafpaktitis 1973).
- Lampanyctus cuprarius* Tåning 1928:68, north Atlantic. (24°30'N, 80°00'W; Lectotype ZMUC P2330213, Nafpaktitis 1973).
- Lampanyctus photonotus* Parr 1928:102, 22°43'N, 74°23'W, Bahamas; Holotype BOC 2261.
- Lampanyctus taaningi* Parr 1929:27, Exuma Sound, Bahamas; Holotype BOC 2301, 1 paratype USNM. (8 paratypes BOC, Krefft and Bekker 1973).
- Lampanyctus omostigma parvicauda* Parr 1931:26, 16°14'N, 99°36'W; Holotype BOC 2682, 27 paratypes BOC.
- Lampanyctus idostigma* Parr 1931:32, 16°14'N, 99°36'W, Holotype BOC 2686, 26 paratypes BOC. (2 paratypes CAS).
- Lampanyctus alatus australis* Tåning 1932:145, off New Zealand, Australia and South Africa. (41°47'S, 176°55'E, off New Zealand; Lectotype ZMUC P2330216, Nafpaktitis 1973).
- Serpa turneri* Fowler 1934:285, Leyte-Mindanao, Philippines; Holotype USNM 92313, 1 paratype. (Holotype and paratype in 1 bottle, USNM 92313, both 57 mm TL).
- Lampanyctus basili* Wisner 1974:11, 6°32'N, 114°16'E (off Malaysia); Holotype SIO 69-20, 265 paratypes: BPBM (15), CAS (16), LACM (7), SIO (220), USNM (7). (Paratypes: BPBM (15), CAS (16), LACM (7), SIO (232), USNM (6); preoccupied by *Lampanyctus basili* Kotthaus 1972).
- Lampanyctus steinbecki* Bolin 1939:140, off Santa Catalina Island, California; Holotype SU 33658. (Holotype now at CAS).
- Lampanyctus achirus* Andriashev 1962:256, 64°36'S, 108°52'W; Holotype ZIANL 36111, 11 paratypes. (Paratypes: CAS (1), ZIANL (11)).
- Lampanyctus hubbsi* Wisner 1963a:16, 2°31'S, 137°04'W, central Pacific; Holotype SIO 60-234-25A, 36 paratypes SIO.
- Lampanyctus iselinoides* Bussing 1965:205, 31°58'S, 73°11'W, Peru-Chile Trench; Holotype LACM 10068, 163 paratypes LACM.
- Lampanyctus lepidolichnus* Bekker 1967:112, 42°17'S, 39°00'W; Holotype ZIANL 37858, 5 paratypes.
- Lampanyctus fernae* Wisner 1971:50, 41°01'N, 155°13'W; Holotype SIO 51-373, 45 paratypes: BCFH (1), CAS (1), OSUDO (1), SIO (29), USNM (13). (Paratypes: BCFH (2), CAS (4), OSUDO (5), SIO (21), USNM (13)).
- Lampanyctus simulator* Wisner 1971:51, 41°01'N, 155°00'W, Holotype SIO 69-17, 12 paratypes: OSUDO (1), SIO (9), USNM (3). (Paratypes: CAS (1), OSUDO (1), SIO (6), USNM (2)).
- Lampanyctus isaacsi* Wisner 1974:14, 1°10'N, 11°36'W, off west Africa; Holotype SIO 63-560, 9 paratypes: SIO (3), USNM (5), ZMUC (1). (USNM and ZMUC paratypes not found 1975, only 2 SIO paratypes in bottle).
- Lampanyctus acanthurus* Wisner 1974:17, 27°25'N, 155°32'W, north Pacific; Holotype SIO 71-305, 20 paratypes: BPBM (1), CAS (3), LACM (2), SIO (12), USNM (2).

LAMPANYCTUS (PARVILUX) Hubbs and Wisner 1964

PARVILUX Hubbs and Wisner 1964:488 (type species *Parvilux ingens* Hubbs and Wisner 1964 by original designation).

Parvilux ingens Hubbs and Wisner 1964:451, 29°09'N, 118°27'W, off Guadalupe Island, Mexico; Holotype SIO 57-207-25A, 76 paratypes: AHF (3), BMNH (4), CAS (2), MCZ (3), MMF (3), RMNH (6), SIO (29), SU (1), USNM (25). (Paratypes: BMNH (1), CAS (3), LACM (3), MCZ (1), RMNH (1), SIO (63), USNM (3)).

Parvilux boschmai Hubbs and Wisner 1964:458, 2°09'N, 84°53'W; Holotype SIO 52-384-25B.

LAMPICHTHYS Fraser-Brunner 1949

LAMPICHTHYS Fraser-Brunner 1949:1095 (type species *Myctophum (Lampanyctus) procerum* Brauer 1904 by original designation).

Myctophum (Lampanyctus) procerum Brauer 1904:402, close to Agulhas Bank. (35°32'S, 18°20'E, south Atlantic; Holotype, Brauer 1906). (Holotype? ZMB 22382, second specimen not mentioned by Brauer ZMB 17609 labelled as type).

Lampichthys rectangularis Fraser-Brunner 1949:103, 44°42'S, 53°32'W; Holotype BMNH Discovery Collections. (Holotype BMNH 1948.5.14.690).

LEPIDOPHANES Fraser-Brunner 1949

LAMPANYCTUS (LEPIDOPHANES) Fraser-Brunner 1949:1090 (as subgenus; type species *Lampanyctus guentheri* Goode and Bean 1896 by original designation).

Lampanyctus guentheri Goode and Bean 1896:79, north Atlantic (Newfoundland Banks); Holotype USNM 43777.

Lampanyctus melanothorax Parr 1928:98, 21°30'N, 71°11'W, Bahamas; Holotype BOC 2260, 54 paratypes BOC. (1 paratype MCZ).

Myctophum (Lampanyctus) gaussi Brauer 1906:235, no type locality given; 4 Syntypes. (Lectotype ZMB 20725, 5 paralectotypes ZMB, Bolin 1959).

?*Lampanyctus gaussi mediterranea* Borodin 1928:12, Sardinia, Mediterranean; Holotype VMM 131.

Lampanyctus subpectoralis Parr 1928:101, 24°29'N, 77°29'W, Bahamas; Holotype BOC 2249.

LOBIANCHIA Gatti 1903

LOBIANCHIA Gatti 1903:28 (type species *Nyctophus gemellarii* Cocco 1838 by monotypy).

PSEUDODIAPHUS Tåning 1918:71 (no type species indicated; *Diaphus gemellari* and *Diaphus dofleini* listed under new genus; *Myctophum (Lampanyctus) dofleini* Zugmayer 1911 here designated as type species).

DIAPHUS (HYPERPHOTOPS) Fraser-Brunner 1949:1066 (as subgenus; type species *Nyctophus gemellarii* Cocco 1838 by original designation).

Nyctophus gemellarii Cocco 1838:26, Sea of Messina. (No type material, Krefft and Bekker 1973).

?*Scopelus uracoclampus* Facciola 1884:51, Messina. (No type material, Krefft and Bekker 1973).

Diaphus nipponensis Gilbert 1913:86, 30°34'N, 129°22'E, Japan; Holotype USNM. (Holotype USNM 74467, Parr 1929).

Myctophum (Lampanyctus) dofleini Zugmayer 1911:3, no localities given; 7 Syntypes. (West of Seine Bank, off Cape Palos and off Cape de Gate; 8 Syntypes MOM 2022, 2699, 2902, 2910, Belloc 1949; only 7 Syntypes found 1975).

LOWEINA Fowler 1925

RHINOSCOPELUS (LOWEINA) Fowler 1925:2 (as subgenus; type species *Scopelus (Rhinoscopelus) rarus* Lütken 1892 by original designation).

Scopelus (Rhinoscopelus) rarus Lütken 1892b:246, 4 localities in north and south Atlantic; Syntypes. (20°00'N, 49°W; Lectotype ZMUC 223, 1 paralectotype ZMUC, Nielsen 1974; Wisner 1976).

Myctophum rarum f. *integer* Brauer 1904:391, no type locality given. (3 localities in Atlantic; 4 Syntypes, Brauer 1906; 1 presumed Syntype ZMB 17585, Krefft and Bekker 1973; 1 Syntype ZMB 17585).

Loweina laurae Wisner 1971:45, 21°32'N, 123°00'W; Holotype SIO 57-99, 47 paratypes: CAS (3), SIO (35), USNM (9).

Myctophum interruptum Tåning 1928:56, north Atlantic. (37°40'S, 120°00'E; Lectotype ZMUC 18, 2 paralectotypes ZMUC, Nafpaktitis 1973; Wisner 1976).

Loweina terminata Bekker 1964:18, 35°00'N, 172°56'E; Holotype ZIANL 37342, 10 paratypes.

MYCTOPHUM Rafinesque 1810

MYCTOPHUM Rafinesque 1810:56 (type species *Myctophum punctatum* Rafinesque 1810 by monotypy).

SCOPELUS Cuvier 1817:169 (type species *Gasteropelecus humboldti* Risso 1810 by subsequent designation of Goode and Bean 1896; = *Myctophum punctatum* Rafinesque 1810).

SCOPELUS (DASYSCOPELUS) Günther 1864:405 (as subgenus; type species *Scopelus asper* Richardson 1845 by subsequent designation of Goode and Bean 1896).

STYLOPHTHALMOIDES Mazzarelli 1912:4 (type species *Stylophthalmus lobiancoi* Mazzarelli 1909 by subsequent designation of Tåning 1932a; = *Myctophum punctatum* Rafinesque 1810).

CTENOSCOPELUS Fraser-Brunner 1949:1059 (type species *Scopelus phengodes* Lütken 1892 by original designation).

Myctophum punctatum Rafinesque 1810:56, Sicily, Mediterranean Sea. (No type material, Krefft and Bekker 1973).

Gasteropelecus humboldti Risso 1810:358, Sea of Amplova, Mediterranean. (Types MNHN, Cuvier and Valenciennes 1849; 3 Syntypes MNHN, Esteve 1947; 3 Syntypes MNHN 1470, Krefft and Bekker 1973).

Scopelus caninianus Cuvier and Valenciennes 1849:455, Italy; Holotype MNHN. (No type material, Krefft and Bekker 1973; Holotype MNHN 88.150, not found 1975).

Scopelus heideri Steindachner 1881:401, Messina; 2 Syntypes. (Holotype NMW 58592, Krefft and Bekker 1973; only one Syntype found 1975 with label indication that 2 specimens existed at one time).

Stylophthalmus lobiancoi Mazzarelli 1909:187, Messina; larval types. (No type material, Krefft and Bekker 1973).

Myctophum asperum Richardson 1845:41, no type locality given. (2 Syntypes BMNH, Günther 1864; type locality unknown; Lectotype BMNH 1855.9.19.1959-30, 1 paralectotype BMNH, Wisner 1970; Lectotype BMNH 1855.9.19.1529).

Dasyscopelus naufragus Waite 1904:154, Lagoon Beach, Lord Howe Island; 25 Syntypes AMS. (5 Syntypes SU, Böhlke 1953; Syntypes: AMS (20) 1.5537-56, IB.4178, BMNH (1) 1926.6.30.80, CAS (5) SU 20171).

Scopelus brachygnathos Bleeker 1856:65, Manado, Makassar, Indonesia; 2 Syntypes. (2 Syntypes RMNH, Nafpaktitis 1973; RMNH 6932).

Dasyscopelus pristilepis Gilbert and Cramer 1897:412, 21°16'N, 157°44'W, Kaiwi Channel, Hawaii; Holotype USNM 47737, 1 paratype. (1 paratype SU, Böhlke 1953; SU paratype now CAS).

Scopelus spinosus Steindachner 1867b:711, China; Holotype. (Holotype NMW 58690).

?*Scopelus cuvieri* Castelnau 1873:106, Knob Island, north of Australia, Torres Strait?; Holotype. (Holotype MNHN, Waite 1904; Holotype MNHN A.4219, not found 1975).

?*Scopelus (Myctophum) indicus* Day 1878:507, Vizagapatam, India; Holotype. (Holotype ZSI 1337, totally disintegrated).

Scopelus affinis Lütken 1892b:252, 38 localities in Atlantic and Indian Oceans and South China Sea. (8°44'N, 21°W; Lectotype ZMUC 16, 67 paralectotypes ZMUC, Bolin 1959; 77 paralectotypes ZMUC, Nielsen 1974).

?*Myctophum opalinum* Goode and Bean 1896:72, no type locality given, number of types not indicated. (Gulf Stream, western Atlantic; Lectotype USNM 43808, Jordan and Evermann 1896; 69 presumed paralectotypes USNM, 1 possible paralectotype MCZ).

?*Rhinoscopelus oceanicus* Jordan and Evermann 1903:168, 10°57'N, 137°35'W, southeast of Hawaii, Holotype USNM 50622, 1 paratype USFC. (USFC paratype now USNM).

Scopelus phengodes Lütken 1892b:253, 25°50'S, 102°50'E (south Pacific); Holotype and paratypes. (Holotype ZMUC 14, 20 paratypes ZMUC, Krefft and Bekker 1973).

Myctophum nitidulum Garman 1899:266, 27°50'N, 145°45'W (north Pacific); Holotype. (Holotype MCZ 28493, Parr 1929).

Myctophum margaritatum Gilbert 1905:596, south of Molokai, Hawaii; Holotype USNM 51536, 62 paratypes. (11+ paratypes SU, Böhlke 1953; paratypes: CAS (26), USNM (29)).

Myctophum aurolaternatum Garman 1899:264, 6°21'N, 80°41'W (eastern Pacific). (25 Syntypes MCZ 28494–5, Parr 1929; Syntypes: MCZ 28494 (3), MCZ 35191 (1), USNM 120276 (4)).

Myctophum aurolaternatum gracilior Fowler 1944:355, 250 miles southwest of Acapulco, Mexico; Holotype ANSP 70262, paratypes ANSP. (16 paratypes ANSP).

?*Scopelus (Myctophum) novaeseelandiae* Steindachner 1901:513, New Zealand; Holotype. (Holotype UMB 4667, lost, von Wahlert 1955).

Dasy Scopelus orientalis Gilbert 1913:70, Misaki, Sagami Bay, Japan; Holotype CMP 6313 or USNM, 125 paratypes. (1 paratype CMP, Henn 1928; 21 paratypes SU, Böhlke 1953; Holotype FMNH 55834, paratypes: CAS (23), FMNH (63), USNM (23)).

Myctophum pristilepis obtusirostre Tåning 1928:54, north Atlantic. (17°54'N, 64°54'W; Lectotype ZMUC P2329232, Nafpaktitis 1973).

?*Myctophum imperceptum* Bekker and Borodulina 1971:422, 9°30'S, 156°30'E, southwest Pacific; Holotype ZIANL 39910, 4 paratypes.

Myctophum selenops Tåning 1928:54, north Atlantic. (23°13'N, 82°21'W; Lectotype ZMUC P2329234, Nafpaktitis 1973).

Myctophum selenoides Wisner 1971:43, west of Keyhole Point, Hawaii; Holotype SIO 60–251, 6 paratypes: BPBM (1), SIO (2), USNM (3).

?*Myctophum lychnobium* Bolin 1946:137, 5°56'N, 76°22'E, off Cape Cormorin, India; Holotype IMC. (Holotype ZSI, lost, Menon and Rao 1971; Holotype ZSI F 7405/2, found).

Myctophum fissunovi Bekker and Borodulina 1971:420, 6°58'S, 39°37'E, Indian Ocean; Holotype ZIANL 39909, 1 paratype.

Myctophum lunatum Bekker and Borodulina 1978:110, 7°26'S, 124°13'E, Indo-Malayan Archipelago; Holotype ZIANL 43261, 14 paratypes IOANM.

NOTOLYCHNUS Fraser-Brunner 1949

VESTULA Bolin 1946:144 (type species *Myctophum valdiviae* Brauer 1904 by original designation; preoccupied by *Vestula* Staal 1865, Hemiptera).

NOTOLYCHNUS Fraser-Brunner 1949:1077 (type species *Myctophum valdiviae* Brauer 1904 by original designation; replacement name for *Vestula* Bolin 1946).

Myctophum valdiviae Brauer 1904:398, Atlantic and Indian Oceans; 66 Syntypes. (23 localities in Atlantic and Indian

Oceans, Brauer 1906; 12 presumed Syntypes ZMB 17586–9, Krefft and Bekker 1973; Syntypes: SMF (6) 2074–5, 11942; SMNS (1) 4477; ZMB (17) 17586–9, 20007).

NOTOSCOPELUS (NOTOSCOPELUS) Günther 1864

SCOPELUS (NOTOSCOPELUS) Günther 1864:405 (as subgenus; type species *Lampanyctus resplendens* Richardson 1845 by subsequent designation of Goode and Bean 1896).

CATABLEMELLA Eigenmann and Eigenmann 1890:24 (type species *Notoscopelus brachychir* Eigenmann and Eigenmann 1889 by original designation; = *Lampanyctus resplendens* Richardson 1845).

Scopelus elongatus Costa 1844:2, off Naples. (No types exist, Moreau 1891; types obviously lost, Krefft and Bekker 1973).

Scopelus pseudocrocodylus Moreau 1891:84, Nice, Mediterranean Sea. (Types MNHN, Esteve 1947; 2 Syntypes MNHN 98–1115, Krefft and Bekker 1973).

Lampanyctus resplendens Richardson 1845:42, no type locality given; 6 Syntypes. (3 Syntypes BMNH, Günther 1864; 3 Syntypes BMNH 1843.3.16, Krefft and Bekker 1973).

Notoscopellus brachychie Eigenmann and Eigenmann 1889:126, Cortez Banks off California; 3 Syntypes. (Emended to *Notoscopelus brachychie*, Eigenmann and Eigenmann 1890; Type USNM 76336, Parr 1929; Lectotype USNM 76336, 1 paralectotype BMNH, Bolin 1959).

Notoscopelus ejectus Waite 1904:150, Lord Howe Island; Holotype AMS. (Holotype AMS 1.5564, Krefft and Bekker 1973).

Serpa hoffmanni Fowler 1934:282, 36°45'N, 74°29'W; Holotype USNM 43790, 1 paratype. (No paratype found ANSP or USNM 1975).

Scopelus kroeyerii Malm 1861:617, Skagerrak, Sweden; Holotype. (Holotype NMG Pi.su. 219, Krefft and Bekker 1973).

Notoscopelus quercinus Goode and Bean 1896:83, north Atlantic; Holotype USNM 43789.

Notoscopelus margaritifera Goode and Bean 1896:84, off Banquero, north Atlantic, 2 Syntypes USNM 43774–5. (Newfoundland Banks; Lectotype USNM 43775, Jordan and Evermann 1896).

Notoscopelus castaneus Goode and Bean 1896:84, 39°57'N, 70°37'W (north Atlantic); Holotype USNM 31706.

Scopelus caudispinosus Johnson 1863:42, Madeira; Holotype BMNH. (Holotype BMNH 1862.2.5.3, Krefft and Bekker 1973).

Macrostoma quercinum japonicum Tanaka 1908:5, off Misaki, Japan; Holotype. (Holotype FMNH 80459, Fujii and Uyeno 1976).

NOTOSCOPELUS (PAREIOPHUS) Nafpaktitis 1975

NOTOSCOPELUS (PAREIOPHUS) Nafpaktitis 1975:83 (as subgenus; type species *Notoscopelus bolini* Nafpaktitis 1975 by original designation).

Notoscopelus (Pareiophus) bolini Nafpaktitis 1975:83, 38°39'N, 04°12'E, Mediterranean; Holotype USNM 212056, 5 paratypes: LACM (2), MCZ (2), USNM (1).

PROTOMYCTOPHUM (PROTOMYCTOPHUM)

Fraser-Brunner 1949

ELECTRONA (PROTOMYCTOPHUM) Fraser-Brunner 1949:1045 (as subgenus; type species *Myctophum tenisoni* Norman 1930 by original designation).

Myctophum anderssoni Lonnberg 1905:763, 48°54'S, 51°40'W; 3 Syntypes. (3 Syntypes NRMS 9022653761).

Myctophum tenisoni Norman 1930:321, 46°25'S, 15°13'E, south Atlantic; Holotype, 8 paratypes BMNH. (Holotype BMNH 1930.1.12.604; of the remaining 13 specimens over 34 mm listed by Norman, the 8 paratypes are not indicated; all specimens are present in BMNH).

Myctophum normani Tåning 1932:127, 41°47'S, 176°55'E, east of New Zealand. (Holotype ZMUC P2329231, Nafpaktitis 1973).

Electrona (Protomyctophum) bolini Fraser-Brunner 1949:1099, 45°18'S, 18°58'S, south Atlantic; Holotype, 4 paratypes BMNH Discovery Collections. (Holotype BMNH 1948.5.14.1).

Protomyctophum andriashevi Bekker 1963:19, 42°16'S, 39°00'W, south Atlantic; Holotype ZIANL 36803, 5 paratypes.

PROTOMYCTOPHUM (HIEROPS) Fraser-Brunner 1949

ELECTRONA (HIEROPS) Fraser-Brunner 1949:1046 (as subgenus; type species *Scopelus arcticus* Lütken 1892 by original designation).

Scopelus arcticus Lütken 1892a:207, off southern Greenland; 5 Syntypes. (Sukkertoppen, Greenland; Lectotype ZMUC 81, Bolin 1959; 4 paralectotypes ZMUC, Nielsen 1974).

Myctophum parallelum Lonnberg 1905:764, 48°27'S, 44°36'W; Holotype. (Holotype NRMS 9022613760).

Myctophum arcticum subparallelum Tåning 1932:128, east of Cook Strait, New Zealand. (41°47'S, 176°55'E; Lectotype ZMUC P2329223, Nafpaktitis 1973).

Electrona crockeri Bolin 1939:98, 33°11'N, 118°21'W, off southern California; Holotype SU 33656. (Holotype now CAS).

Electrona thompsoni Chapman 1944:54 (replacement name for *Myctophum oculium* Chapman 1939).

Myctophum oculium Chapman 1939:524, 54°15'N, 158°23'W, northeast Pacific; Holotype USNM 108146, 37 paratypes. (Preoccupied by *Myctophum oculium* Garman 1899; 1 paratype SU, Böhlke 1953; paratypes: CAS (32), USNM (2)).

Protomyctophum (Hierops) chilensis Wisner 1971:39, 33°07'S, 73°09'W, off Chile; Holotype SIO 65–665, 23 paratypes: CAS (1), LACM (7), SIO (14), USNM (1).

Protomyctophum (Hierops) beckeri Wisner 1971:39, 17°09'N,

153°57'W; Holotype SIO 60–249, 4 paratypes: BPBM (1), SIO (2), USNM (1).

SCOPELOPSIS Brauer 1906

SCOPELOPSIS Brauer 1906:146 (type species *Scopelopsis multipunctatus* Brauer 1906 by monotypy).

Scopelopsis multipunctatus Brauer 1906:146, 33°23'S, 16°19'E, south Atlantic; Holotype. (Holotype ZMB 17560).

Lampanyctus longipinnis Regan 1916:140, 33°12'S, 171°05'E, northeast of Three Kings Island, New Zealand; larval Holotype BMNH. (Holotype BMNH 1916.3.20.90).

Scopelopsis caudalis Whitley 1932:333, Lord Howe Island; Holotype AMS 1A.2427.

STENOBRACHIUS Eigenmann and Eigenmann 1890

MYCTOPHUM (STENOBRACHIUS) Eigenmann and Eigenmann 1890:5 (as subgenus; type species *Myctophum leucopsarum* Eigenmann and Eigenmann 1890 by original designation).

Myctophum (Stenobranchius) leucopsarum Eigenmann and Eigenmann 1890:5, off Point Loma, California; 23 Syntypes. (Lectotype USNM 41916, Jordan and Evermann 1896; 2 types MCZ, Parr 1934; paralectotypes: BMNH (3), CAS (1), MCZ (2)).

Lampanyctus beringensis Schmidt 1933:131, off Cape Severny, Bering Island; Holotype ZIANL 23745.

Myctophum nannochir Gilbert 1890:51, Pacific coast of United States; Syntypes. (Lectotype SU 1459, Gilbert 1895; 8 types USNM, Parr 1929; 9 paralectotypes SU, Böhlke 1953; paralectotypes: CAS (9), MCZ (1), USNM (7)).

Lampanyctus nannochir laticauda Kulikova 1954:196, Okhotsk Sea and Kurile Islands; 67 Syntypes. (Syntypes not at ZIANL).

SYMBOLOPHORUS Bolin and Wisner in Bolin 1959

SYMBOLOPHORUS Bolin and Wisner in Bolin 1959:11 (type species *Myctophum californiense* Eigenmann and Eigenmann 1889 by original designation).

?*Myctophum boops* Richardson 1845:39, Tasman Sea; Syntypes. (Holotype BMNH, Günther 1864; type locality in error, Whitley 1953; Syntype BMNH 1948.1.12.1).

Scopelus veranyi Moreau 1888:108, Nice, Mediterranean Sea; Syntypes. (No type material, Krefft and Bekker 1973; no types recorded in MNHN).

Stylophthalmus mediterraneus Mazzarelli 1909:187, Messina; larval Syntypes.

Myctophum californiense Eigenmann and Eigenmann 1889:124, Cortez Banks off California; several Syntypes. (Type USNM 41920, Parr 1929; Syntypes: BMNH (1) 1891.5.17.4, CAS (1) SU 20172, USNM (1) 41920).

Myctophum evermanni Gilbert 1905:597, south of Oahu, Hawaii; Holotype USNM 51521, 34 paratypes. (19 paratypes SU,

Böhlke 1953; paratypes: CAS (19), USNM (6)).

Myctophum rufinum Tåning 1928:54, north Atlantic. (15°50'N, 26°32'W; Lectotype ZMUC P2330210, Nafpaktitis 1973).

?*Myctophum humboldti barnardi* Tåning 1932:128, off South Africa. (Lectotype ZMUC P2329227, Nafpaktitis 1973).

?*Scopelus hookeri* Whitley 1953:134, Tasman Sea (Lord Howe Island); Holotype AMS 1A.1406.

TAANINGICHTHYS Bolin 1959

TAANINGICHTHYS Bolin 1959:25 (type species *Lampadena bathyphila* Tåning 1928 by original designation).

Lampadena bathyphila Tåning 1928:63, north Atlantic. (25°11'N, 20°57'W; Lectotype Bolin 1959; Lectotype ZMUC P2329220, Nafpaktitis 1973).

Lampadena minima Tåning 1928:63, north Atlantic. (15°50'N, 26°32'W; Lectotype ZMUC P2329221, Nafpaktitis 1973).

Taaningichthys paurolychnus Davy 1972:71, 31°N, 119°W, northeast Pacific; Holotype SIO 70-19, 12 paratypes: MMF (1), NIO (1), NMFS (1), SIO (2), SOSC (1), IOANM (1), ZMUC (4). (Paratypes: BMNH (1), LACM (3), MMF (8), USNM (2), ZIANL (1), ZMUC (1)).

TARLETONBEANIA Eigenmann and Eigenmann 1890

TARLETONBEANIA Eigenmann and Eigenmann 1890:6 (type species *Tarletonbeania tenua* Eigenmann and Eigenmann 1890 by original designation; = *Myctophum crenulare* Jordan and Gilbert 1880).

Myctophum crenulare Jordan and Gilbert 1880:274, Santa Barbara Channel, California; Holotype. (Holotype USNM 27402, Jordan and Evermann 1896).

Myctophum procellarum Bean in Jordan and Gilbert 1881:457 (NOMEN NUDUM).

Tarletonbeania tenua Eigenmann and Eigenmann 1890:7, probably near Coronado Islands, California; Holotype USNM 41882.

?*Tarletonbeania taylori* Mead 1953:105, 39°21'N, 142°56'E, off Ohakozake, Japan; Holotype USNM 164970, 5 paratypes: USNM (2). (3 paratypes CAS).

TRIPHOTURUS Fraser-Brunner 1949

LAMPANYCTUS (TRIPHOTURUS) Fraser-Brunner 1949:1083 (as subgenus; type species *Myctophum (Lampanyctus) micropterum* Brauer 1906 by original designation).

Myctophum mexicanum Gilbert 1890:51, Gulf of California and west coast of Baja California, Mexico; 6 Syntypes. (Type USNM 44289, Jordan and Evermann 1896; (invalid as a lectotype designation, as 44289 is not part of the syntypic series); type USNM 76343, Parr 1929; Lectotype USNM 76343, 3 paralectotypes SU, Böhlke 1953).

?*Myctophum oculum* Garman 1899:260, 12 localities in eastern Pacific. (8 Syntypes MCZ 28500, Parr 1934; 19

Syntypes: MCZ 28500 (7), 34945 (1), 34946 (4), 35162 (1), 35182 (1), 35185 (1), 35187 (1), 35189 (2), USNM 120422 (1)).

Myctophum (Lampanyctus) nigrescens Brauer 1904:403, Indian Ocean. (2 localities east of Seychelles; 2 Syntypes, Brauer 1906; 2 Syntypes ZMB 17617, 22379).

?*Lampanyctus microchir* Gilbert 1913:101, Suruga Bay, Japan; Holotype USNM. (Holotype USNM 74468, Parr 1929).

?*Myctophum (Lampanyctus) micropterum* Brauer 1906:239, 11 localities in tropical Atlantic and Indian Oceans; 9 Syntypes. (3 Syntypes ZMB 17614-16).

Myctophidae unplaceable to genus

?*Scopelus tenuicauda* Steindachner 1867a:590, China Sea. (Type not found NMW 1975).

?*Scopelus langerhansi* Johnson 1890:454, Madeira; Holotype ZMB. (Holotype not found ZMB 1975).

ALPHABETICAL LIST OF RECENT MYCTOPHID SPECIES

Species, present genus, original genus, year of description (senior synonym year).

acanthurus, *Ceratoscopelus*, *Scopelus*, 1882, (1864)
acanthurus, *Lampanyctus*, *Lampanyctus*, 1974
achirus, *Lampanyctus*, *Lampanyctus*, 1962
adenomus, *Diaphus*, *Diaphus*, 1905
aeolochrus, *Diaphus*, *Myctophum*, 1927, (1896)
affinis, *Myctophum*, *Scopelus*, 1892
agassizi, *Diaphus*, *Diaphus*, 1908
ahlstromi, *Electrona*, *Metelectrona*, 1963, (1963)
alatus, *Lampanyctus*, *Lampanyctus*, 1896
aliciae, *Diaphus*, *Diaphus*, 1934
altifrons, *Diaphus*, *Diaphus*, 1961
anderseni, *Diaphus*, *Diaphus*, 1932
anderssoni, *Protomyctophum*, *Myctophum*, 1905
andreae, *Centrobranchus*, *Scopelus*, 1892
andriashevi, *Protomyctophum*, *Protomyctophum*, 1963
anomala, *Lampadena*, *Lampadena*, 1928
antarcticus, *Electrona*, *Scopelus*, 1878
antelucens, *Diaphus*, *Diaphus*, 1961
anteorbitalis, *Diaphus*, *Diaphus*, 1913, (1905)
antonbruuni, *Diaphus*, *Diaphus*, 1978
aphya, *Gymnoscopelus*, *Gymnoscopelus*, 1873
arabicus, *Diaphus*, *Diaphus*, 1978
arcticus, *Protomyctophum*, *Scopelus*, 1892
argenteus, *Lampanyctodes*, *Scopelus*, 1904, (1876)
ashmeadi, *Diaphus*, *Diaphus*, 1934, (1906)
asperum, *Myctophum*, *Myctophum*, 1845
astridae, *Diaphus*, *Diaphus*, 1929, (1897)
ater, *Lampanyctus*, *Lampanyctus*, 1928
atkinsoni, *Diaphus*, *Diaphus*, 1934, (1934)
atlanticum, *Diogenichthys*, *Myctophum*, 1928
atlantica, *Lampadena*, *Lampadena*, 1969, (1963)

- atratum*, *Hygophum*, *Myctophum*, 1899
aurolaternatum, *Myctophum*, *Myctophum*, 1899
australis, *Lampanyctus*, *Lampanyctus*, 1932
barnardi, *Symbolophorus*, *Myctophum*, 1932
barnesi, *Gonichthys*, *Gonichthys*, 1943
basili, *Lampanyctus*, *Lampanyctus*, 1972, (1904)
basili, *Lampanyctus*, *Lampanyctus*, 1974, (1934)
bathyphila, *Taaningichthys*, *Lampadena*, 1928
beckeri, *Protomyctophum*, *Protomyctophum*, 1971
benoitii, *Hygophum*, *Scopelus*, 1838
bensoni, *Lampanyctus*, *Serpa*, 1934, (1928)
beringensis, *Stenobranchius*, *Lampanyctus*, 1933, (1890)
bertelseni, *Diaphus*, *Diaphus*, 1966
blacki, *Bolinichthys*, *Serpa*, 1934, (1891)
bolini, *Protomyctophum*, *Electrona*, 1949
bolini, *Gymnoscopelus*, *Gymnoscopelus*, 1962
bolini, *Notoscopelus*, *Notoscopelus*, 1975
bonapartii, *Lampanyctus*, *Nyctophus*, 1838, (1810)
boops, *Symbolophorus*, *Myctophum*, 1845
boschmai, *Lampanyctus*, *Parvilux*, 1964
brachycephalus, *Diaphus*, *Diaphus*, 1928
brachyichir, *Notoscopelus*, *Notoscopelus*, 1889, (1845)
brachygnathos, *Myctophum*, *Scopelus*, 1856
braueri, *Gymnoscopelus*, *Myctophum*, 1905
braueri, *Hygophum*, *Myctophum*, 1905, (1892)
braueri, *Lampadena*, *Lampadena*, 1914, (1896)
brevirostris, *Centrobranchus*, *Centrobranchus*, 1964
bruuni, *Hygophum*, *Hygophum*, 1971
bryani, *Diaphus*, *Diaphus*, 1934, (1934)
burtoni, *Diaphus*, *Diaphus*, 1934
californiense, *Symbolophorus*, *Myctophum*, 1889
candens, *Hintonia*, *Hintonia*, 1949
caninianus, *Myctophum*, *Scopelus*, 1849, (1810)
carlsbergi, *Electrona*, *Myctophum*, 1932
carlsoni, *Diaphus*, *Diaphus*, 1934, (1932)
castaneus, *Notoscopelus*, *Notoscopelus*, 1896, (1861)
caudalis, *Scopelopsis*, *Scopelopsis*, 1932, (1906)
caudispinosus, *Notoscopelus*, *Scopelus*, 1863
chavesi, *Lampadena*, *Lampadena*, 1905
chilensis, *Protomyctophum*, *Protomyctophum*, 1971
choerocephalus, *Centrobranchus*, *Centrobranchus*, 1904
chrysorhynchus, *Diaphus*, *Diaphus*, 1897
cocco, *Gonichthys*, *Scopelus*, 1829
coeruleus, *Diaphus*, *Scopelus*, 1871
colletti, *Electrona*, *Scopelus*, 1892, (1878)
conspicua, *Lampanyctus*, *Serpa*, 1936, (1928)
coruscans, *Gonichthys*, *Myctophum*, 1845, (1943)
crameri, *Diaphus*, *Diaphus*, 1934, (1932)
crenulare, *Tarletonbeania*, *Myctophum*, 1880
crockeri, *Protomyctophum*, *Electrona*, 1939
crocodilus, *Lampanyctus*, *Gasteropelecus*, 1810
cuprarius, *Lampanyctus*, *Lampanyctus*, 1928
cuvieri, *Myctophum*, *Scopelus*, 1873, (1867)
dahlgreni, *Diaphus*, *Diaphus*, 1934
danae, *Diaphus*, *Diaphus*, 1932
dea, *Lampadena*, *Lampadena*, 1949
dehaveni, *Diaphus*, *Diaphus*, 1934
diademetus, *Diaphus*, *Diaphus*, 1932
diademophilus, *Diaphus*, *Diaphus*, 1978
distofax, *Bolinichthys*, *Bolinichthys*, 1975
doderleini, *Ceratoscopelus*, *Scopelus*, 1882, (1864)
dofleini, *Lobianchia*, *Myctophum*, 1911
draclmanni, *Diaphus*, *Diaphus*, 1932
dumerili, *Diaphus*, *Scopelus*, 1856
effulgens, *Diaphus*, *Aethoprora*, 1896
ehrhorni, *Diaphus*, *Diaphus*, 1934
ejectus, *Notoscopelus*, *Notoscopelus*, 1904, (1845)
elongatus, *Notoscopelus*, *Scopelus*, 1844
elucens, *Diaphus*, *Myctophum*, 1904, (1898)
engraulis, *Diaphus*, *Scopelus*, 1887, (1871)
evermanni, *Symbolophorus*, *Myctophum*, 1905
faustinoi, *Diaphus*, *Diaphus*, 1934
fernae, *Lampanyctus*, *Lampanyctus*, 1971
festivus, *Lampanyctus*, *Lampanyctus*, 1928
fibulatum, *Benthosema*, *Myctophum*, 1897
fissunovi, *Myctophum*, *Myctophum*, 1971
florenti, *Gymnoscopelus*, *Myctophum*, 1933, (1931)
fragilis, *Diaphus*, *Diaphus*, 1928
fraserbrunneri, *Bolinichthys*, *Lampanyctus*, 1946, (1906)
fraseri, *Gymnoscopelus*, *Lampanyctus*, 1931
freta, *Lampanyctus*, *Serpa*, 1936, (1904)
fulgens, *Diaphus*, *Myctophum*, 1904
garmani, *Diaphus*, *Diaphus*, 1906
gaussi, *Lepidophanes*, *Myctophum*, 1906
gemellarii, *Lobianchia*, *Nyctophus*, 1838
gemmifer, *Lampanyctus*, *Lampanyctus*, 1896, (1810)
gigas, *Diaphus*, *Diaphus*, 1913, (1896)
gilberti, *Benthosema*, *Myctophum*, 1907, (1891)
glacialis, *Benthosema*, *Scopelus*, 1837
glandulifer, *Diaphus*, *Diaphus*, 1913, (1913)
gracilicaudus, *Centrobranchus*, *Centrobranchus*, 1905, (1892)
gracilior, *Myctophum*, *Myctophum*, 1944, (1899)
gracilis, *Gonichthys*, *Scopelus*, 1892, (1829)
gracilis, *Diaphus*, *Diaphus*, 1961
grayi, *Bolinichthys*, *Macrostoma*, 1938, (1906)
gudgeri, *Diaphus*, *Diaphus*, 1934, (1932)
guentheri, *Lepidophanes*, *Lampanyctus*, 1896
handi, *Diaphus*, *Diaphus*, 1934
hanseni, *Hygophum*, *Myctophum*, 1932
harveyi, *Diaphus*, *Diaphus*, 1934, (1932)
hectoris, *Lampanyctodes*, *Scopelus*, 1876
heideri, *Myctophum*, *Scopelus*, 1881, (1810)
hians, *Gonichthys*, *Myctophum*, 1845, (1829)
hoffmanni, *Notoscopelus*, *Serpa*, 1934, (1845)
hollandi, *Benthosema*, *Myctophum*, 1922, (1897)
holti, *Diaphus*, *Myctophum*, 1918
hookeri, *Symbolophorus*, *Scopelus*, 1953, (1932)
hubbsi, *Lampanyctus*, *Lampanyctus*, 1963
hudsoni, *Diaphus*, *Diaphus*, 1976
humboldti, *Myctophum*, *Gasteropelecus*, 1810, (1810)
hygomei, *Hygophum*, *Scopelus*, 1892
hypolucens, *Diaphus*, *Diaphus*, 1928, (1928)
idostigma, *Lampanyctus*, *Lampanyctus*, 1931
imitator, *Benthosema*, *Myctophum*, 1928, (1913)
imperceptum, *Myctophum*, *Myctophum*, 1971, (1928)
indicus, *Myctophum*, *Scopelus*, 1878
indicus, *Bolinichthys*, *Lepidophanes*, 1969
ingens, *Lampanyctus*, *Parvilux*, 1964
integer, *Loweina*, *Myctophum*, 1904, (1892)
intermedius, *Diaphus*, *Diaphus*, 1930, (1838)
interruptum, *Loweina*, *Myctophum*, 1928
intricarius, *Lampanyctus*, *Lampanyctus*, 1928

- isaacsi*, *Lampanyctus*, *Lampanyctus*, 1974
iselini, *Lampanyctus*, *Lampanyctus*, 1934, (1810)
iselinoides, *Lampanyctus*, *Lampanyctus*, 1965
jagorii, *Gonichthys*, *Scopelus*, 1845, (1829)
japonicum, *Notoscopelus*, *Macrostoma*, 1908
jenseni, *Diaphus*, *Diaphus*, 1932
jordani, *Lampanyctus*, *Lampanyctus*, 1913
jouani, *Diaphus*, *Diaphus*, 1934, (1934)
joubini, *Bolinichthys*, *Lampanyctus*, 1931, (1906)
kendalli, *Diaphus*, *Diaphus*, 1934, (1932)
knappi, *Diaphus*, *Diaphus*, 1978
knipovitschi, *Benthosema*, *Myctophum*, 1939, (1837)
kroeyerii, *Notoscopelus*, *Scopelus*, 1861
kuroshio, *Diaphus*, *Diaphus*, 1978
kylei, *Diaphus*, *Diaphus*, 1932, (1932)
lacerta, *Diaphus*, *Lampanyctus*, 1896, (1856)
langerhansi, ?, *Scopelus*, 1890
laternatum, *Diogenichthys*, *Myctophum*, 1899
laticauda, *Stenobranchius*, *Lampanyctus*, 1954, (1890)
latus, *Diaphus*, *Diaphus*, 1913
laurae, *Loweina*, *Loweina*, 1971, (1892)
layi, *Diaphus*, *Diaphus*, 1934, (1934)
lepidolichnus, *Lampanyctus*, *Lampanyctus*, 1967
leucopsarum, *Stenobranchius*, *Myctophum*, 1890
lewisi, *Diaphus*, *Diaphus*, 1966, (1906)
lineatus, *Lampanyctus*, *Lampanyctus*, 1928
lobatus, *Diaphus*, *Diaphus*, 1978
lobiancoi, *Myctophum*, *Stylophthalmus*, 1909, (1910)
longipes, *Bolinichthys*, *Myctophum*, 1906
longipinnis, *Scopelopsis*, *Lampanyctus*, 1916, (1906)
longleyi, *Diaphus*, *Diaphus*, 1934, (1932)
loricata, *Gonichthys*, *Alysia*, 1839, (1829)
lucida, *Diaphus*, *Aethoprora*, 1896
lucifrons, *Diaphus*, *Diaphus*, 1934
luetkeni, *Diaphus*, *Myctophum*, 1904
luminosum, *Lampadena*, *Myctophum*, 1899
lunatum, *Myctophum*, *Myctophum*, 1978
lychnobium, *Myctophum*, *Myctophum*, 1946
macdonaldi, *Lampanyctus*, *Nannobranchium*, 1896
macrochir, *Hygophum*, *Scopelus*, 1864
macroptus, *Diaphus*, *Diaphus*, 1928, (1896)
macropterum, *Lampanyctus*, *Myctophum*, 1904
maderensis, *Ceratoscopelus*, *Scopelus*, 1839
malayanus, *Diaphus*, *Diaphus*, 1913
margaritanum, *Myctophum*, *Myctophum*, 1905, (1899)
margaritiferus, *Notoscopelus*, *Notoscopelus*, 1896, (1861)
meadi, *Diaphus*, *Diaphus*, 1978
mediterranea, *Lepidophanes*, *Lampanyctus*, 1928, (1906)
mediterraneus, *Symbolophorus*, *Stylophthalmus*, 1909, (1888)
megalops, *Diaphus*, *Diaphus*, 1978
megalops, *Electrona*, *Myctophum*, 1865, (1864)
melanothorax, *Lepidophanes*, *Lampanyctus*, 1928, (1896)
metopoclampum, *Diaphus*, *Myctophum*, 1829
mexicanum, *Triphoturus*, *Myctophum*, 1890
meyeri, *Diaphus*, *Diaphus*, 1934, (1913)
microchir, *Triphoturus*, *Myctophum*, 1913, (1904)
microps, *Diaphus*, *Myctophum*, 1904
micropterum, *Triphoturus*, *Myctophum*, 1906
micropunctatus, *Lampanyctus*, *Lampanyctus*, 1939, (1892)
minax, *Diaphus*, *Diaphus*, 1968
minima, *Taaningichthys*, *Lampadena*, 1928
mollis, *Diaphus*, *Diaphus*, 1928
monodi, *Diaphus*, *Diaphus*, 1934, (1896)
mulleri, *Benthosema*, *Scopelus*, 1861, (1837)
multipunctatus, *Scopelopsis*, *Scopelopsis*, 1906
nannochir, *Stenobranchius*, *Myctophum*, 1890
nanus, *Diaphus*, *Diaphus*, 1908, (1904)
naufragus, *Myctophum*, *Dasyscopelus*, 1904, (1845)
nicholsi, *Gymnoscopelus*, *Lampanyctus*, 1911, (1873)
nielsenii, *Diaphus*, *Diaphus*, 1978
nigrescens, *Triphoturus*, *Myctophum*, 1904
nigroocellatus, *Centrobranchus*, *Scopelus*, 1873
nigrum, *Lampanyctus*, *Nannobranchium*, 1887
nikolayi, *Bolinichthys*, *Bolinichthys*, 1978
nipponensis, *Lobianchia*, *Diaphus*, 1913, (1838)
nitida, *Lampadena*, *Lampadena*, 1928, (1899)
nitidulum, *Myctophum*, *Myctophum*, 1899
nobilis, *Lampanyctus*, *Lampanyctus*, 1928
nocturnum, *Diaphus*, *Myctophum*, 1861, (1856)
normani, *Protomyctophum*, *Myctophum*, 1932
notialis, *Lampadena*, *Lampadena*, 1968
novaeguineae, *Lampanyctus*, *Lampanyctus*, 1958, (1904)
novaeseelandiae, *Myctophum*, *Scopelus*, 1901
obtusirostre, *Myctophum*, *Myctophum*, 1928
oceanicus, *Myctophum*, *Rhinoscopelus*, 1903, (1892)
oculeum, *Triphoturus*, *Myctophum*, 1899
oculeum, *Protomyctophum*, *Myctophum*, 1939, (1944)
omostigma, *Lampanyctus*, *Lampanyctus*, 1908
opalinum, *Myctophum*, *Myctophum*, 1896, (1892)
opisthopterus, *Gymnoscopelus*, *Gymnoscopelus*, 1949
orientalis, *Myctophum*, *Dasyscopelus*, 1913
ostenfeldi, *Diaphus*, *Diaphus*, 1932
pacificus, *Diaphus*, *Diaphus*, 1961, (1904)
pacificus, *Diaphus*, *Diaphus*, 1931
panamense, *Benthosema*, *Myctophum*, 1932
panurgus, *Diogenichthys*, *Diogenichthys*, 1946
parallelum, *Protomyctophum*, *Myctophum*, 1905
parri, *Diaphus*, *Diaphus*, 1932
parvicauda, *Lampanyctus*, *Lampanyctus*, 1931
parvimanus, *Benthosema*, *Scopelus*, 1864, (1837)
paucirastra, *Electrona*, *Electrona*, 1962
paurolychnus, *Taaningichthys*, *Taaningichthys*, 1972
peccatus, *Hygophum*, *Serpa*, 1939, (1932)
peculiaris, *Lampanyctus*, *Lampanyctus*, 1929, (1810)
perspicillata, *Diaphus*, *Aethoprora*, 1898
phengodes, *Myctophum*, *Scopelus*, 1892
phillipsi, *Diaphus*, *Diaphus*, 1934
photonotus, *Lampanyctus*, *Lampanyctus*, 1928
photothorax, *Bolinichthys*, *Lampanyctus*, 1928
piabilis, *Gymnoscopelus*, *Lampanyctus*, 1931
pinchoti, *Benthosema*, *Benthosema*, 1932, (1897)
polyphotis, *Ceratoscopelus*, *Lampanyctus*, 1932, (1892)
pontifex, *Lampadena*, *Lampadena*, 1970
pristilepis, *Myctophum*, *Dasyscopelus*, 1897, (1856)
problematicus, *Diaphus*, *Diaphus*, 1928
procellarum, *Tarletonbeania*, *Myctophum*, 1881, (1880)
procerum, *Lampichthys*, *Myctophum*, 1904
protoculus, *Diaphus*, *Myctophum*, 1891, (1890)
proximum, *Benthosema*, *Myctophum*, 1929, (1913)
proximum, *Hygophum*, *Hygophum*, 1965
pseudoalatus, *Lampanyctus*, *Lampanyctus*, 1918, (1896)
pseudocrocodilus, *Notoscopelus*, *Scopelus*, 1891, (1844)

pterotus, *Benthoosema*, *Scopelus*, 1891
punctatissimus, *Lampanyctus*, *Lampanyctus*, 1913, (1896)
punctatum, *Myctophum*, *Myctophum*, 1810
pusillus, *Lampanyctus*, *Scopelus*, 1890
pyrsobolus, *Bolinichthys*, *Scopelus*, 1891
quercinus, *Notoscopelus*, *Notoscopelus*, 1896, (1861)
rafinesquii, *Diaphus*, *Nyctophus*, 1839
rarus, *Loweina*, *Scopelus*, 1892
rassi, *Diaphus*, *Diaphus*, 1961, (1932)
readi, *Diaphus*, *Diaphus*, 1934, (1896)
rectangularis, *Lampichthys*, *Lampichthys*, 1949, (1904)
regale, *Lampanyctus*, *Myctophum*, 1892
regani, *Diaphus*, *Diaphus*, 1932
regularis, *Centrobranchus*, *Myctophum*, 1904, (1873)
reinhardtii, *Hygophum*, *Scopelus*, 1892
reinhardtii, *Lampanyctus*, *Nyctimaster*, 1921
remiger, *Hygophum*, *Myctophum*, 1896, (1892)
renschii, *Benthoosema*, *Myctophum*, 1929, (1897)
resplendens, *Notoscopelus*, *Lampanyctus*, 1845
richardsoni, *Diaphus*, *Diaphus*, 1932
risso, *Electrona*, *Scopelus*, 1829
ritteri, *Lampanyctus*, *Myctophum*, 1915
roei, *Diaphus*, *Diaphus*, 1974
rolfbolini, *Diaphus*, *Diaphus*, 1971, (1934)
rufinum, *Symbolophorus*, *Myctophum*, 1928
sagamiensis, *Diaphus*, *Diaphus*, 1913, (1897)
salubris, *Electrona*, *Electrona*, 1933, (1829)
scapulofulgens, *Diaphus*, *Diaphus*, 1934, (1904)
schmidti, *Diaphus*, *Diaphus*, 1932
schmizi, *Diaphus*, *Scopelus*, 1890, (1856)
scofieldi, *Diogenichthys*, *Diogenichthys*, 1939, (1928)
scoticus, *Benthoosema*, *Scopelus*, 1889, (1837)
selenoides, *Myctophum*, *Myctophum*, 1971, (1928)
selenops, *Myctophum*, *Myctophum*, 1928
septilucis, *Lampanyctus*, *Lampanyctus*, 1932, (1928)
sibogae, *Lampanyctus*, *Promacheon*, 1913
signatus, *Diaphus*, *Diaphus*, 1908
simile, *Benthoosema*, *Myctophum*, 1928, (1913)
similis, *Diaphus*, *Diaphus*, 1974
simulator, *Lampanyctus*, *Lampanyctus*, 1971
speculigera, *Lampadena*, *Lampadena*, 1896
spinosus, *Myctophum*, *Scopelus*, 1867
splendidum, *Diaphus*, *Myctophum*, 1904
steadi, *Diaphus*, *Diaphus*, 1934, (1904)
steinbecki, *Lampanyctus*, *Lampanyctus*, 1939
stellatus, *Electrona*, *Scopelus*, 1840, (1864)
stilbius, *Bolinichthys*, *Lampanyctus*, 1908 (1928)
streetsi, *Diaphus*, *Diaphus*, 1934, (1913)
subasper, *Electrona*, *Scopelus*, 1864
suborbitale, *Benthoosema*, *Myctophum*, 1913
suborbitalis, *Diaphus*, *Diaphus*, 1913
subparallelum, *Protomyctophum*, *Myctophum*, 1932
subpectoralis, *Lepidophanes*, *Lampanyctus*, 1928, (1906)
subtilis, *Diaphus*, *Diaphus*, 1968
supralateralis, *Bolinichthys*, *Lampanyctus*, 1928
taaningi, *Lampanyctus*, *Lampanyctus*, 1929, (1928)
taaningi, *Diaphus*, *Diaphus*, 1930
taaningi, *Hygophum*, *Hygophum*, 1965
taningi, *Lampanyctus*, *Lampanyctus*, 1931, (1928)
tanakae, *Diaphus*, *Diaphus*, 1913
taylori, *Tarletonbeania*, *Tarletonbeania*, 1953

tenisoni, *Protomyctophum*, *Myctophum*, 1930
tenua, *Tarletonbeania*, *Tarletonbeania*, 1890, (1880)
tenuicauda, ?, *Scopelus*, 1867
tenuiculum, *Gonichthys*, *Myctophum*, 1899
tenuiforme, *Lampanyctus*, *Myctophum*, 1906
termophilus, *Diaphus*, *Diaphus*, 1928
terminata, *Loweina*, *Loweina*, 1964
theta, *Diaphus*, *Diaphus*, 1890
thiollierei, *Diaphus*, *Diaphus*, 1934
thompsoni, *Protomyctophum*, *Electrona*, 1944
thori, *Benthoosema*, *Myctophum*, 1918, (1837)
townsendi, *Ceratoscopelus*, *Myctophum*, 1889
trachops, *Diaphus*, *Diaphus*, 1974
turneri, *Lampanyctus*, *Serpa*, 1934
umbroculus, *Diaphus*, *Diaphus*, 1934
uracocampus, *Lobianchia*, *Scopelus*, 1884, (1838)
urolampus, *Idiolychnus*, *Diaphus*, 1897
uophaos, *Lampadena*, *Lampadena*, 1963
valdiviae, *Notolychnus*, *Myctophum*, 1904
vanhoeffeni, *Diaphus*, *Myctophum*, 1906
venetus, *Gonichthys*, *Gonichthys*, 1964
ventralis, *Electrona*, *Electrona*, 1963
veranyi, *Symbolophorus*, *Scopelus*, 1888
vitazi, *Diaphus*, *Diaphus*, 1961
warmingii, *Ceratoscopelus*, *Scopelus*, 1892
watasei, *Diaphus*, *Diaphus*, 1904
weberi, *Diaphus*, *Diaphus*, 1932, (1928)
whitleyi, *Diaphus*, *Diaphus*, 1934
yaquinae, *Lampadena*, *Dorsadena*, 1972

ALPHABETICAL LIST OF FOSSIL MYCTOPHID SPECIES

acutirostrum, *Myctophidarum* Holec 1975
acutus, *Myctophum*, *Nyctophidarum* Weiler 1959 (Weiler 1968)
aemilianus, *Myctophidarum* Anfossi and Mosna 1972
agatense, *Hygophum* Robba 1970
an, *Myctophum*, *Scopelus* Sulc 1932 (Weiler 1968)
angulatus, *Diaphus* Ohe and Araki 1973
austriacus, *Myctophum*, *Berycidarum* Koken 1891 (Weiler 1968)
appeninicus, *Lampanyctus* Anfossi and Mosna 1971
bartonicus, *Myctophum*, *Scopelus* Shepherd 1916 (Weiler 1968)
biarritzensis, *Myctophum*, *Scopelus* Priem 1912 (Weiler 1968)
biatlanticus, *Symbolophorus*?, *Nyctophum* Weiler 1959 (Fitch 1969)
bolini, *Diaphus*, *Lampanyctus* David 1943 (Fitch 1969)
borneensis, *Scopelidarum* Posthumus 1929
carpaticus, *Myctophidarum* Brzobohaty 1965
cassidiformis, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
circularis, *Myctophum*, *Scopelus* Frost 1924 (Weiler 1968)
columnae, *Myctophum*, *Aspius* Sauvage 1873 (Weiler 1968)
concentricus, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
daimellii, *Nyctophus* d'Erasmus 1930
debilis, *Diaphus*, *Berycidarum* Koken 1891 (Nolf 1977)
dorsalis, *Myctophum*, *Leuciscus* Sauvage 1870 (Weiler 1968)
ecnomi, *Lampanyctus*?, *Aspius* Sauvage 1870 (Weiler 1971)
edwardsi, *Lampanyctus*?, *Rhodeus* Sauvage 1870 (Weiler 1971)
ellipticus, *Myctophum*, *Scopelus* Sulc 1932 (Weiler 1968)
ellipticus, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)

- excavatus*, *Myctophum*, *Scopelus* Sulc 1932 (Smigielska 1966)
excisus, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
frosti, *Myctophum*, *Scopelus* Vorstmann 1927 (Weiler 1968)
germanicum, *Hygophum?* Heinrich 1969
gracile, *Eomyctophum* Daniltshenko 1962
gracilis, *Myctophum* Schubert 1912
hawaii, *Diaphus* Ohe and Araki 1973
incertus, *Myctophum*, *Berycidarum* Priem 1911 (Weiler 1968)
incisus, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
insoletum, *Myctophum*, *Berycidarum* Prochazka 1893 (Smigielska 1966)
intermedius, *Hygophum*, *Hygophus* Weiler 1959 (Fitch 1969)
italicus, *Diaphus* Anfossi and Mosna 1971
kokeni, *Diaphus?*, *Berycidarum* Prochazka 1893 (Nolf 1977)
kongararuensis, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
koraensis, *Protomyctophum-Electrona?*, *Eomyctophum* Daniltshenko 1947 (Fitch pers. comm.)
kuboensis, *Lampanyctus* Ohe and Araki 1973
laminatus, *Myctophum?*, *Scopelus* Frost 1933 (Weiler 1968)
larteti, *Diaphus*, *Leuciscus* Sauvage 1870 (Weiler 1968)
latirostratus, *Myctophum*, *Scopelus* Weiler 1950 (Smigielska 1966)
licatae, *Lampanyctus?*, *Leuciscus* Sauvage 1870 (Weiler 1971)
limicola, *Eomyctophum* Daniltshenko 1960
longirostris, *Myctophidarum* Brzobohaty 1964
makutaensis, *Myctophidarum* Aoka 1971
mammatus, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
marwicki, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
mediterraneus, *Myctophum*, *Berycidarum* Koken 1891 (Smigielska 1966)
meneliticus, *Diaphus* Kalabis 1948
meneri, *Protomyctophum-Electrona?*, *Eomyctophum* Daniltshenko 1947 (Fitch, pers. comm.)
microsoma, *Lampanyctus?*, *Clupea* Sauvage 1870 (Weiler 1971)
mimiensis, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
moravicus, *Myctophum*, *Berycidarum* Prochazka 1893 (Smigielska 1966)
muraii, *Diaphus* Sato 1962
murbani, *Myctophum*, *Scopelus* Weinfurter 1952 (Smigielska 1966)
nanae, *Lampadena* Sato 1962
nicolisi, *Scopeloides* Bassani 1889
obliquus, *Myctophum*, *Scopelus* Weiler 1943 (Weiler 1968)
orbicularis, *Myctophum*, *Apogoninarum* Priem 1906 (Weiler 1968)
roseinum, *Myctophum* Dieni 1968
ovatus, *Scopelus* Stinton 1957
pabloensis, *Myctophum*, *Ceratoscopelus?* Weiler 1959 (Fitch 1969)
papuense, *Myctophum*, *Scopelus* Schubert 1910 (Weiler 1968)
petrolifer, *Lepidophanes*, *Lampanyctus* David 1943 (Fitch 1969)
polygonium, *Myctophum* Aoki 1971
polysarcus, *Diaphus?*, *Leuciscus* Kramberger 1879 (Kalabis 1948)
praerafinesquii, *Diaphus* Weiler 1971
probenoiti, *Hygophum*, *Myctophum* Arambourg 1927 (Weiler 1968)
prolaternatum, *Myctophum* Arambourg 1921
pulcher, *Myctophum*, *Berycidarum* Prochazka 1893 (Weiler 1968)
regulare, *Myctophum* Smigielska 1966
regularis, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
rossiae, *Myctophum* Robba 1970
rotundum, *Hygophum* Ohe and Araki 1973
sauvagei, *Diaphus* Arambourg 1925
serratus, *Lampanyctus* Stinton 1957
shizukuishiensis, *Diaphus* Sato 1962
spinatum, *Myctophum* Aoki 1971
splendidus, *Myctophum*, *Berycidarum* Prochazka 1893 (Smigielska 1966)
sulcatus, *Myctophum*, *Berycidarum* Bassoli 1960 (Weiler 1968)
tenuis, *Myctophum*, *Berycidarum* Schubert 1905 (Weiler 1968)
tuberculatus, *Myctophum*, *Berycidarum* Bassoli 1906 (Weiler 1968)
tutamoensis, *Myctophum*, *Scopelus* Frost 1933 (Weiler 1968)
vastus, *Myctophum* Aoki 1971
vexillifer, *Lampanyctus?*, *Aspius* Sauvage 1870 (Weiler 1971)
weileri, *Ceratoscopelus?* Brzobohaty 1965

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NOTE ADDED IN PROOF

The following new species of fossil Myctophidae based on otoliths have recently been published: *Myctophum unicum*, *Diaphus crassus*, *Gymnocephalus fitchi*, *Hygophum agrigen-tensis*, *Hygophum? orcianensis*, and *Electrona anfossimosnai* by Schwarzahans, W., 1978, Otolithen aus dem Unter-Pliozän von Süd-Sizilien und aus der Toscana. *Berliner geowiss. Abh.*, (A)8:1–52.

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CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

SIZE VARIATION IN FOOT ELEMENTS OF *BISON* FROM RANCHO LA BREA

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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

Prior to November 30, 1973, publications of the Natural History Museum have appeared under various titles — *Leaflet Series*, *Museum Graphic*, *Education Series*, *History Series*, *Science Series*, *Study Guides*, *Contributions in History*, *History Bulletin*, *Science Bulletin*, unnumbered catalogs of exhibitions, and other miscellaneous publications.

The publication program of the Natural History Museum continues to publish a series of reports that give accounts of new discoveries in history and science as well as new advances in museum knowledge. The theme of the Natural History Museum serials will emphasize basic research through the continuing active series:

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Edward Ostermeyer
Editor

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SIZE VARIATION IN FOOT ELEMENTS OF *BISON* FROM RANCHO LA BREA¹

By Wade E. Miller² and Jack D. Brotherson³

ABSTRACT: Measurements, in the form of statistical summaries, are given for the foot elements of all available specimens of *Bison antiquus* and *Bison ? latifrons* from the Rancho La Brea collection at the Natural History Museum of Los Angeles County. These elements show only moderate variability in measurements, and variability in morphology seems generally slight. Sexual dimorphism appears in only the metacarpal. Rare *Bison ? latifrons*' metapodials can possibly, but not easily, be distinguished from those of *B. antiquus*.

INTRODUCTION

Foot bones probably represent the most commonly recovered bison fossils in Rancho La Brea; therefore, it is desirable to furnish data on one of the largest known collections. This paper provides data on the size variability for a very large sample of foot elements of *Bison antiquus* (recognized as *B. bison antiquus* by Flerov 1967) as well as limited information on *B. ? latifrons*. Foot bones studied include carpals, tarsals, metacarpals, metatarsals and phalanges of both front and hind feet. The carpal, tarsal, metapodial and phalanx data are summarized in Table 1. All available specimens from the Rancho La Brea collection at the Natural History Museum of Los Angeles County were used in the present study.

Although the Rancho La Brea fauna has been known for many years, only a few of its taxa have actually been thoroughly studied. The bison included in this fauna are mentioned in numerous scientific articles, including the general Rancho La Brea faunal paper by Stock (1968), but a comprehensive study has not yet been made. Miller (1971) gave measurements of a few Rancho La Brea bison skeletal elements, including some foot bones, in comparison with bison from Costeau Pit in southern California.

The Rancho La Brea sample of *Bison antiquus* ranks among the largest assemblages of fossil *Bison* from any presently described locality. Skinner and Kaisen (1947, p.131) discussed the Alaskan collections of bison in which over 1,200 individuals are present. However, many different sites were evidently involved and four species were included. Skinner and Kaisen did not separate these species in their tables for Alaskan fossil bison metapodials, the only postcranial bones they measured.

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tory Museum of Los Angeles County, for permission to study the bison material presented in this paper. The senior author enlisted the aid of Dr. Jack D. Brotherson as biometrician and co-author. Appreciation for assistance in mathematical computations is extended to Mr. Gary Heaston of Brigham Young University. Miss Jill Olsen of Brigham Young University drew figures of the foot bones.

METHODS

With the exception of sesamoids, all available foot bones of bison (carpals, tarsals, metapodials and phalanges) from the Rancho La Brea fauna at the Natural History Museum of Los Angeles County were studied. 2,756 bones representing all 15 foot elements were measured and are statistically summarized in Table 1 (individual measurements taken for each bone, which includes specimen number, pit number from which specimens were obtained and depths of recovery, are not given here due to bulk, but they are currently on file in the Earth Sciences Division at the above museum). Figures 10 through 24 show precisely where each measurement was taken. Only adult specimens were considered in this study. Epiphyseal fusion, definition of processes and bone density were used in determination of maturity.

Means, standard deviations and coefficients of variation (Ostle 1963) were computed on all measurements taken (Table 1). Histograms (Figs. 1 and 2) and scatter diagrams (Figs. 3-9) were

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constructed for metacarpals and metatarsals as these bones permitted the greatest possible absolute disparity in measurements and might most readily reflect sexual dimorphism and/or presence of more than one species. The Kolmogorov-Smirnoff test (Ostle 1963) was run on these elements in order to determine whether normality in distribution patterns existed. Should they occur in the Rancho La Brea fauna, *Bison latifrons*' metapodials would presumably be among the longest and almost certainly would be the most robust. Correlation analysis (Ostle 1963) was employed in order to determine which combination of metapodial measurements (Table 2) would be most ideal in constructing the scatter diagrams (some elements have identical coordinates in these diagrams but have been shown as contiguous dots for discernment). Discriminant analysis (Klecka 1975) was used to ascertain whether the bones thought to represent a second species could be independently classified. An S-360 Mod. 65 I.B.M. computer was used in both correlation and discriminant analysis.

RESULTS AND DISCUSSION

Visual inspection of the 2,756 bison foot bones examined showed only minor morphologic variations, mostly in the shapes of articular surfaces and processes. According to Skinner and Kaisen (1947, p. 134-135), isolated *Bison* metapodials can be sexed on the relative heaviness of shafts. However, sexual dimorphism is not clearly evident on this basis as seen in figures 3 through 9. It may be present in the metacarpals as evinced in the bimodal length distribution (Fig. 1) but not in metatarsals (Fig. 2). The Kolmogorov-Smirnoff test (Ostle 1963) was run on all specimens included in these two figures at the 0.01 significance level. It showed a condition of normality for the distribution of metatarsals but one of non-normality for the metacarpals. Male bison might have been relatively larger in their forequarters than females to present a more formidable image when facing any threat, intraspecific or otherwise. According to Guthrie (1970, p.10), bison, presumably only males, use a frontolateral display when confronting other members of the species in an attempt to intimidate. This could help account for sexual dimorphism appearing in the metacarpals but not in the metatarsals. One disturbing factor in the supposed sexual dimorphism of the metacarpals is the ratio between males and females. Males, as interpreted from the histogram (Fig. 1), are approximately three-fourths as abundant as females. Thirty eight complete and partial skulls in the Rancho La Brea collection at the Natural History Museum of Los Angeles County indicate that males are less than half as abundant as females, 11 to 27. If the interpretation of the above histogram is correct, the discrepancy in the male-female ratio between metacarpals and skulls might be due to the relatively small sample size of the skulls, an unknown bias in the accumulation of the respective elements, or bias in the selection of skulls for loans or exchanges with other institutions. The male-female ratio in herds of the Recent bison is not given in most published literature. Also, statements conflict as to the composition of small bands which comprise or comprised major herds. For example Allen (1876, p. 57) stated that at no time of the year did the sexes form separate herds, while Mc Hugh (1972, p.156-157) and Meagher (1973, p. 46) both reported that they did. The only known sex ratios on bison are from modern herds. Meagher (1973, p. 56-60) related that in the Yellowstone population, which has been left in a wild state since

the 1930's, the male-female ratio is variable depending upon age. She reported that there are more males than females in some age groups, while the reverse is true for others; with females slightly exceeding males in the overall population. Mr. Kendall Nelson (1976, personal communication), of the Utah Wildlife Division, indicated that the small state herd of bison (now about 200 individuals) has a sex ratio of 1.2 cows per bull. This herd has been left in a wild condition since its introduction into Utah in the 1940's. The sex ratio interpreted from Rancho La Brea *Bison* metacarpals is roughly similar to that found in living herds of bison.

A complicating factor in the present study is the possible inclusion of *Bison latifrons*' foot elements. As previously reported (Wyman 1926; Miller 1968), this giant bison existed as a rare component of the Rancho La Brea fauna. Schultz and Hillerud (1977) evidently did not accept the possibility of *Bison latifrons*' presence at Rancho La Brea. They commented (p.104) on Miller reporting (1968) this species from the Rancho La Brea fauna and stated that the specimens were probably large *B. antiquus*, similar to *B. antiquus barbouri*. However, they did not mention Wyman's report (1926) of a *B. latifrons*' skull from Rancho La Brea which had a six foot horn core spread. Also, Miller gave (1971) additional information on the probability of *Bison latifrons* from Rancho La Brea to which Schultz and Hillerud made no reference. The presence of *B. latifrons* at Rancho La Brea is further strengthened by LACM HC 6013, a distal horn core fragment, which has not previously been reported. This fragment, which measures 233 mm along its outer curvature, falls within the variation noted for *B. latifrons* but not *B. antiquus*. Recorded data indicate that this specimen was recovered from pit 4 between 11 and 12 feet below ground level. Unpublished radio-carbon dates for pit 4 on file at the Natural History Museum of Los Angeles County indicate a time range from approximately 13,000 years B.P. to 35,000 years B.P. based on both wood and collagen. The depths from which dated *Bison ?latifrons* samples were collected range from 5 to 23.5 feet. The scatter diagrams given in this paper (Figs. 3-9) show a few individuals, indicated by lettered dots, which may represent this species. Surprisingly, the presumed *B. ?latifrons*' metapodials are not the longest ones. Discriminant analysis showed, however, that they can be classified as a distinct group. This analysis revealed that 100% of both the metacarpals and metatarsals of possible *Bison latifrons* were properly grouped as shown by the scatter diagrams. It also showed that the groupings of *B. antiquus*' metacarpals and metatarsals were, respectively, 97% and 89% correctly placed (Table 2 gives means and standard deviations for metapodial measurements relating to these two bison groups). the discriminant analysis further verified the importance of some metapodial parameters over others in distinguishing *B. antiquus* from *B. latifrons*. The most discriminating measurements for the metacarpals in order of importance are: greatest transverse width of distal end, least anteroposterior width of shaft, least transverse width of shaft and greatest transverse width of proximal end; and for the metatarsals, greatest transverse width of distal end, greatest length, greatest anteroposterior width of proximal end and greatest anteroposterior width of distal end. All the above parameters were shown to be significant at the 0.01 level. Carpals, tarsals and phalanges, because of smaller disparity in measurements, apparently do not allow distinctions to be made between *Bison latifrons* and *B. antiquus*.

A major purpose of this study is to provide a basic data base

which will show proportions as well as size. This will become more significant with the planned study of additional bison postcranial elements from Rancho La Brea. Previously it was suggested (Miller 1971, p. 29) that the body proportions of *Bison antiquus* differed from those of *B. ? latifrons*. Further research still needs to be done to confirm this, although some proportions of the metapodials do suggest distinctions as noted above. Examples of proportional body differences exist among modern bison species, as the European bison (the wisent), *B. bonasus*, is distinctly longer limbed and has a larger pelvis than the more massive American form, *B. bison*.

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TABLE 1
 Statistical summary of *Bison* foot elements from Rancho La Brea (in mm).

	N	OR	X	s	s/X	s-X
METACARPAL	76					
1. Greatest length		205-235	221.22	7.02	0.03	0.81
2. Greatest anteroposterior width of proximal end		39-57	45.00	2.85	0.06	0.33
3. Greatest transverse width of proximal end		65-94	76.99	4.95	0.06	0.57
4. Least anteroposterior width of shaft		27-36	30.24	1.57	0.05	0.18
5. Least transverse width of shaft		38-59	47.59	3.41	0.07	0.39
6. Greatest anteroposterior width of distal end		37-49	42.69	2.27	0.05	0.26
7. Greatest transverse width of distal end		70-94	79.03	4.78	0.06	0.55
CALCANEUM	80					
1. Greatest length		155-201	173.21	7.77	0.04	0.87
2. Greatest height across sustentacular facet		59-75	65.79	3.55	0.05	0.40
3. Greatest overall height		64-76	68.88	3.40	0.05	0.38
ASTRAGALUS	143					
1. Greatest length		80-97	88.15	3.79	0.04	0.32
2. Greatest transverse diameter		50-67	58.06	3.31	0.06	0.28
3. Greatest anteroposterior diameter		46-59	50.47	2.52	0.05	0.21
NAVICULAR-CUBOID	146					
1. Greatest anteroposterior diameter		62-82	70.27	3.76	0.05	0.31
2. Greatest transverse diameter		64-85	72.01	4.07	0.06	0.34
3. Greatest height		52-77	63.76	4.10	0.06	0.34
MESO-ECTOCUNEIFORM	101					
1. Greatest anteroposterior diameter		42-54	47.65	2.55	0.05	0.25
2. Greatest transverse diameter		26-37	30.79	1.88	0.06	0.19
3. Greatest height		18-25	19.93	1.38	0.07	0.14
PISIFORM	67					
1. Greatest anteroposterior diameter		30-42	35.06	2.16	0.06	0.26
2. Greatest transverse diameter		20-31	23.81	2.36	0.10	0.29
3. Greatest height		31-42	34.28	2.26	0.07	0.28
CUNEIFORM	113					
1. Greatest anteroposterior diameter		27-40	31.90	2.83	0.09	0.27
2. Greatest transverse diameter		47-65	54.88	3.45	0.06	0.32
3. Greatest height		37-56	45.13	3.84	0.09	0.36
LUNAR	158					
1. Greatest anteroposterior diameter		50-71	57.51	3.74	0.07	0.30
2. Greatest transverse diameter		34-46	38.56	2.42	0.06	0.19
3. Greatest height		35-51	40.94	2.87	0.07	0.23
SCAPHOID	125					
1. Greatest anteroposterior diameter		50-68	56.33	3.73	0.07	0.33
2. Greatest transverse diameter		30-44	35.35	2.68	0.08	0.24
3. Greatest height		36-50	40.58	2.72	0.07	0.24
UNCIFORM	109					
1. Greatest anteroposterior diameter		36-51	42.18	2.86	0.07	0.27
2. Greatest transverse diameter		35-47	39.40	2.50	0.06	0.24
3. Greatest height		28-36	31.70	1.81	0.06	0.17

MAGNUM	126					
1. Greatest anteroposterior diameter		40-52	45.29	2.59	0.06	0.23
2. Greatest transverse diameter		42-60	48.47	3.50	0.07	0.31
3. Greatest height		25-33	28.14	1.74	0.06	0.16
METATARSAL	64					
1. Greatest length		258-287	271.45	6.71	0.02	0.84
2. Greatest anteroposterior width of proximal end		54-74	61.30	3.76	0.06	0.47
3. Greatest transverse width of proximal end		55-68	60.58	3.16	0.05	0.39
4. Least anteroposterior width of shaft		34-40	36.00	1.58	0.04	0.20
5. Least transverse width of shaft		33-48	39.34	2.95	0.07	0.37
6. Greatest anteroposterior width of distal end		39-49	43.11	2.01	0.05	0.25
7. Greatest transverse width of distal end		67-83	73.03	3.70	0.05	0.46
ANTERIOR PROXIMAL PHALANX	282					
1. Greatest length		63-82	72.60	5.22	0.07	0.31
2. Greatest anteroposterior diameter		37-51	43.02	3.17	0.07	0.19
3. Greatest transverse diameter		36-48	41.62	2.48	0.06	0.15
POSTERIOR PROXIMAL PHALANX	279					
1. Greatest length		64-85	74.95	3.46	0.05	0.21
2. Greatest anteroposterior diameter		36-48	41.43	2.21	0.05	0.13
3. Greatest transverse diameter		30-49	36.94	2.33	0.06	0.14
MEDIAL PHALANX	555					
1. Greatest length		43-60	49.94	2.93	0.06	0.12
2. Greatest anteroposterior diameter		30-49	38.69	2.98	0.08	0.13
3. Greatest transverse diameter		30-50	38.57	3.29	0.09	0.14
UNGUAL PHALANX	337					
1. Greatest length		70-101	85.65	6.14	0.07	0.33
2. Greatest transverse diameter		27-41	33.15	2.60	0.08	0.14

Points of measurement shown in Figures 10-24

N = number of specimens s = standard deviation
OR = observed range s/X = coefficient of variation
X = mean s-X = standard deviation of the mean

TABLE 2

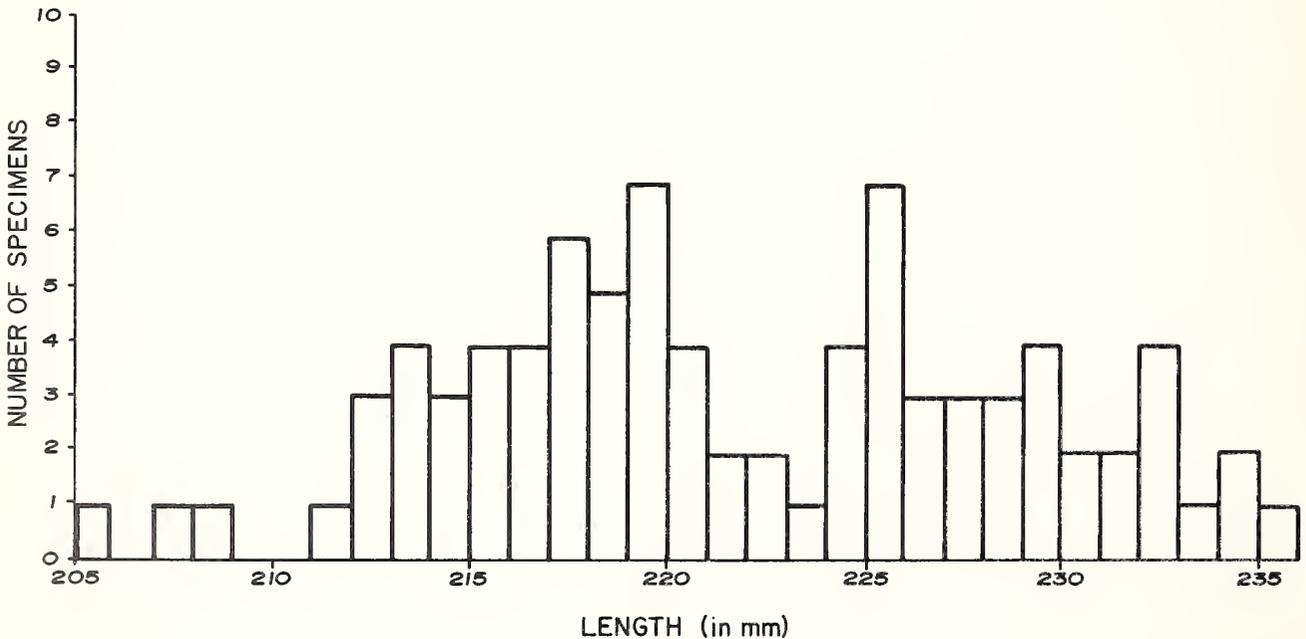
Means and standard deviations of *Bison antiquus* and *Bison ? latifrons* metapodials from Rancho La Brea (in mm).

	METACARPALS					
	<i>Bison antiquus</i>			<i>Bison ? latifrons</i>		
	N	X	s	N	X	s
1. Greatest length	69	220.51	6.79	7	228.28	5.41
2. Greatest anteroposterior width of proximal end		44.59	2.40		49.00	3.96
3. Greatest transverse width of proximal end		76.07	4.01		86.00	4.51
4. Least anteroposterior width of shaft		29.94	1.12		33.14	1.86
5. Least transverse width of shaft		46.94	2.71		54.00	3.00
6. Greatest anteroposterior width of distal end		41.65	5.41		46.86	1.35
7. Greatest transverse width of distal end		78.06	3.59		88.57	4.72
	METATARSALS					
	59			5		
1. Greatest length		271.41	6.82		271.45	6.28
2. Greatest anteroposterior width of proximal end		60.69	3.21		67.17	3.92
3. Greatest transverse width of proximal end		60.10	2.81		65.17	2.72
4. Least anteroposterior width of shaft		35.90	1.59		37.00	1.26
5. Least transverse width of shaft		38.93	2.52		43.33	3.98
6. Greatest anteroposterior width of distal end		42.95	2.00		44.67	2.01
7. Greatest transverse width of distal end		72.34	2.81		79.67	3.70

N = number of specimens

X = mean

s = standard deviation

FIGURE 1. Length-frequency histogram of *Bison* metacarpals from Rancho La Brea.

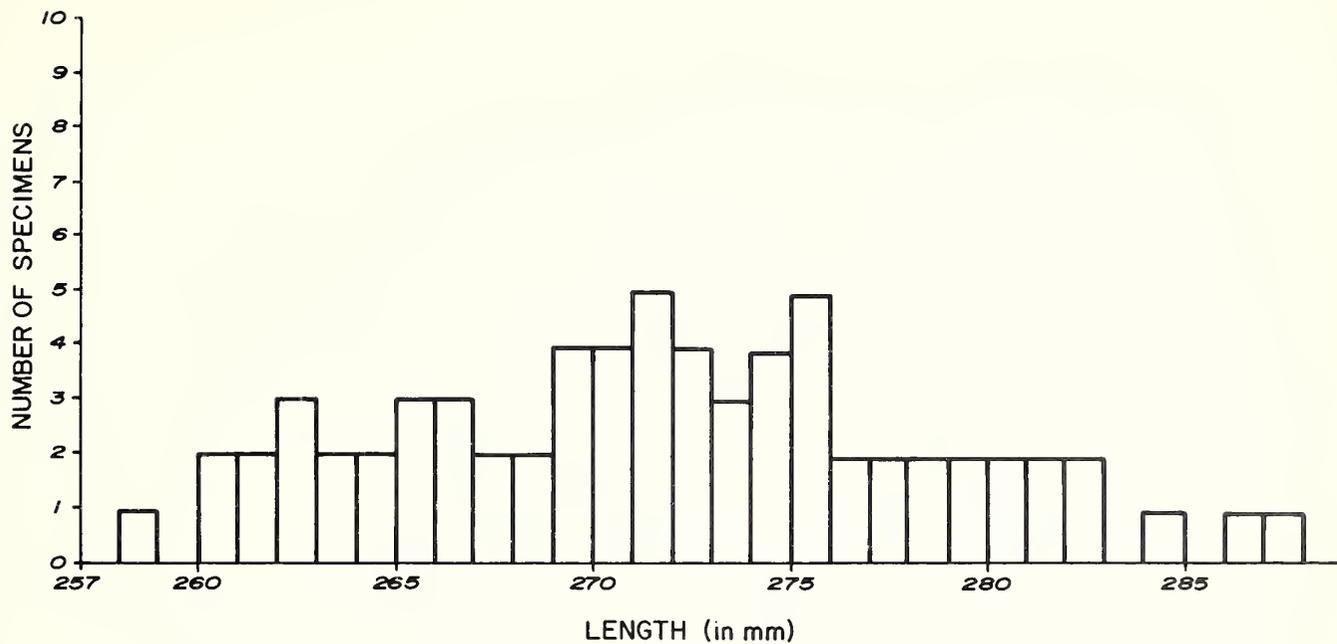


FIGURE 2. Length-frequency histogram of *Bison* metatarsals from Rancho La Brea.

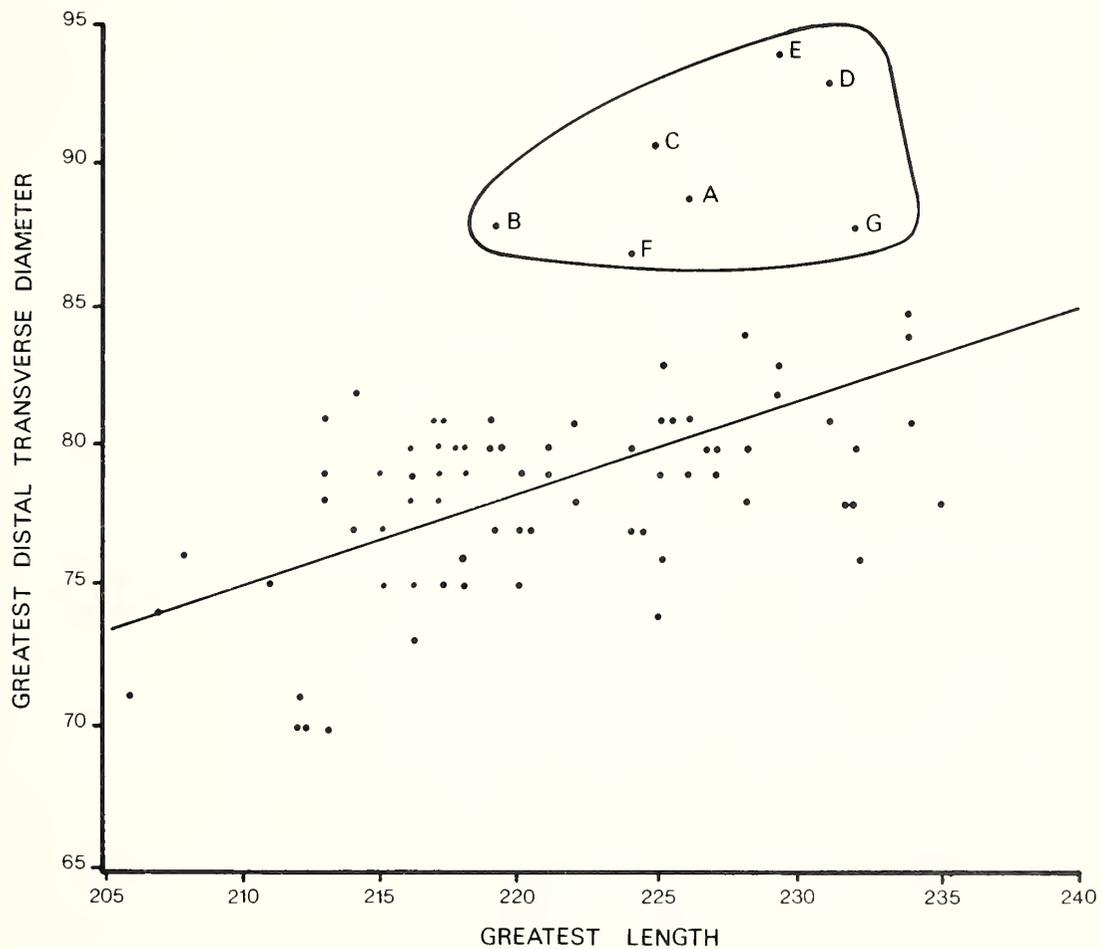


FIGURE 3. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

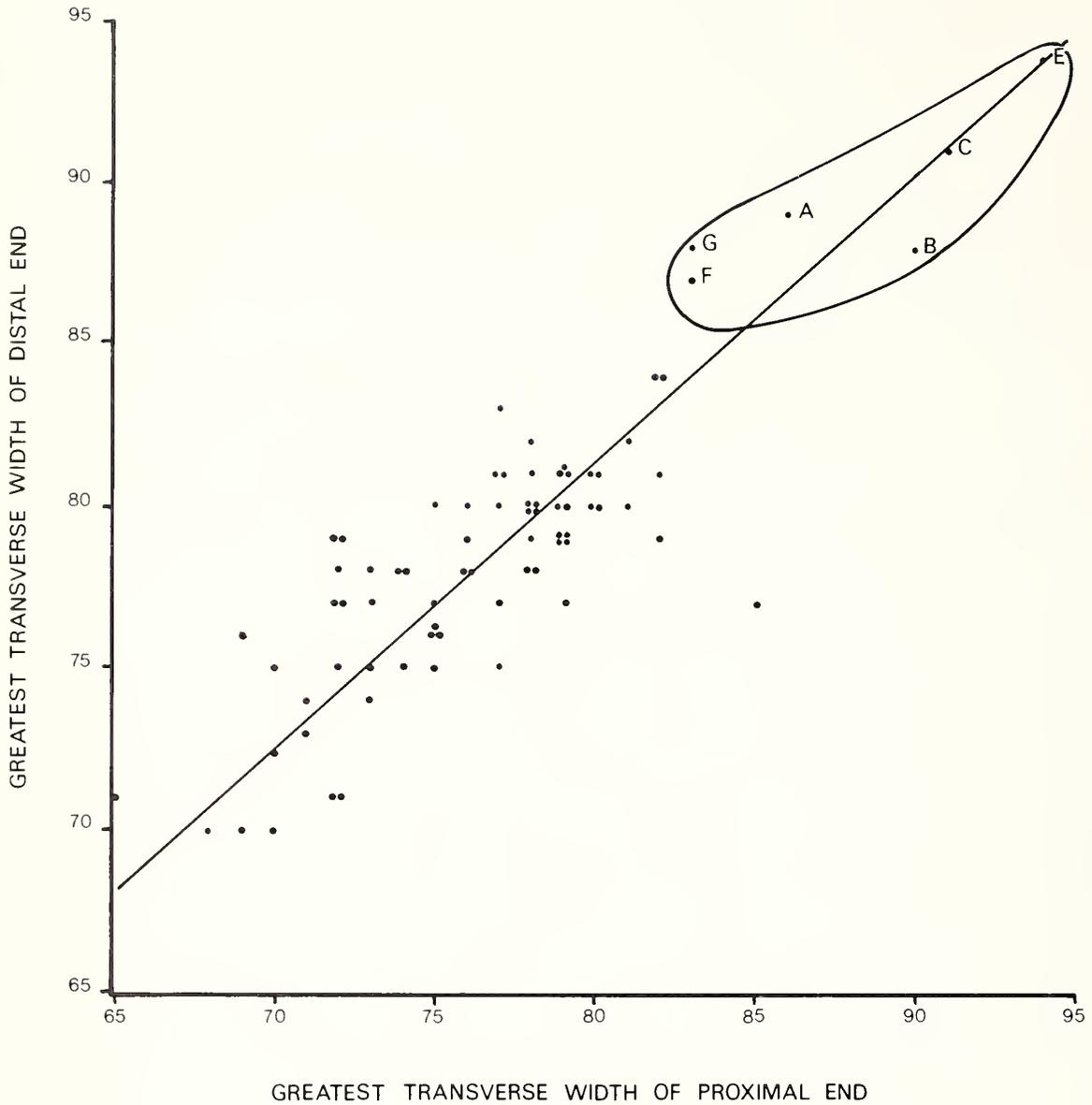


FIGURE 4. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

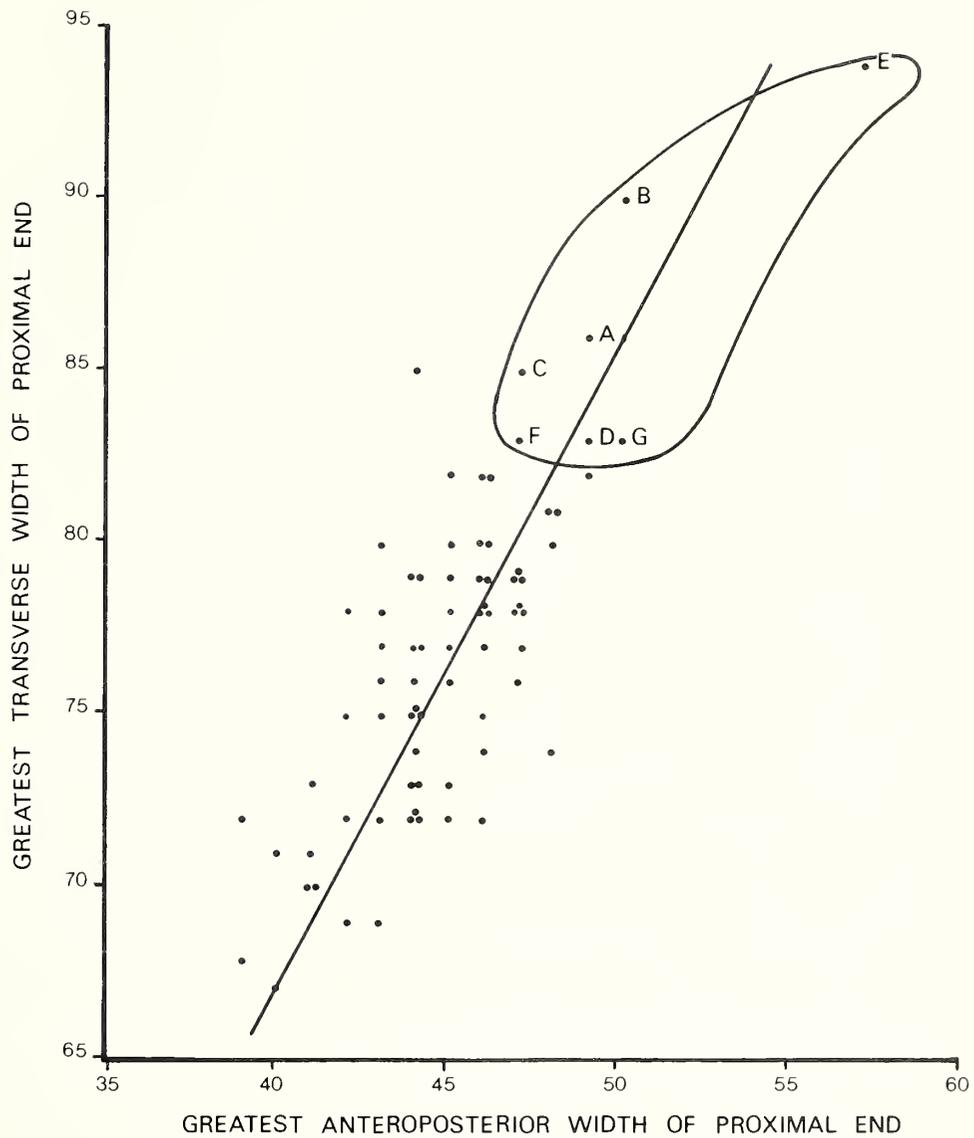


FIGURE 5. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

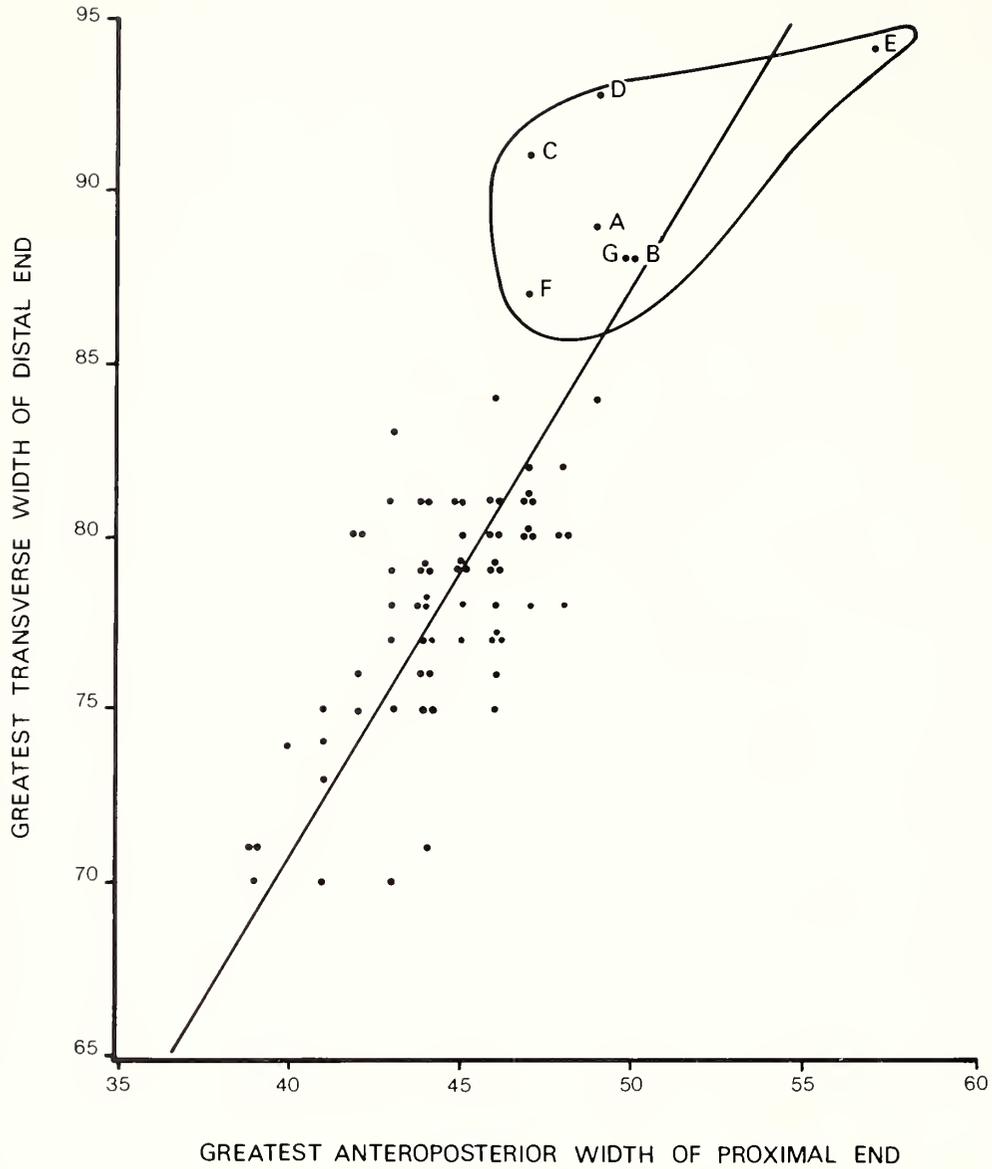


FIGURE 6. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

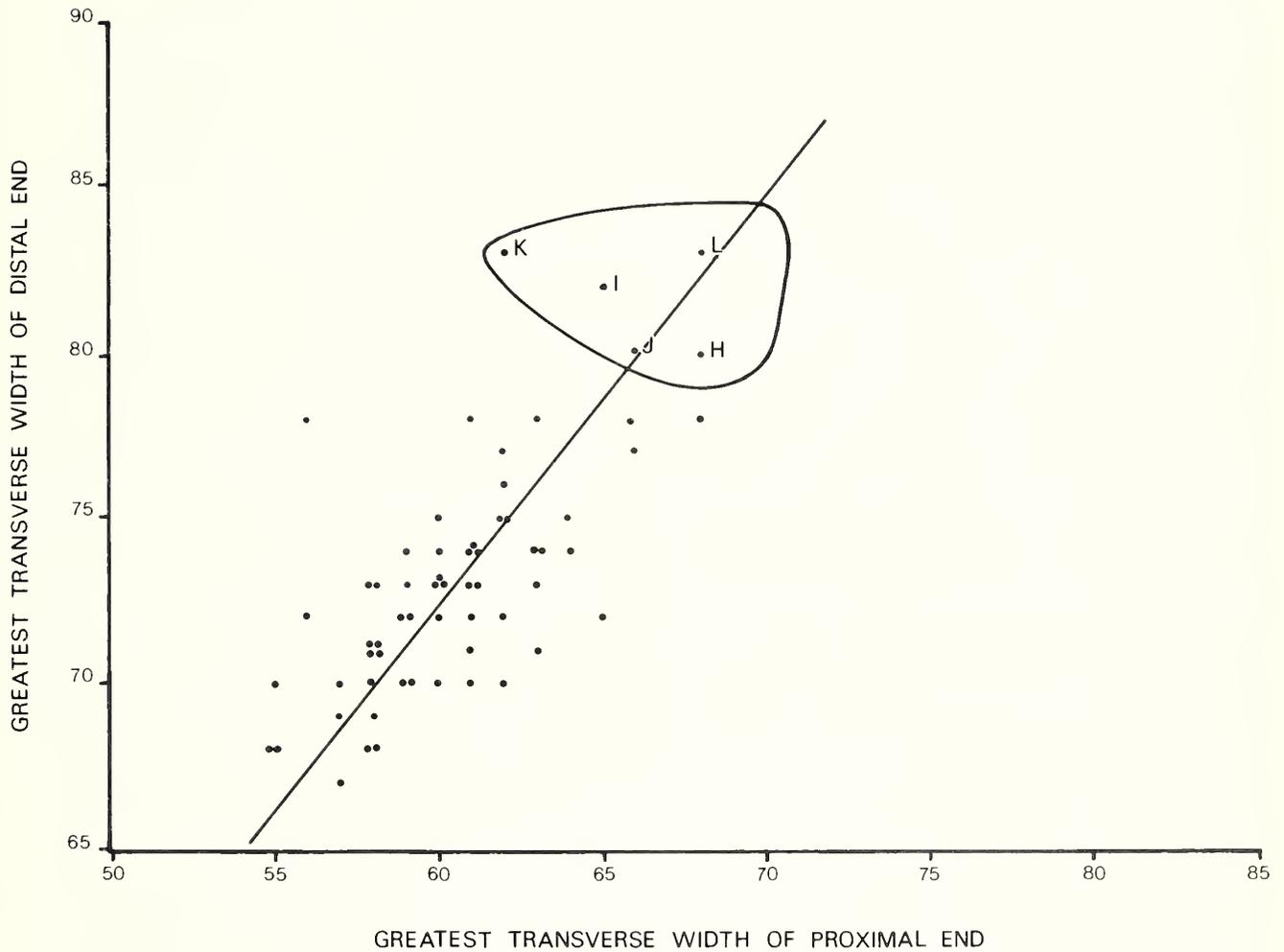


FIGURE 7. Bivariate scatter diagram of *Bison* metatarsals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

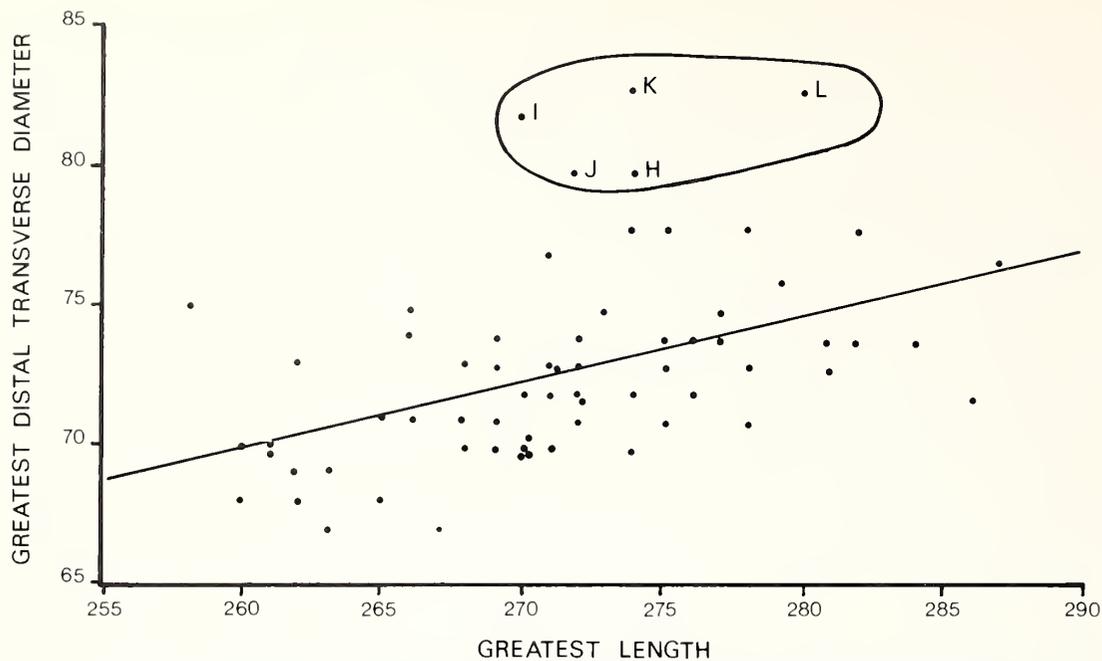


FIGURE 8. Bivariate scatter diagram of *Bison* metatarsals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

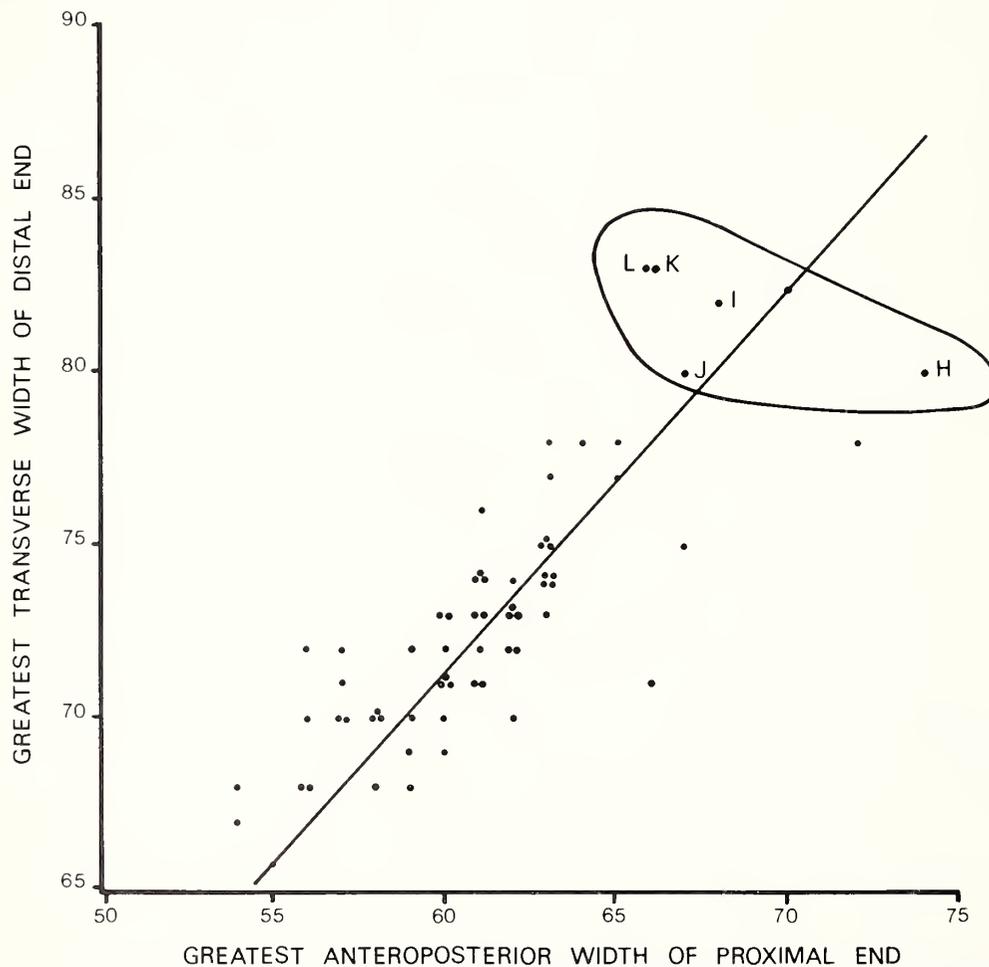


FIGURE 9. Bivariate scatter diagram of *Bison* metatarsals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

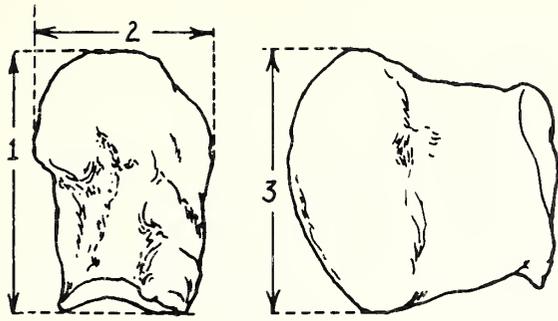


FIGURE 10. *Bison antiquus* pisiform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

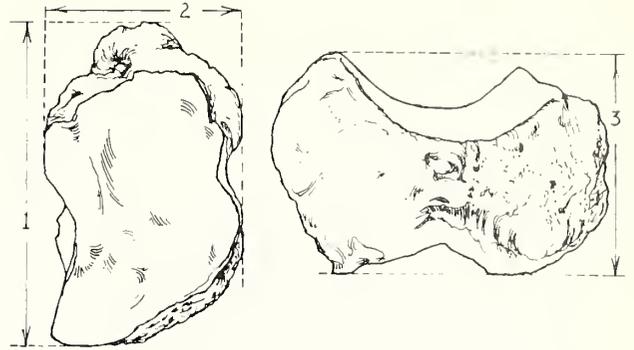


FIGURE 13. *Bison antiquus* scaphoid (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

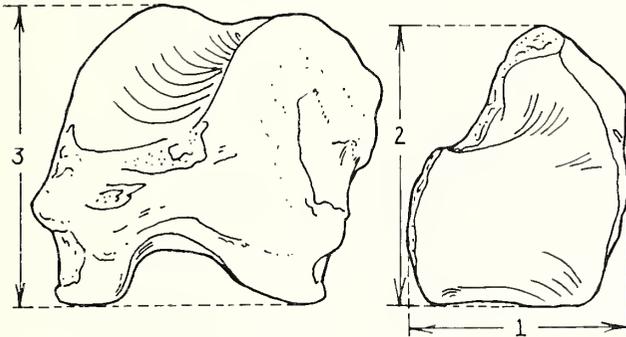


FIGURE 11. *Bison antiquus* cuneiform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

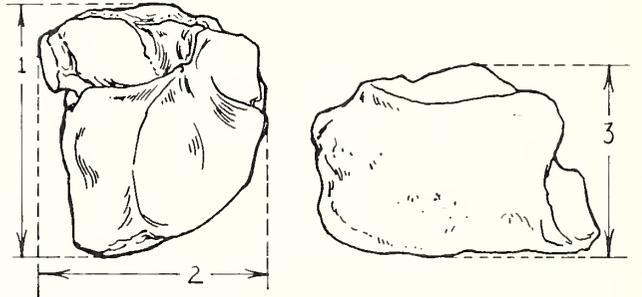


FIGURE 14. *Bison antiquus* unciform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

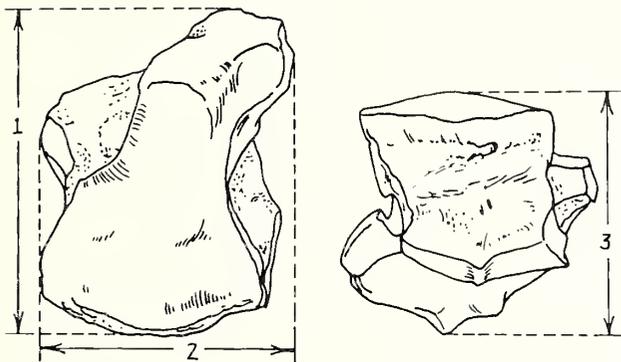


FIGURE 12. *Bison antiquus* lunar (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

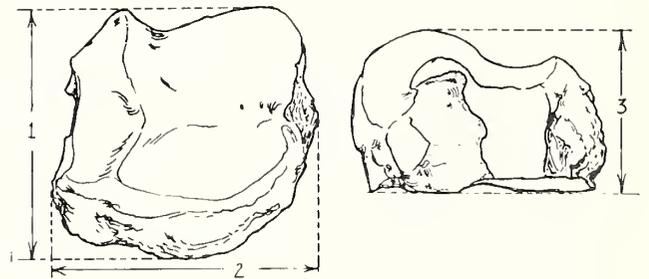


FIGURE 15. *Bison antiquus* magnum (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

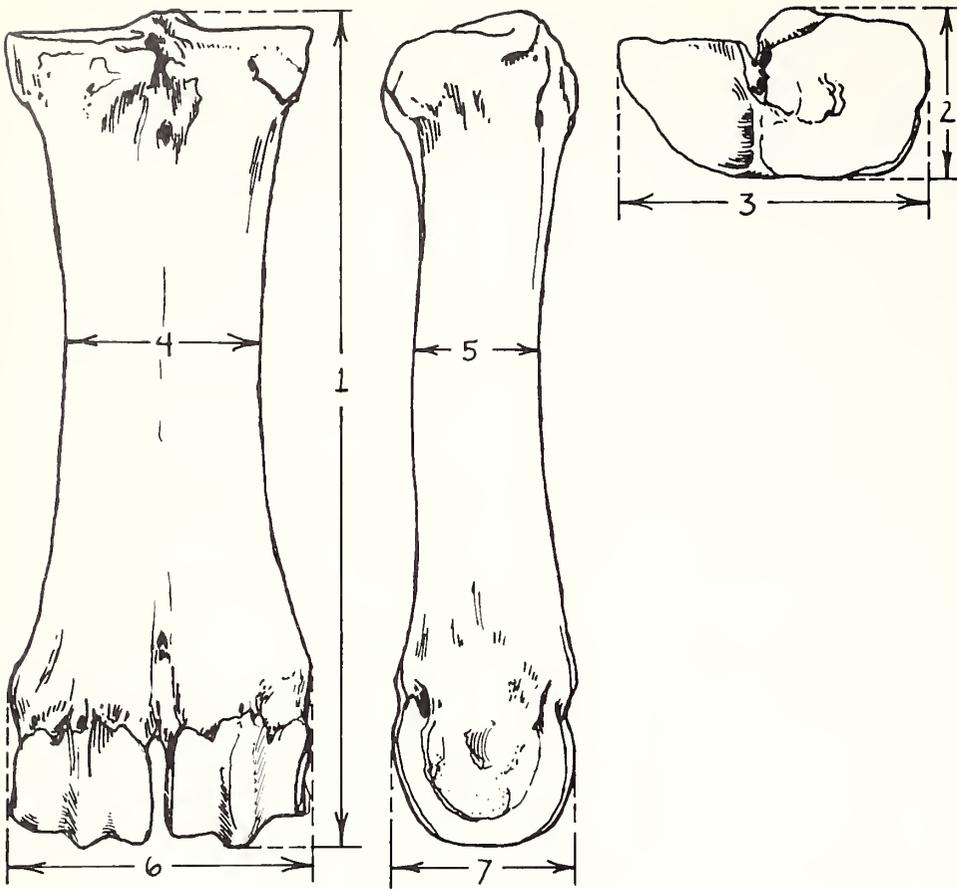


FIGURE 16. *Bison antiquus* metacarpus (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

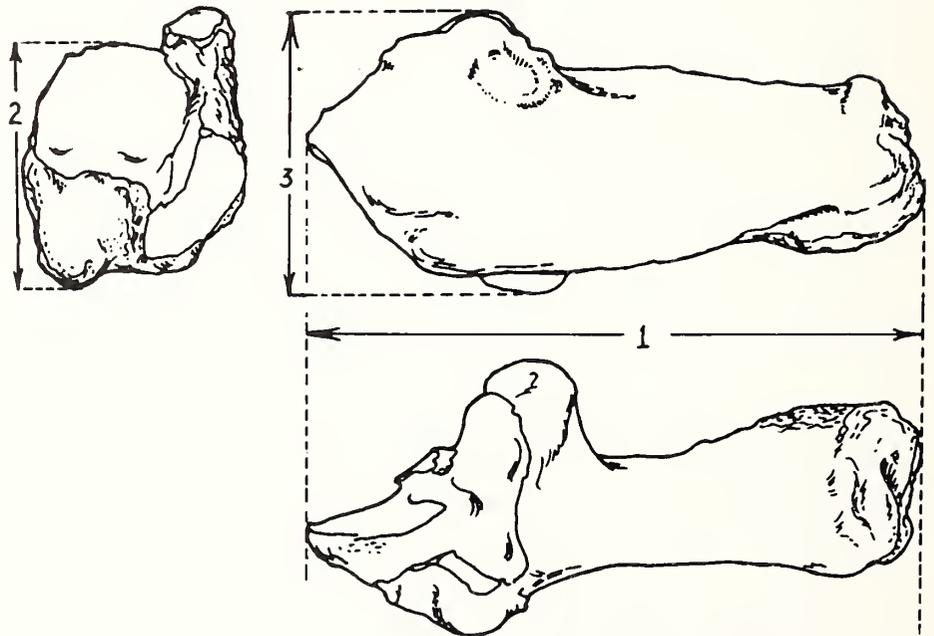


FIGURE 17. *Bison antiquus* calcaneum (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

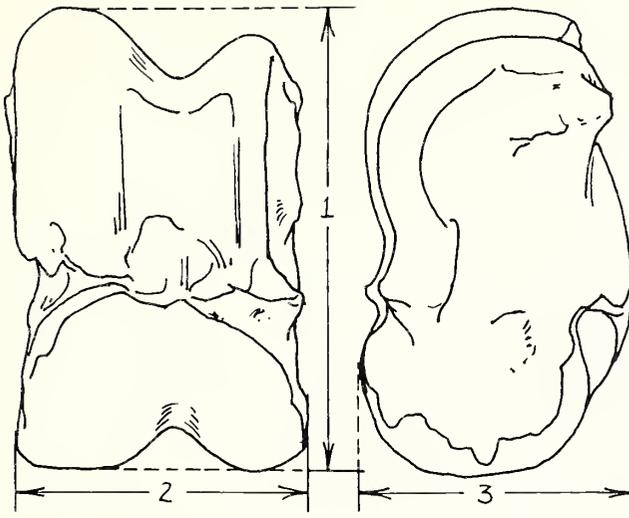


FIGURE 18. *Bison antiquus* astragalus (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

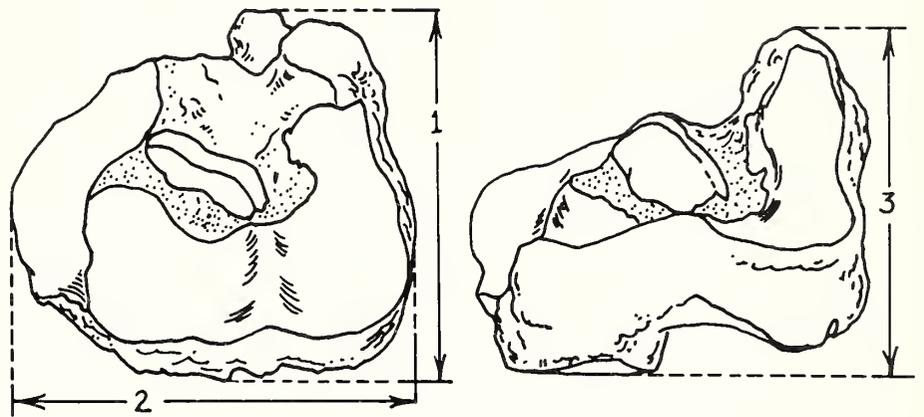


FIGURE 19. *Bison antiquus* navicular-cuboid (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

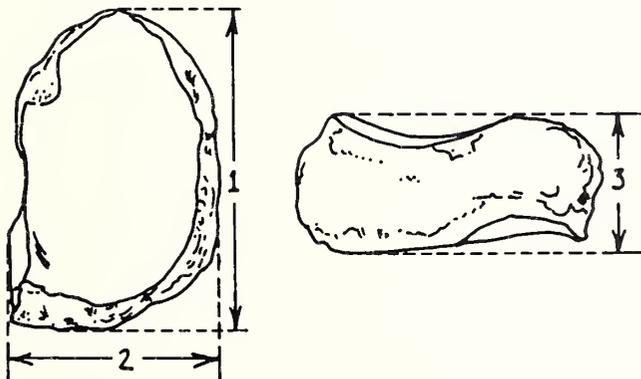


FIGURE 20. *Bison antiquus* meso-ectocuneiform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

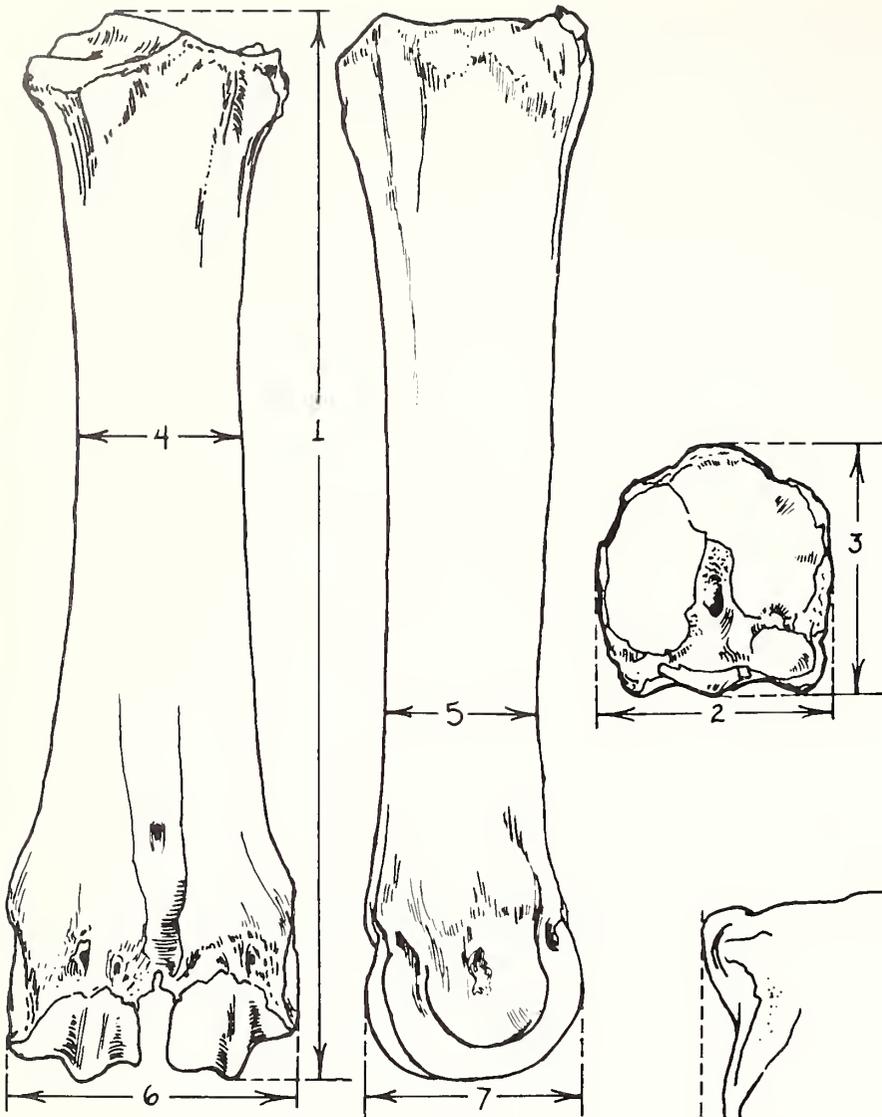


FIGURE 21. *Bison antiquus* metatarsus (not to scale). Numbers on drawing correspond to measurements on Table I. Approximate measurements are given in parentheses.

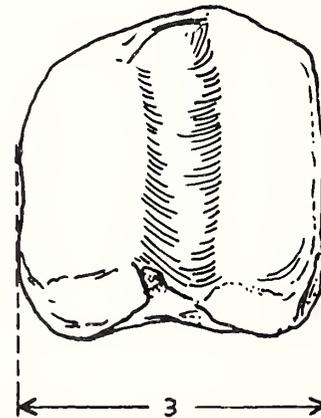
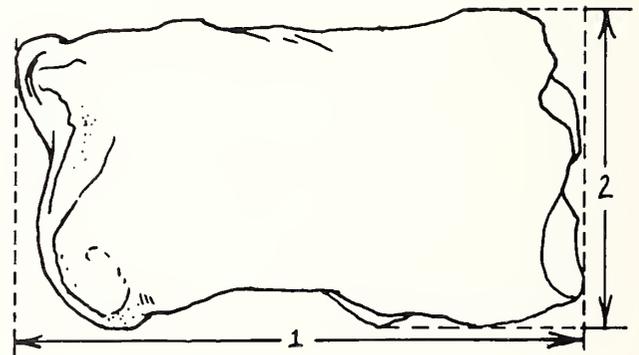


FIGURE 22. *Bison antiquus* proximal phalanx (not to scale). Numbers on drawing correspond to measurements on Table I. Approximate measurements are given in parentheses.

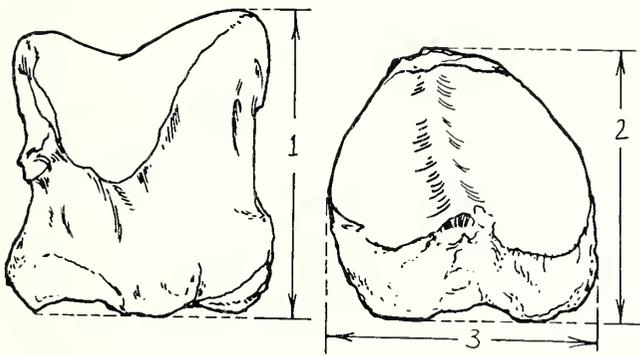


FIGURE 23. *Bison antiquus* medial phalanx (not to scale). Numbers on drawing correspond to measurements on Table I. Approximate measurements are given in parentheses.

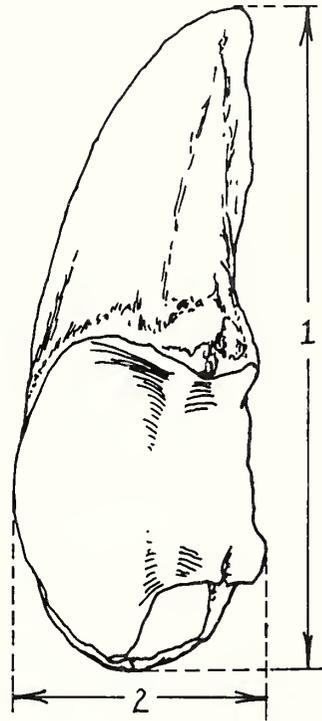


FIGURE 24. *Bison antiquus* ungual phalanx (not to scale). Numbers on drawing correspond to measurements on Table I. Approximate measurements are given in parentheses.

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