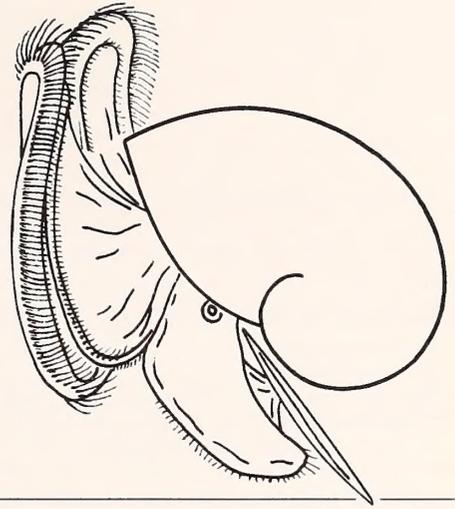




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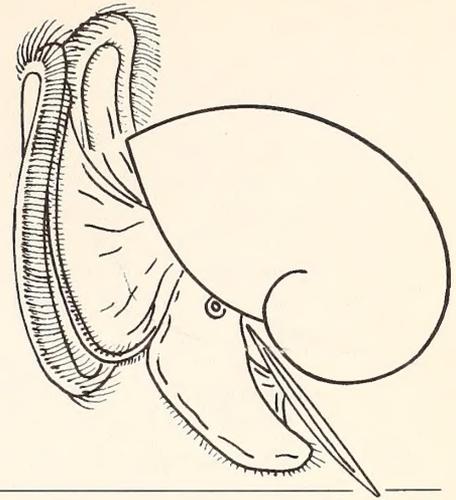
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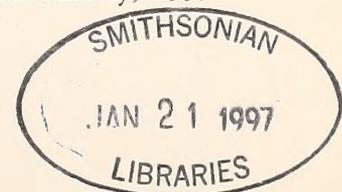
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THE VELIGER

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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Inventorying the Molluscan Diversity of the World: What Is Our Rate of Progress?

by

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Abstract. Levels and trends in the naming of new mollusk species over the last 30 years are reviewed through analysis of a sample of 12,561 names extracted from nine volumes of *Zoological Record*. On average, 1395 new species-group mollusks are being named each year, of which 69% are fossils (average yearly increment: 366 Recent gastropods, 292 fossil gastropods, 42 Recent bivalves, 316 fossil bivalves, 320 fossil cephalopods, and 59 other Recent and fossil mollusks). Using a smaller sample of 1996 names, the synonymy ratio of Recent taxa is calculated to be 1.6, i.e., about 265 new valid species are named each year. Over the past 25 years, the number of new marine species described each year has increased by 68%, whereas the number of new non-marine species has decreased by 15%. The most significant decrease concerns tropical continental faunas. Possibly as many as half of the new descriptions of Recent species are by people not funded for this purpose, with amateurs authors of 28% of the descriptions. The United States has the most active scientific professional and non-professional community, being responsible for over 20% of new Recent species. Nearly half of the new species worldwide are described in malacological journals. With a collecting effort of marine mollusks increased by several orders of magnitude in the last few decades, there is no sign of leveling off in the inventory of molluscan diversity. For the foreseeable future, micromollusks, the deep-sea, and the marine and non-marine tropics will remain effectively inexhaustible reservoirs of undescribed species. From a conservation perspective, the loss of knowledge of and attention to tropical land and freshwater faunas is dramatic, considering loss of habitat and extinction.

INTRODUCTION

In this age of shrinking natural habitats and an unprecedented extinction crisis (Ehrlich, 1995), biodiversity has become a buzzword of grant applications and conservation programs. The baseline for all biodiversity studies is an inventory of the species that inhabit this planet and where they live, a goal that has been championed by projects such as Systematics Agenda 2000 (Anonymous, 1994). Whereas birds, and to a lesser extent mammals, are now virtually completely inventoried, the diversity of invertebrates is still far from being adequately surveyed. A significant part of malacological research effort continues to involve alpha-taxonomy and descriptions of new species.

In the present paper, I address the question of how malacologists are achieving the goal of global species inventories? Which areas of the world are receiving most, and least, attention? Which national communities are most active in this research effort? I first address these questions through a quantitative analysis of descriptions of new species. In a more qualitative approach, I summarize what

have been the major fronts in the last decades. In conclusion, I discuss where I believe our efforts should go to in the next few decades.

METHODS

I have used the *Zoological Record* (hereafter *ZR*) to extract data on descriptions of new species-group taxa, their geographical and stratigraphical location, and the type of publication outlet containing the description. As a representation of research activity, I have sampled sets of 2 consecutive years in the 1960, 1970, 1980, and 1990 decades, as they are recorded by *ZR*: volumes 104 (1967) and 105 (1968); volumes 114 (1977) and 115 (1978); volumes 124 (1987) and 125 (1988); volumes 129 (1992) and 130 (1993). The year 1978 was found to deviate anomalously (and inexplicably) from other years in having a considerably higher number of fossil species described, therefore data were researched for *ZR* volume 116 (1979) to balance, if necessary, the effect of 1978.

I am here using the word species as an equivalent of

Table 1

Numbers of new species of Recent and fossil mollusks described during 9 sample years. Source: Zoological Record.

	Fossil	Recent	Total
1967	1102	396	1498
1968	682	346	1028
1977	828	406	1234
1978	1792	525	2317
1979	1352	327	1679
1987	671	457	1128
1988	809	504	1313
1992	820	376	1196
1993	635	533	1168
Total 9 years	8691	3870	12,561
Average/year	965.5	430	1395.5

the species-group category (i.e., my counts include new subspecies as well as species), but they do not include *nomina nova*, since these represent the result of nomenclatural rather than taxonomical discoveries. Subspecies account for between 3 and 10% of all new species-group names, depending on the year considered. There are at least two problems with this approach: (1) Each volume of *ZR* records not only papers and names published during the nominal year for that volume, but also a number of names omitted from earlier volumes. However, it is assumed that all volumes are affected in the same way and represent the scientific output of equivalent periods of time; (2) It has been demonstrated elsewhere (Bouchet & Rocroi, 1992) that the coverage of new supraspecific names by *ZR* misses about 23% of the names. I have not tried here to evaluate an omission rate for species-group names, but it is safe to assume that it is not negligible. Based on my experience with genus-group names, omission appears to affect considerably more fossil than Recent taxa. Since much of the present paper deals with data on Recent mollusks, I believe that my results are valid within an acceptable margin of error.

RESULTS

Naming New Molluscan Species

Numbers of new Recent and fossil species are tabulated separately for each of the 9 years sampled (Table 1). For each of the major classes, the distinction between Recent and fossil taxa is tabulated separately (Table 2), the 9 study years being pooled together. A number of results emerge from the tables:

(1) During the last 30 years, the average yearly output stands at 1395 new species (366 Recent gastropods, 292 fossil gastropods, 42 Recent bivalves, 316 fossil bivalves, 320 fossil cephalopods, and 59 other Recent and fossil mollusks). This average has remained remarkably stable over the last 3 decades. In 7 years out of 9, the number of new species described ranges between 1000 and 1500.

Table 2

Average numbers of new fossil and Recent mollusks described yearly (for 9 sample years, 1967–1993), partitioned by class.

	Fossil	Recent	Total
Aplacophora	—	10	10
Monoplacophora	9.5	0.7	10.2
Polyplacophora	2.1	6.2	8.3
Cephalopoda	320.4	3.9	324.3
Scaphopoda	2.9	1.5	4.4
Bivalvia	315.8	41.9	357.7
Gastropoda	292	365.8	657.8
Other classes*	22.8	—	22.8
Total	965.5	430	1395.5

* Rostroconchia, Hyolitha, Tentaculita.

(2) Fossils account for 69.2% of the new species, with individual values ranging from 54.3% (1993) to 80.5% (1979). The high number of fossils is caused to a large extent by fossil cephalopods: these alone account for one-third of all new fossil species and for 23% of all new mollusk species. Also, 88.3% of all new bivalves are fossils. The proportion between fossil and Recent is more balanced in gastropods: only 44.4% of all new gastropods are fossils.

(3) The average number of new Recent species stands at 430 per year. Despite much variance in the data concerning successive years, it appears that the average has slowly but regularly increased: it stood at 371 per year in the 1960s, rose to 419 in the 1970s, and has reached 467.5 in the last 10 years. This increase is not paralleled in fossils, with results for individual years showing still more variance. There was an unexplained peak in the 1970s (1324 per year), and the number of new fossil species has in the last 10 years reached a level well below the 1960s average (734 vs. 892 per year, respectively).

Where Do the New Species Come from?

The slow increase in naming of new Recent mollusk species since the 1960s masks two different trends (Figure 1). Marine mollusks, which in the 1960s accounted for 184.5 new species per year, or 49.7% of the total of Recent species, in the last 10 years (1987–93) accounted for 310.5 new species or 66.4% of the total. By contrast, non-marine mollusks slipped from 186.5 new species in the 1960s to 157 in the last 10 years. The global increase in naming activity noticed above therefore results from a steep increase in the naming of marine mollusks (+ 68% in 25 years) and a recession (–15.8%), or at best a stagnation, in the naming of non-marine mollusks.

The proportions for individual biogeographical regions are rather erratic from decade to decade (Table 3; Figure 2). The Indo-Pacific and the Caribbean account respectively for 34.5% and 16% of all new marine mollusks. The Panamic and West African tropical regions account for 7% each, but they have followed different trends since the

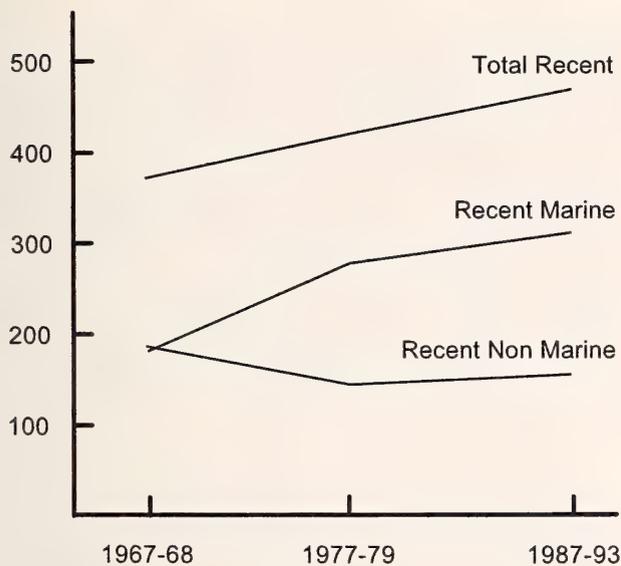


Figure 1

The number of new Recent species described yearly over the last 30 years.

1960s. The Panamic region dropped from 11.1% (1967–1968) to 3.9% (1992–1993), while West Africa was increasing from 3.8% (1967–1968) to 12.3% (1992–1993). Another possibly significant trend is discernible in Europe, which has dropped from a peak 16.3% in the 1970s to just 4.3% in 1992–1993. The figures for the other regions may

Table 3

Partitioning of new Recent mollusks to major biogeographic regions. Weight of individual regions indicated as percentage of total within discrete time periods. Total number of names involved in italics.

	1967–68	1977–79	1987–88	1992–93
Indo-Pacific	38.7	36.3	22.9	43
North Pacific	7.9	2.5	2.9	4.8
S. Australia/N. Zealand	11.9	8	6.3	1.4
Panamic	11.1	8.4	5.4	3.9
South Africa	1.4	2.8	11	6.4
West Africa	3.8	5.2	6	12.3
Europe	6.2	16.3	10.4	4.3
Caribbean	13.8	7.5	27.3	16.4
Antarctic	—	9.8	0.3	1.4
Other	5.1	3.2	7.5	5.9
<i>Total marine</i>	<i>369</i>	<i>828</i>	<i>682</i>	<i>560</i>
Palaearctic	27.6	39.5	53.4	37.8
Nearctic	5.4	7.4	23.7	1.4
Neotropical	23.9	14.2	6.1	4.9
Africa	11.3	9.8	6.1	15.2
Australasia-Pacific	6.4	25.3	5.7	34.7
Oriental	25.5	3.7	5	6
<i>Total non-marine</i>	<i>373</i>	<i>430</i>	<i>279</i>	<i>349</i>

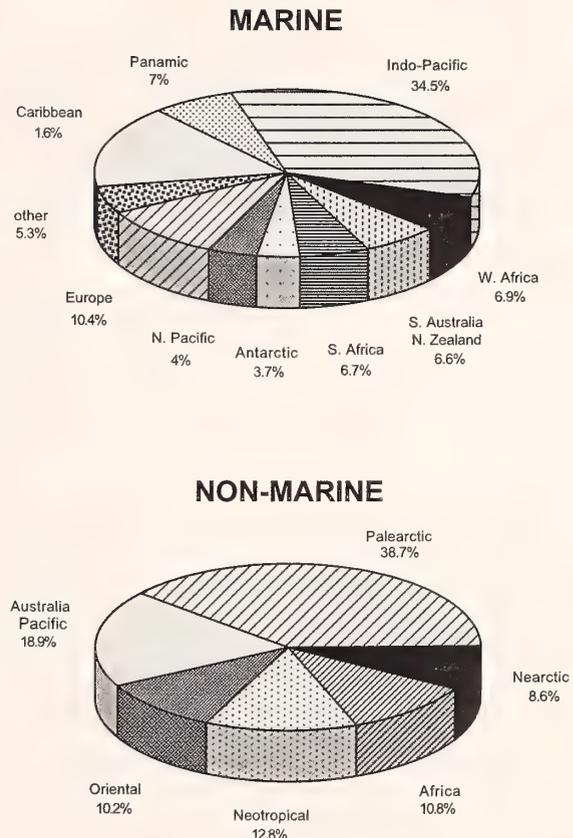


Figure 2

Partitioning of new Recent mollusks to major biogeographic regions. Percentages calculated globally for the period 1967–1993, based on data in Table 3.

not be significant as they probably reflect the much smaller number of malacologists involved in their study.

The results for non-marine mollusks also exhibit much variance, but some tendencies can possibly be discerned (Table 3; Figure 2). In the 1960s, the Palaearctic, Neotropical, and Oriental regions each accounted for one-fourth of the total effort. Since then, the Palaearctic is the only region which has experienced a regularly high output of descriptions, surpassing well over 25% of the total for any period of time considered. Conversely, the proportions occupied by the Neotropical and Oriental regions have collapsed well below 10% each. The only tropical region which may possibly have experienced an increased research effort is the Australasia-Pacific.

New Species and Synonyms

How many of the species described as new were really new, and how many will end up as synonyms of already named species? Because there are usually very few specialists working simultaneously on any given family or geographical region, there are few, if any, taxonomists that can provide an expert opinion on the validity of a new

Table 4
Synonymy ratio of new nominal species described in the last decades for selected samples.

Sample	Period	No. nominal species	No. valid species	Synonymy ratio	Source
Eulimidae	1965-1995	173	167	1.04	Warén, personal communication
Muricidae	1972-1993	384	316	1.22	Houart, 1994
Volutidae	1960-1992	116	82	1.41	Poppe & Goto, 1992
Terebridae	1960-1985	65	49	1.33	Bratcher & Cernohorsky, 1987
<i>Conus</i>	1965-1994	164	81	2.02	Röckel et al., 1995
European marine mollusks	1967-1995	1094	539	2.03	Gofas & Le Renard, personal communication
Total		1996	1234	1.62	

species immediately after it has been described. Synonymization usually occurs in the context of genus or family revisions. Such revisions may occur many years after the description of a new species (Solow et al. (1995) estimate that it takes on average 43 years to identify a synonym in the Thysanoptera). It is therefore too early to quantify globally the validity of new species described in the last 3 decades. I have however tried to approach the synonymy ratio [= number of names/number of valid taxa] based on selected samples (Table 4). My sources are published revisions as well as unpublished information in the CLEMAM database on the European marine mollusks (Gofas & LeRenard, personal communication) and a catalogue of taxa in the family Eulimidae (Warén, personal communication). The result is a synonymy ratio of 1.62, based on a sample of 1996 names. My feeling is that the sample used leads to an overestimation of the number of synonyms because, with the exception of Eulimidae, it concerns taxa or regions where a high number of authors are involved. They are also taxa, again with the exception of Eulimidae, where many species have commercial value as "specimen shells." As a consequence, competition among authors is high, and there are numerous examples of a new species being described almost simultaneously by competing authors, or being described without proper research in an attempt to win priority. In the vast majority of land and freshwater mollusks or marine micromollusks, this competition does not occur, but as a consequence, the validity of recently described taxa has not yet been evaluated. Therefore, for lack of a better approximation, I keep 1.62

as a working figure. If this ratio is projected over the average number of new species (430) described each year, we find that 265 valid new species are added each year to the inventory of molluscan diversity. Based on a different data set (i.e., all the names proposed since Linnaeus for selected groups of bivalves and gastropods), Boss (1971) calculated a synonymy ratio of 4, i.e., three synonyms for every valid species. My results thus confirm the opinion of Solem (1978) who had criticized Boss' synonymy ratio as being too high, and suggest that at least 62% of the new species described in the last 30 years were indeed new species. In fact, my result is remarkably close to that of Solow et al. (1995), who estimated that the proportion of valid species in the Thysanoptera is around 61%.

Who Describes?

I have studied two samples (1977-1978 and 1992-1993) to quantify the descriptive effort by author and by country. Table 5 shows that the number of authors involved in naming new Recent mollusk species has increased over the last 15 year period. For the most recent sample (1992-1993), a total of 284 authors named 909 species. One hundred and twenty-five authors (44%) were involved in 1992 only, and 107 authors (37.7%) in 1993 only, and just 52 authors (18.3%) were involved in each of these 2 consecutive years.

I then counted the number of new species described by authors from different countries. In doing so, I considered the nationality of an author to be that of the country where he/she works, not that of his/her birth. In the case of co-authored new species, I have credited each author with one-half, one-third, etc. of the number of co-authored names. Not unexpectedly, the result (Table 6) shows that USA is the most productive country, with over 20% of the new species. Germany, Japan, Netherlands, and Belgium have also had a stable and steady output over the last 15 years. The output of other countries has varied considerably. Some of this variation may reflect real trends, but it may also reflect the inadequacy of the data set, especially when it involves single large papers from countries with few

Table 5

Number of authors and co-authors involved in the naming of new Recent mollusks.

Year	No. authors	No. names
1977	114	406
1978	100	525
1992	177	376
1993	159	533

malacologists. In the case of the former Soviet Union, the observed trend may reflect diminished resources for taxonomists as a result of political changes. It is noteworthy, and regrettable, that mega-diversity countries such as Mexico, Brazil, India, Indonesia, the Philippines, and China have such a low profile on the international scene of molluscan species inventorying, none of them contributing more than 1% of the global descriptive effort.

Descriptive malacology is but a small field of zoology and a still smaller field of biology. I have thus compared the malacological ranking of countries with their ranking based on publication counts extracted from the 1989–1993 annual cumulations of the Science Citation Index (Braun et al., 1995), a scientometric index that privileges mainstream journals and ignores many journals published by institutions and amateur societies. I have used the ranking for General Biology, which includes the subject categories Biology, Biophysics, Botany, Entomology, Ornithology, Parasitology, and Zoology. The comparison (Table 6) shows that Austria, Belgium, Germany, Netherlands, New Zealand, and South Africa have a higher weight in descriptive malacology than in “general biology” as defined above. Conversely, the USA and United Kingdom have a much higher scientometric weight than their output in descriptive malacology indicates. It is remarkable that Canada ranks number 4 in terms of scientometric weight, but has a negligible output in the field of descriptive malacology.

Malacologists may describe new species from their own biogeographical region (an activity that may be qualified as “internal”) or from more distant regions (an activity that may be qualified as “external”). It is interesting to note that much of the research by malacologists from Europe (including ex-USSR) and the United States is external (Figure 3), whereas it is mainly internal in Australasia, Japan, and the rest of the world. These data suggest that taxonomists in Europe and the United States judge, correctly or incorrectly, that their faunas are adequately inventoried and turn to other parts of the world to discover new mollusks.

The vast majority of papers contain the descriptions of only one or two new species. Of 320 articles that were published in 1992–1993, 193 (60.3%) contain the description of a single new species, and 248 (77.5%) contain the descriptions of one or two, i.e., 77.5% of all papers contribute to the naming of just 33.3% of the species. This situation may reflect the pressure for publication, especially on postgraduate or untenured younger taxonomists. At the opposite extreme, 34 papers (10.6%) alone contain the descriptions of more than half the species (467 species, i.e., 51.3%). A reasonable assumption would be that short papers describing single new species are the work of single authors, whereas major papers with many new species are the result of collaborative work by several authors. In fact, an examination of the distribution of article-author pairs shows that 43.5% of papers describing one or two new species are co-authored by two or more authors (average 2.3 authors), whereas 38.2% of papers with five or more

Table 6

Naming activity on new Recent mollusk species, as a percentage of the total output, in the top 14 countries compared with their scientometric weight in general biology (after Braun et al., 1995).

	1977–78		1992–93		Scientometric weight	
	%	Rank	%	Rank	%	Rank
Australia	2.3	11	9.7	3	3.3	8
Austria	9.2	3	0.7	13	0.4	26
Belgium	2.4	10	2.4	11	0.8	16
France	3.1	9	10	2	4.7	6
Germany	11.1	2	9.1	4	5.8	5
Italy	1.9	12	4.7	7	2.1	9
Japan	7.6	4	8.8	5	7.0	3
Netherlands	7.5	5	7.1	6	2.1	10
New Zealand	6.3	7	0.6	14	0.6	21
South Africa	3.9	8	1.8	12	0.8	17
Spain	1.7	13	4.3	8	1.8	12
United Kingdom	1.5	14	2.5	10	7.7	2
USA	23.2	1	20.3	1	36.5	1
ex USSR	6.6	6	4.3	8	4.0	7

new species have more than one author (average 1.4 authors). Co-authorship of single species descriptions may reflect collector-describer and/or amateur-professional collaboration. To summarize, the description of new species of Recent mollusk takes place principally in two kinds of publications: (a) many small, scattered papers with a large number of co-authors, containing the descriptions of one or two new species; (b) a few major papers, mostly single-authored, containing the descriptions of 15 or more new species.

Descriptive malacology has had a long history of interaction with amateurs, and I have therefore evaluated their involvement in the naming of new molluscan species. For this purpose, I have followed Coan (1988) in classifying as amateur anyone who is not paid specifically for his/her work in malacology. In doing so, I have found it difficult to ascertain the professional position of some authors and, despite advice from colleagues, errors may have crept into my counts. Authors who are researchers or even taxonomists in other fields of science have had their contributions counted with those of amateurs. A number of professional malacologists remain active after their retirement, so that in one sense they are not “paid to study mollusks.” I have, however, considered their contributions with those of professionals. In the case of co-authored papers, I have considered only the professional situation of the first author. In a sample of 931 names published in 1977–1978, 265 species (28.5%) were described by amateurs. In a second sample of 909 names published in 1992–1993, 251 species (27.6%) were described by amateurs. Despite the uncertainties mentioned above, this result shows that amateurs play a very significant role in the inventorying and naming of new mollusk species. Although I have

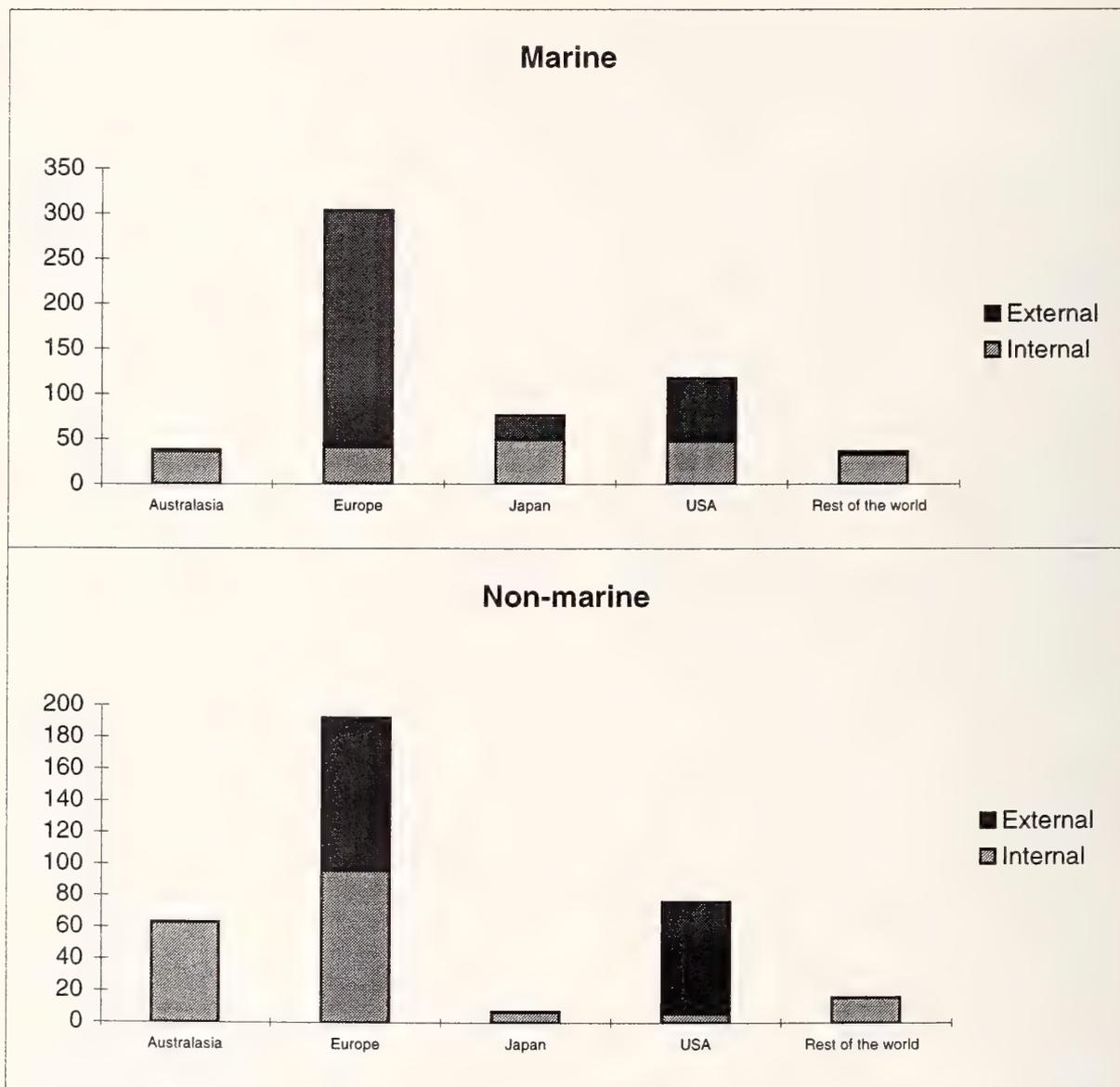


Figure 3

The efforts of malacologists from different parts of the world to describe new species from their own region (internal activity) and from regions other than their own (external activity).

not attempted a precise evaluation, it is likely that the contributions of retired professionals and amateurs pooled together may reach the 50% mark. The diversity of professional positions of authors of new species might be viewed as healthy in that people from different backgrounds take an interest in inventorying molluscan biodiversity. But the important contribution of amateurs and retired professionals may also be taken, despite some official statements on the importance of inventories, as a sign of the low esteem of alpha-taxonomy by many academic institutions and funding agencies.

Where Are Descriptions of New Species Published?

I have recognized four main categories of publication outlet: malacological journals, institutional (museums, universities, etc.) journals, journals published by learned societies and corporate publishers, and other publications (e.g., books). Based on the sample of 909 new Recent species described in 1992–1993, malacological journals form the main category, with nearly half (47.7%) of the new species contained in 28 serials (Table 7). Six of these (*Venus*, *La Conchiglia*, *Archiv für Molluskenkunde*, *Nauti-*

Table 7

Publication outlets used for descriptions of new Recent species. Sample: 909 names published in 1992-93.

Malacological journals	47.7%
Institutional journals	21.7%
Other journals	22.1%
Other publications (books)	8.5%

lus, *Apex* and *The Veliger*) are the malacological journals most frequently used for descriptions of new species, concentrating 28.6% of the new species, although no single journal has more than 8% of the total.

Inventorying the Biosphere

To visualize the effect of the current activity on the global inventorying of mollusks, I have charted the progress of knowledge on various groups of mollusks since Linnaeus (1758). Taking the current number of known species as a reference, I have plotted the number of species known at the end of every decade since 1758 as a percentage of that total (Figure 4) for selected groups of mollusks (Table 8), with different accessibility and different levels of interest to amateur malacologists.

Cypraeidae and the hydrobiid subfamily Cochliopinae might serve as examples to characterize patterns in inven-

tories. The family Cypraeidae has been included because it is probably the mollusk group with the longest tradition for scientific inventorying, even in pre-Linnaean days. Not unexpectedly, the 50% mark of cowrie inventorying was reached as early as the 1820s, and a plateau phase has lasted since 1850. Quite another pattern is shown by the Cochliopinae, a group of small to minute snails living in specialized freshwater and brackish habitats. In 1830, when already half of the cowries were known, only two species of Cochliopinae, representing 0.7% of the total number of species known today, had already been described. The 50% mark of Cochliopinae inventorying was reached in the 1930s. The curve is still steeply ascending, and it seems quite impossible from the graph to predict the number that will be finally reached when the inventory of Cochliopinae has been reasonably completed. In fact, the recent taxonomic literature abounds with examples demonstrating the inadequacy of mollusk inventories in many parts of the world (Table 9).

One frustrating conclusion from results of this kind is that they do not help reach an irrefutable estimate on the number of mollusk species in the biosphere. In a recent review of organism inventory (Hammond, 1995), Mollusca was singled out as a group where "the number of described species currently accepted is particularly problematic, with quoted figures ranging from some 45,000 to 150,000."

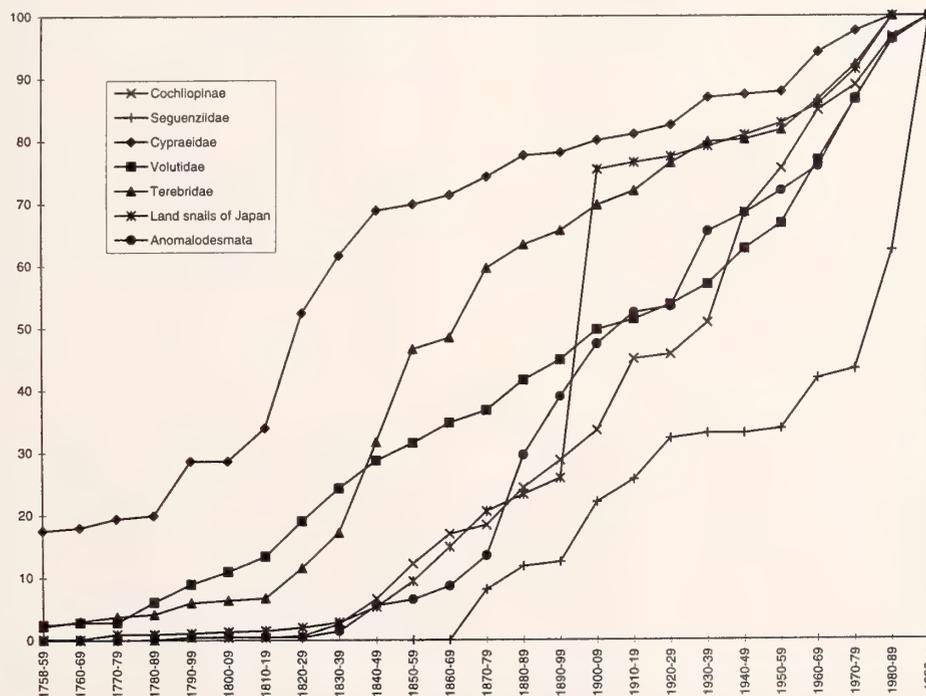


Figure 4

Progression of species inventorying in selected groups of Recent mollusks since 1758, plotted as a percentage of the known number of species (1995 = 100%). Only species currently recognized as valid are considered. Sources: see Table 7.

Table 8

Materials used to establish curves illustrating the progress of species inventorying since 1758. Results see Figure 4.

Taxon	No. known species	Source	Habitat	Interest to amateurs
Seguenziidae	136	Marshall, 1991	marine, 150–6000 m	nil
Cochliopinae	271	Hershler & Thompson, 1992	freshwater	nil
Cypraeidae	206	Lorenz & Hubert, 1993	marine, 0–30 m	very high
Volutidae	247	Poppe & Goto, 1992	marine, 0–500 m	high
Terebridae	268	Bratcher & Cernohorsky, 1987	marine, 0–200 m	low
Land snails of Japan	733	Minato, 1988	terrestrial	low
Anomalodesmata	415	Poutiers & Bernard, 1995	marine, 200–5000 m	nil

The Sources of the New Species

The steady naming activity results in part from application of new techniques (e.g., scanning electron microscopy, scuba diving, research submersibles), but also to a very large extent from a continuation of classical biological exploration, using the same methods as the generations before us. Despite the emphasis on cellular and molecular approaches in modern curriculums, very few new mollusk species have been *established* by research involving such new characters (e.g., Burch 1972; Murphy 1978; Gofas & Backeljau 1994; Bogan & Hoeh, 1995). More frequently, molecular characters are used *a posteriori* to evaluate the distinctness of cryptic taxa initially segregated on the basis of morphology (e.g., Backeljau et al. 1994; Kojima et al. 1995, reviewed by Davis 1994). In fact, the vast majority of new species named in the last few decades were recognized and described based on morphological characters.

A remarkable characteristic of marine mollusk inventorying of the last 30 years is the phenomenal comeback of amateur interest in collectable seashells. The number of known specimens of *Conus gloriamaris* Chemnitz, 1777, can be used as an example of the change in scale of collecting effort: this number has increased from a total of approx. 40 specimens known before 1968, to over 30 col-

lected each year after 1968 (Poppe, personal communication), i.e., about three orders of magnitude. The increasing demand for collector items has elicited the availability of material from new or little known collecting grounds all over the world, particularly in the tropics. Despite the very narrow interest area of most amateurs, amateur malacology has generated descriptions, not only of new, showy species by non-professionals, but of all kinds of mollusks by amateurs and professionals alike, based on diverse and abundant material brought together by commercial dealers and enthusiast collectors.

The hydrothermal vents and cold seeps represent a spectacular example of a recently explored environment. The mollusk fauna associated with these habitats is remarkable in terms of novelty of species (nearly all were unnamed) and relationships (new families or superfamilies). However, it is not particularly diverse. A little more than 100 species have been described since 1981 (Warén & Bouchet, 1993), which represents a rather insignificant proportion of the global mollusk naming effort. In fact, the continued exploration of the ambient deep sea (below 200–300 m), although much less popular with the media, is yielding considerably more new species. Even in the North-East Atlantic, probably the best explored and inventoried of deep-sea basins, the proportion of new species named in the last 20 years exceeds 20% of the total fauna. New deep-

Table 9

Examples of papers containing the descriptions of large numbers of new Recent mollusk species.

Author	Taxon/Region	Species covered	New species
Salvini-Plawen, 1978	Solenogastres Antarctic	90	75
Kilburn, 1988	Turridae South Africa	71	42
Marshall, 1991	Seguenziidae New Caledonia	55	50
Vermeulen, 1991, 1994	Diplommatinidae Borneo	81	46
Ponder et al., 1993	Hydrobiidae Australia	64	51
Solem, 1993	Camaenidae Australia	65	39
Fischer-Piette et al., 1994	Pulmonata Madagascar	334	92
Rudman, 1995	Chromodorididae New Caledonia	*	11
Cosel, 1995	Bivalves West Africa	*	51

* Only new species described in paper.

sea species result from government-funded expeditions, mostly in South Africa (Kilburn & Herbert, 1995), the North Atlantic, the North Pacific, New Zealand, and New Caledonia (Richer de Forges, 1990); as by-products of commercial fishing in the Philippines, Somalia, and the Caribbean; or a combination of both research and commercial fishing, as in Japan and Australia.

In the last few decades, an extraordinary biological, anatomical, and ecological diversity of marine micromollusks has been revealed. For example, in Europe, the shallow-water mollusk fauna was reputed to be completely inventoried since the turn of the century until, rather unexpectedly, new species started to be named and described in the late 1960s. Since then, several hundred new species have been named, but few are larger than 10 mm, and most are smaller than 5 mm. Japan, the Caribbean, the Mediterranean, Australia, and New Zealand are regions where many new micromollusks have been described. During the same period, taxonomic research on nudibranchs has been revolutionized by the advent of SCUBA diving and color photography, eventually opening new areas of interest to dedicated amateurs and divers. The main geographical sources of new species of sea slugs have been Australia, Japan, Central America (both Panamic and Caribbean), the Mediterranean, and Brazil.

With regard to freshwater faunas, the study of waterborne diseases has maintained a steady level of malacological research in tropical regions. Although much of this research is non-taxonomical, the inventorying of freshwater mollusks has progressed in Africa, Southeast Asia, and China, clearly as a consequence of medical and parasitological programs. Hydrobioids certainly represent the least known segment of freshwater mollusk faunas, because they live in groundwater, springs and resurgences, caves, etc. and require specialized collecting. Interest in hydrobioids is being maintained at a rather high level, with speciose radiations recently described from Australia, southern Europe, Turkey, tropical China and Indochina, and the United States.

Inventorying of land snail faunas has progressed unevenly. The 1960s were a continuation of the colonial era, with northern hemisphere malacologists active in the Andes, Madagascar, Africa, and the Middle East. More recently, publication of major monographs on the Endodontidea of the Pacific Islands and the Camaenidae of Australia rightly focuses our attention on the Australasia-Pacific region, which is the only tropical region to have experienced an acceptable level of land snail inventorying. New species have also been named from southern subtropical Japan, its offshore islands, and Taiwan. The most unexpected developments, however, have come from the Palearctic region, where numerous new species have been discovered and described in the Atlantic archipelagoes, the Balkan area and the Aegean archipelagoes, Turkey, the Caucasus, and the Tian-Shan mountain ranges of Central Asia. By contrast, vast areas of Central and West Africa,

the tropical Andes, Brazilian Atlantic forest, and most of the Oriental region have remained outside the stream of mollusk inventorying.

PERSPECTIVES

The results amply demonstrate that the inventory of molluscan biodiversity is far from achieved. Consequently, there is ample justification for high levels of research time, institutional support, and journal space to continue to be devoted to alpha-taxonomy. As an example, based on preliminary examination of sublittoral (below 100 m) material dredged in New Caledonia in 1984–1994, Bruce Marshall and I estimate that about 80% of the 2000+ species are still undescribed. Considering that approx. 190 valid new marine species (310 nominal species/synonymy ratio 1.62) are described each year worldwide, there remains an unlimited perspective for alpha-taxonomy. The era of discovery of very large species (e.g., *Turbinella laffertyi* Kilburn, 1975, size 280 mm, or *Tridacna tevoroo* Lucas, Ledua & Braley, 1990, size 500 mm) is however probably coming to an end. Micromollusks, deep-sea faunas, and the non-marine and marine tropics obviously constitute the main reservoirs of unknown species, and the Indo-Pacific, both in shallow and deep water, is likely to remain a major frontier for many decades.

The most distressing perspective is the loss of knowledge about and attention given to tropical non-marine faunas. Europe, North America, and Japan contain most of the experts on land and freshwater mollusks available worldwide, but most of this work is directed toward their local faunas, although the Palearctic and Nearctic are already the best inventoried. Despite declarations on the necessity to preserve the biological diversity of our planet, it is certain that many tropical land and freshwater snail radiations will become extinct through loss of habitat before they have been described, even before they have been collected (Emberton, 1995). Regrettably, there is no passive method for collecting land snails comparable to the trapping and/or knock-out fogging methods used to collect many arthropods that can be efficiently operated by general ecologists and other non-specialists. Surveys and collections of land and freshwater mollusks can only be done by experienced collectors, and it is important that more sensitive and threatened geographical areas are properly surveyed and inventoried before their faunas have been devastated like those, for example, of Hawaii (Solem, 1990) or Rodrigues Island (Griffiths, 1994).

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Using Shell Parameters as Complementary Data in Phylogenetic Systematic Analyses: Evolution of Form in Five Species of Littorinids (Mollusca: Gastropoda)

by

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Abstract. Gastropod shells contain records of ontogeny and so, house a wealth of biological information. In this paper, I present a methodology for the analysis of shell forms which yields data that may be used in phylogenetic systematic analyses. I use a mathematical model which considers two aspects of a shell's aperture throughout growth, the "aperture trajectory" and the "aperture scaling," to describe shell shape and size. The aperture trajectory describes the path in space followed by the center of the aperture from the apex to the final lip of a shell, while the aperture scaling represents the changes in the dimensions of the aperture along the trajectory. I treat each whorl of a shell as a separate entity, consider horizontal and vertical components of the trajectory and scaling as characters, code character states in a conservative manner, and use them in a cladistic analysis. As an example, I apply the method to shells of five species of periwinkles (Gastropoda: *Littorina*). I obtain a phylogeny (interpreted cladogram) that differs from recently published hypotheses derived from other types of data, and I compare, contrast, and combine my results with these. Finally, I discuss the assumptions and limitations of the methodology I present.

INTRODUCTION

Periwinkles are prosobranch gastropods that inhabit intertidal zones worldwide; the most well-known genus is *Littorina* Férussac, 1827. Recently, two mutually incompatible hypotheses of interspecific relationships in *Littorina* have been published. Reid (1990) used soft body anatomical features, with special emphasis on reproductive systems, to derive a cladogram for all 18 species currently recognized in the genus, while Boulding et al. (1993) used allozyme loci data to derive a distance-Wagner tree for different populations of six species. In this study, I present a phylogenetic hypothesis (interpreted cladogram) based on shell features for five species of *Littorina* and compare, contrast, and finally, combine it with the other hypotheses. My primary objectives are to demonstrate that, in general, shells provide a rich source of biologically relevant morphometric data and to provide a methodology for obtaining and using these data in a phylogenetic context.

Obtaining Phylogenetic Data from Shell Morphometrics

Shell growth and form: Researchers have identified and classified snails by analyzing features of shell form (Raup, 1966; Vermeij, 1971; Kohn & Riggs, 1975; Rex & Boss, 1976; Murray, 1982; Janson & Sundberg, 1983). An assumption made implicitly by each researcher, a distinction I wish to state explicitly, was that shell form results from shell growth. In other words, the shape and size of a shell are the products of the cumulative accretion of calcium carbonate onto a snail's aperture. Although the preceding statement may appear to be trivial, I will show that an explicit distinction and recognition of the relationship between growth and form directs morphologists toward measuring biologically significant features of shells.

During the secretion of its shell, a gastropod extends its mantle edge just beyond the lip of its shell aperture. The shape of the mantle edge at the time of secretion depends

on the internal stress of the mantle (Morita, 1991) and the shape of the aperture (Hutchinson, 1989). Along its periostracal groove, a snail secretes a calcareous matrix which hardens onto the aperture and becomes a permanent part of the previously accreted shell surface. Internally, the shell may be thickened or resorbed, but, once laid down, its external form remains unchanged.

As a result of this accretionary process, the form of a shell records its history of growth (Stasek, 1963; Gould, 1989). If accretionary processes are genetically determined and are heritable, similarities in shell form among closely related taxa result from common evolutionary histories. This is the implicit philosophical link between analyses of shell form and their use in identification and classification. In this paper, I explicitly represent similar shell forms by numerically identical (i.e., presumed homologous) character states in a data set with which I perform a cladistic analysis.

Reconstruction of shell growth from shell form: Traditionally, researchers have oriented shell specimens in axial view and measured features such as length, width, and aperture dimensions. These measurements describe shell form (shape and size), but consider no aspects of (accretionary) growth explicitly. Therefore, while they may aid in the identification of shells, the connection between analyses performed on these measurements and evolution (i.e., between ontogeny and phylogeny), at least in a developmental sense, is tenuous at best.

An axial orientation represents a Ptolemaic view (Ackery, 1989) of a shell's world (Figure 1), in which it appears that the aperture "coils around" an imaginary vertical axis. In reality, a shell's aperture rests upon or adheres to a surface, and the rest of the shell rotates during accretion. Nevertheless, by selecting measurements that link the process of growth with its product, form, one can reconstruct growth history from an axial view of a shell.

The external form of a shell is composed of whorls. Each whorl is the result of accretion for a period of a snail's life during which its shell rotates through an angle of 2π radians (360 degrees). This is readily observable from a radiograph or section of a specimen in axial orientation (Figure 1).

In order to take morphometric measurements of shell form, I consider the position of the apex of a shell in axial orientation to coincide with the origin of a Cartesian coordinate system (x, y, z). I define the set of positions of aperture centers from the apex to the final lip as the "aperture trajectory" and the changes in the dimensions of the aperture along the trajectory as the "aperture scaling" (Figure 1). I further separate the trajectory and scaling of the aperture into horizontal and vertical components, each under the influence of an independent parameter: offset (O) affects the radial migration of the aperture; translation (T), the abapical migration; horizontal expansion (H), the change in horizontal dimensions of the aperture; and vertical expansion (V), the change in vertical dimensions.

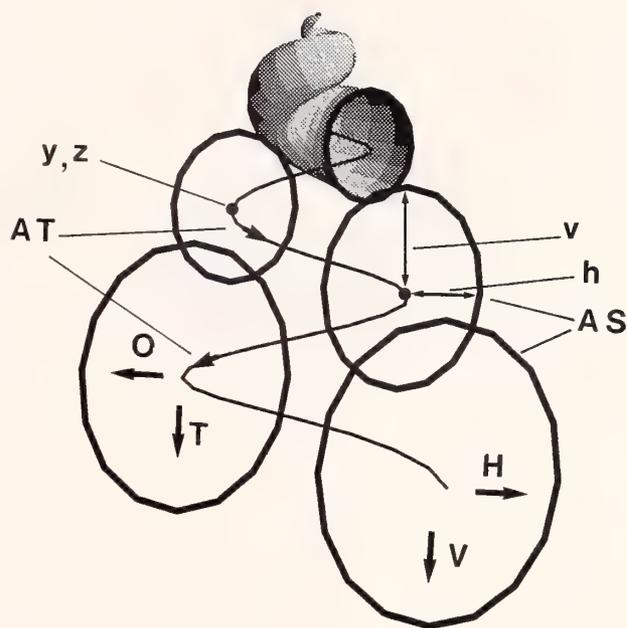


Figure 1

Axial orientation that facilitates the morphometric analysis of shell form (only the surface of the initial whorl of the shell is simulated completely). The aperture trajectory (AT) represents the path taken by the aperture during growth. The mathematical description of the radial migration of the aperture is affected by the parameter offset (O), while that of the abapical motion is affected by the parameter translation (T). The aperture scaling (AS) represents the changes in dimensions of the aperture throughout growth. The mathematical description of changes in the horizontal dimension of the aperture is affected by horizontal expansion (H), while that of the vertical dimension is affected by vertical expansion (V). The initial form of the shell (based on raw data) is produced when all parameters have a value of 1.0. Also shown is an example of apertural measurements taken from specimens: coordinate positions of centers ($\{y, z\}$) and horizontal and vertical dimensions ($\{h, v\}$).

Phylogenetic application: The preceding geometric analysis enables one to generate images of shells using computer graphics (Stone, 1995). The separation of form into aperture trajectories and scalings facilitates the description and thereby, the simulation of different shells. By changing the parameter values (O, T, H, and V), one can change the form of a shell's image. Because it permits the transformation of one shell form into another, this type of analysis is amenable to outgroup comparison (Watrous & Wheeler, 1981; Maddison et al., 1984): outgroup shell forms can be analyzed and compared morphometrically to ingroup shell forms. The character states derived from these comparisons can be ordered and used as cladistic data (see MATERIALS AND METHODS).

The five littorinid species studied in this analysis (the ingroup) have been hypothesized (Reid, 1989) to be more closely related to one another than any of them is to *Littoraria fasciata* (Gray, 1839) or *Nodilittorina aspersa* (Phi-

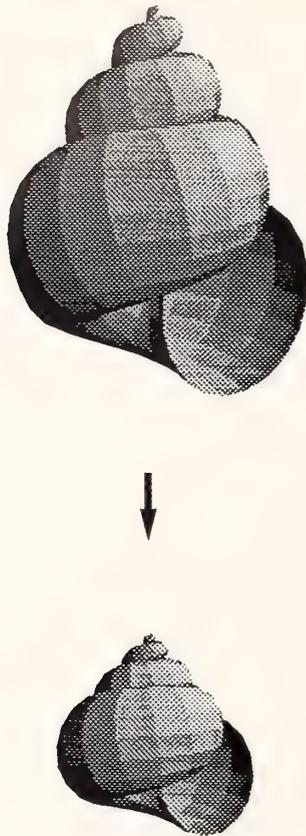


Figure 2

Transformation of shell image of *Littoraria fasciata* into shell image of *Littorina littorea* by varying the parameter values in a mathematical model.

lippi, 1846) (the outgroups). Differences in shell forms presumably result from changes in the growth geometries of the five ingroup species with respect to the two outgroup species. Therefore, I represent shells of each of the ingroup species as combinations of changes of parameter values in the equations describing shell forms of the outgroups (Figure 2). Every change in a parameter value provides a character state that may be used in a cladistic analysis. Therefore, by determining the equations that describe the trajectory and scaling of apertures for outgroup shells, calculating the parameter values required to "evolve" each member of the ingroup, and using these data in a cladistic analysis, I can develop a hypothesis of the evolutionary history (interpreted cladogram) of these taxa.

To recapitulate, I have proposed a methodology that includes several explicit assumptions: two aspects of shell form (or shape and size), the aperture trajectory and aperture scaling, may be described mathematically; these are the consequences of the process of shell growth (or accretion); accretionary processes are genetically determined and heritable; hence, mathematical descriptions of shell forms may be used to define characters and character states

that can be analyzed cladistically and therefore reflect evolutionary relationships among closely related taxa.

I emphasize that the parameters I have defined describe only (but accurately) shell shape and size and therefore are architectural morphometric variables (*sensu* Schindel, 1990), as opposed to landmark data (Bookstein et al., 1985). Although Johnston et al. (1991) have developed methods for the measurement of landmark data for (*Epitonium*) shells with easily identified homologous points, such data have yet to be used in cladistic analyses (but see Wagner, 1995). In contrast, much has been written supporting the use of meristic morphometric data in cladistic analyses (Archie, 1985; Goldman, 1988). However, because this area of research is controversial (Farris, 1990), I code shell parameter data in a conservative manner (see section entitled Coding and Polarizing Shell Character States).

MATERIALS AND METHODS

I borrowed the following samples from the Department of Invertebrate Zoology at the Royal Ontario Museum (ROM) or the California Academy of Sciences (CAS) (sample catalogue numbers, sub-sample sizes of adult shells, and collection localities for each species are indicated): *Littoraria fasciata* (Gray, 1839), ROM CAT M503, 3, El Salvador; *Nodilittorina aspersa* (Philippi, 1846), CAS 1045476, Panama; *Littorina littorea* (Linnaeus, 1758), ROM CAT M455, 15, Prince Edward Island; *Littorina obtusata* (Linnaeus, 1758), ROM CAT M499, 15, Prince Edward Island; *Littorina saxatilis* (Olivi, 1792), ROM CAT M478, 15, New Brunswick; *Littorina sitkana* Philippi, 1846, ROM CAT M493, 15, British Columbia; and *Littorina scutulata* Gould, 1849, ROM CAT M490, 15, British Columbia. I took radiographs, with specimens in axial orientation on a sheet of photographic emulsion (Kodak Industrex SR), using an HP Faxitron Model 43805N X-Ray machine at 60 keV for 180 seconds.

I oriented the radiographs beneath a sheet of transparent graph paper on a light table. I considered the position of a shell's apex as coincident with the origin of an x-y-z coordinate system and recorded two pairs of apertural data: one designated the coordinate positions ($\{y, z\}$, the x coordinate for a given radiograph was constant) of aperture centers; the other, apertural horizontal and vertical dimensions ($\{h, v\}$). Assuming that apertures were elliptical, I readily obtained these data as aperture centers (for $\{y, z\}$, Figure 1) and semi-major and semi-minor axes (for $\{h, v\}$, Figure 1). Though the conceptualization of whorls may be arbitrary, I took measurements at one-whorl intervals. Schindel (1990) suggested that longitudinal sections (hence whorls) could be used to analyze ontogenetic histories of apertural motions. Furthermore, Johnston et al. (1991) found evidence for oscillatory patterns in shell shape with periodicity 2π . Hence, whorls are appropriate intervals within which features of shell form can be measured. To ensure homology between whorls of the same number across species, this methodology should be applied only to specimens in which apices are well preserved.

An Example

Using a modified least-squares linear regression of logarithmically transformed y , z , h , and v values against whorl number, I determined parametrized allometric equations describing the aperture trajectory of *Littoraria fasciata*, one of the outgroups, to be

$$\begin{aligned} \{x, y, z\} = \{ & O(\theta) (0.0868 \theta^{1.29}) \text{Sin}[\theta], \\ & O(\theta) (0.0868 \theta^{1.29}) \text{Cos}[\theta], \\ & T(\theta) - (0.0525 \theta^{1.81}) \} \end{aligned} \quad (1)$$

and the aperture scaling to be

$$\{h, v\} = \{H(\theta) (0.0418 \theta^{1.47}), V(\theta) (0.0512 \theta^{1.50})\}, \quad (2)$$

where initially, I set $O(\theta)$, $T(\theta)$, $H(\theta)$, and $V(\theta)$ each to a value of 1.00. Hence, after the first whorl ($\theta = 2\pi$) has been accreted, one would expect the center of an aperture for a typical *L. fasciata* shell to be situated 0.929 mm radially from the central axis and 1.46 mm vertically from the apex, and the aperture, itself, to have a horizontal dimension of 0.623 mm and a vertical dimension of 0.806 mm. One of the ingroup species, *Littorina littorea*, however, has an aperture trajectory described by

$$\begin{aligned} \{x, y, z\} = \{ & O(\theta) (0.0130 \theta^{1.75}) \text{Sin}[\theta], \\ & O(\theta) (0.0130 \theta^{1.75}) \text{Cos}[\theta], \\ & T(\theta) (-0.0436 \theta^{1.63}) \}, \end{aligned} \quad (3)$$

and an aperture scaling described by

$$\{h, v\} = \{H(\theta) (0.112 \theta^{0.994}), V(\theta) (0.0324 \theta^{1.47})\}. \quad (4)$$

Therefore, after its first whorl has accreted, a typical *L. littorea* shell has its aperture situated 0.324 mm radially from its central axis and 0.872 mm vertically from its apex, with a horizontal dimension of 0.696 mm and a vertical dimension of 0.483 mm. One can determine if these two sets of morphometric predictions (one for *L. fasciata* and one for *L. littorea*) are significantly different, in a statistical sense, by calculating confidence intervals around each. Also, one can transform the mathematical description of the first whorl of a typical individual of *L. fasciata* into that of *L. littorea* by setting the parameter values of *L. fasciata* to $O1 = 0.349 (= 0.324/0.929)$, $T1 = 0.597 (= 0.872/1.46)$, $H1 = 1.12 (= 0.696/0.623)$, and $V1 = 0.599 (= 0.483/0.806)$. This type of analysis provides four morphometric parameters that, combined with statistical analyses, can be used as character states in a cladistic analysis. Similar considerations for the second, third, and fourth whorls provides 12 (three whorls · four parameters) additional characters.

If, during evolution, differences in shell form resulted from changes in the trajectory and scaling of shell apertures during growth, then setting the parameter values to $O1 = 0.349$, $T1 = 0.597$, $H1 = 1.12$, $V1 = 0.599$, $O2 = 0.480$, $T2 = 0.527$, $H2 = 0.803$, $V2 = 0.587$, $O3 = 0.578$, $T3 = 0.490$, $H3 = 0.662$, $V3 = 0.579$, $O4 = 0.660$, $T4 = 0.465$, $H4 = 0.577$, and $V4 = 0.574$ evolves an image representing *L. fasciata* into an image representing *L. lit-*

torea (Figure 2). I performed this type of analysis, using the two outgroup species and five ingroup species, to derive a set of parameter values. In effect, this set of parameter values transforms a typical outgroup shell into that of each species among the various members of the ingroup. After some statistical analysis (see below), I recorded and polarized these parameter values, to create a data set that could be analyzed by numerical cladistic software.

Coding and Polarizing Shell Character States

Parameter values of 1.0 leave the mathematical description or image of a shell unchanged; therefore, this is the plesiomorphic state for all parameters. Ideally, the parameter values of ingroup members would sort naturally into discrete values. For example, if the radial migration of the aperture during the secretion of the first whorl increased twofold in the ingroups relative to the outgroups, one would code character O1 as 1 for the outgroups and 2 for each member of the ingroup. However, such convenient natural sorting of parameter values probably is rare—*natura non facit saltum*. Hence, one must employ some other means of coding them.

To this end, I calculated the coordinate position ($\{y, z\}$) and linear dimensions ($\{h, v\}$) of the aperture at one whorl intervals for each species, as predicted by its allometric equations of form, and determined 90% confidence intervals around each. I chose the 90% level of confidence as a compromise between two complementary aspects of using morphological data conservatively in a cladistic analysis: character states should represent statistically sound aspects of morphology (high level of confidence), but, to provide resolution, confidence intervals must be numerically distinct to some extent (lower level of confidence). In other words, I compromised a small amount of statistical robustness to ensure conservative but informative character codings. I then compared confidence intervals of each ingroup species with corresponding confidence intervals of the outgroups. I separated each of the four predicted measures into one of three statistically distinct states: those less than the outgroups, those overlapping with the outgroups, or those greater than the outgroups. Thus, only those predicted measurements that had non-overlapping confidence intervals with corresponding measurements of the outgroups were apomorphic states (Figure 3). Finally, I recorded the parameter values: those corresponding to statistically apomorphic conditions became 0 if they were smaller in the ingroup or 2 if they were greater, while those that statistically were indistinguishable from the outgroups were coded as 1 (Table 1).

Other Data

I reanalyzed Reid's (1990) data set, based on soft body anatomical features, for species used in this study only, in the following manner. First, I recoded the states of multistate characters in cases wherein taxa bearing some of

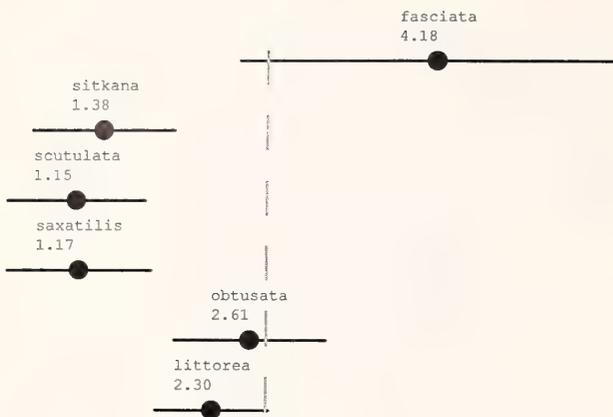


Figure 3

Statistical analysis used to polarize measurements predicted from allometric equations of shell form. Measurements (values and large dots) with confidence intervals (here 90%, horizontal lines) that are distinct from the outgroup intervals are apomorphic. Apomorphic measurements are used as a basis to recode parameter values: parameter values for measurements that are greater (or less than) than corresponding measurement in the outgroups are recoded as 2 (or 0). The plesiomorphic state of a parameter is coded as 1; this is also the parameter value for which a particular aspect of the graphically simulated image of a shell form remains unchanged. Here, because the confidence intervals for this parameter of *Littorina obtusata* and *Littorina littorea* overlap (vertical line) with those of the outgroups (*Littoraria fasciata* and *Nodilittorina aspersa*, not shown), states are coded as 1 (plesiomorphic). The character shown is V3 (see Table 1 for coding).

the states were excluded (characters 10 and 14, Table 2). For example, Reid (1990) interpreted character 14 in his analysis, the coiling of egg grooves within the lumen of the oviduct, as having seven states, depending on the complexity of coiling, the number of loops, and the size of the capsule gland. Since all taxa bearing states 1 and 2 were excluded in this study, I reinterpreted this character as having five states: 0, 1, 2, 3, and 4 (character 14, Table 2). Second, although Reid (1990) ran the states of characters 9, 10, and 14 ordered, I ran the states of all multistate characters (characters 9, 10, 14, and 16, Table 2) un-

dered. This avoided the construction of non-falsifiable hypotheses of character state order and allowed for all hypotheses of character state order to be tested against congruence with the states of other characters used (Hauser, 1992). Third, due to the deletion of taxa, seven characters became cladistically uninformative (characters 5, 6, 12, and 25 are zero column vectors, while characters 7, 19, and 22 are autapomorphies, Table 2). And finally, I excluded shell characters (characters 1 through 3, Table 2) from the analysis, by running them as inactive.

I then combined Reid's (1990) soft body anatomical data with the shell parameter data presented in this paper to construct a "whole animal" data set. Because the data sets had different outgroups, I had to derive a hypothetical sister-species of the ingroup. I left the states of shell parameter characters (the first 16 characters, Table 3) alone. States of the final 26 characters for the outgroups, from Reid (1990), I re-polarized using outgroup comparison rules (Maddison et al., 1984; Wiley et al., 1991). This provided the character states for the hypothetical sister-species of the ingroup (Hyp, Table 3). Again, I recoded the states of Reid's (1990) multistate characters 10 and 14 (characters 26 and 30, Table 3), ran multistate characters (characters 25, 26, 30, and 32, Table 3) unordered (though the use of a hypothetical outgroup made the unordering of character 25 inconsequential to the analysis), and excluded shell characters (characters 17 through 19, Table 3) from the analysis, by running them as inactive.

Boulding et al. (1993) published a distance-Wagner tree, using Cavalli-Sforza and Edwards' chord distance, Swofford's multiple addition criterion, and no optimization. The disadvantage of this approach is that information gets lost during the recoding of data into distance measures; thereafter, these data cannot be combined with other types of cladistic data. To make the results of Boulding et al. (1993), based on allozyme data, comparable to those based on shell parameters, I deleted two taxa not used in this study from their data set and recoded it using the 10 loci as characters and alleles as character states. This provided one cladistically informative character (character 10, Table 4), three potentially cladistically informative characters (i.e., informative using functional ingroups and out-

Table 1

Data matrix derived from shell parameters. Symbols used for species: Lfa = *Littoraria fasciata*, Nas = *Nodilittorina aspersa*, Lli = *Littorina littorea*, Lob = *Littorina obtusata*, Lsa = *Littorina saxatilis*, Lsc = *Littorina scutulata*, Lsi = *Littorina sitkana*.

	O1	T1	H1	V1	O2	T2	H2	V2	O3	T3	H3	V3	O4	T4	H4	V4
Lfa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Nas	1	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1
Lli	1	1	1	1	1	0	1	1	0	0	1	1	0	0	1	0
Lob	1	1	1	1	1	0	1	1	1	0	1	1	—	—	—	—
Lsa	1	1	1	1	1	0	1	1	0	0	1	0	0	0	0	0
Lsc	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0
Lsi	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0

Table 2

Data matrix derived from Reid's (1990) morphological data (his characters 1 through 26 in order). The symbols for the species used are identical to those in Table 1 except: NFo = *Nodolittorina (Fossarilittorina)*, NEc = *Nodolittorina (Echinolittorina)*, and NNo = *Nodolittorina (Nodolittorina)*.

NFo	1 1 0 1 0	0 1 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0 0
NEc	1 0 0 1 0	0 0 1 2 1	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0 0
NNo	1 0 0 1 0	0 0 1 2 1	0 0 1 0 0	0 0 0 0 0	0 0 0 0 0 0
Lsc	2 1 1 0 0	0 0 0 1 0	1 0 0 1 0	3 1 0 0 0	0 0 0 0 0 1
Lli	1 1 1 0 0	0 0 0 1 2	1 0 0 1 0	1 1 0 0 1	1 0 1 1 0 1
Lsi	1 1 1 0 0	0 0 0 1 2	1 0 1 2 1	1 0 1 0 1	1 0 1 1 0 1
Lob	0 1 1 0 0	0 0 0 1 2	1 0 1 3 1	2 ? 1 0 0	1 1 1 1 0 1
Lsa	1 1 1 1 0	0 0 0 1 2	1 0 1 4 1	2 ? 1 1 0	1 0 1 1 0 1

groups—characters 2, 4, and 8, Table 4), and six cladistically uninformative characters (characters 1, 3, 5, 9, and the two autapomorphies, characters 6 and 7, Table 4). Once again, I ran the states of all multistate characters unordered, as the computer algorithm performs functional ingroup/outgroup analyses on the states of each character using the states of other characters. Finally, I coded losses of alleles as independent, ordered states for character 4 (Table 4, parentheses), and, together with the other nine characters, coded and unordered as above, ran this as another data set.

I performed all cladistic analyses for this study using Hennig86 (Farris, 1988) and invoking the implicit enumeration algorithm. This guaranteed that all shortest (most parsimonious, or most economical, and therefore falsifiable) cladograms were found. I excluded autapomorphies from analyses because they inflate consistency indices (Wiley et al., 1991). I included autapomorphies on cladograms because non-homoplasious apomorphies may suggest the existence of missing (possibly fossil) taxa that may change the position of terminal taxa (Donoghue et al., 1989; see DISCUSSION).

As an estimate of node-support for the cladogram obtained from the analysis of shell parameter data, I performed a bootstrap analysis across characters (Felsenstein, 1985). The bootstrap is useful in the estimation of confidence for data in which the distribution is unknown or for which statistical estimation is too complex, as is the case with cladistic data. In this randomization technique, characters (column vectors in Table 1) are randomly resampled "c" times with replacement from a data set containing "c"

characters, to form a new data set. This new data set is analyzed to give an estimate of phylogeny. This procedure is replicated "r" times, providing a distribution of estimates of phylogeny. The rationale of the bootstrap here is that this distribution of estimated phylogenies provides a basis for an estimation of node-support contained in the data from which the cladogram was derived. In employing a bootstrap, I made the assumption that shell parameter characters were independent of one another (see section on Assumptions and Limitations of This Study).

Two valid criticisms of the bootstrap are that, as a randomization technique, any given analysis is unlikely to be reproduced, and the data sets, although based on real character states, are fictitious. As a brute force method of estimating node-support, however, the results of a bootstrap become more robust as the number of replicates increases. With the increasing availability of powerful personal computers, many replicates (i.e., large r values) now can be achieved rapidly, and the effects due to these problems can be made negligible.

I employed the bootstrap in a conservative manner: I performed 10,000 replications (using the mhennig and branch-breaking algorithms of Random Cladistics (Siddal, 1993) of the data in Table 1 and mapped the proportion of times (calculated as a percentage) each monophyletic group from the original cladogram occurred on cladograms representing bootstrapped data, back onto the original cladogram (Figure 4a). This cladogram differs from a bootstrap cladogram, which represents a phylogeny estimated by resampling data (Felsenstein, 1985).

I performed all statistical analyses of the raw data in

Table 3

Combined data matrix derived from shell form parameters (first 16) and Reid (1990; last 26). The symbols for the species used are identical to those in Table 1 except: Hyp = Hypothetical outgroup with states derived by outgroup comparison.

Hyp	1111	1111	1111	1111	11?10	000?0	?00?0	?0000	00000?
Lli	1111	1011	0011	0010	11100	00012	10010	11001	101101
Lob	1111	1011	1011	----	01100	00012	10131	2?100	111101
Lsa	1111	1011	0010	0000	11110	00012	10141	2?110	101101
Lsc	1111	0011	0010	0000	21100	00010	10010	31000	000001
Lsi	1111	1011	0010	0010	11100	00012	10121	10101	101101

Table 4

Data of Boulding et al. (1993) recoded using loci as characters and alleles as character states (in the order presented in their paper). Column of parenthetical values represents fourth locus when losses of alleles are considered independent states. The symbols for the species appear as they do in Table 1.

Lli	0	0	0	0 (0)	0	0	0	0	0	0
Lob	0	2	0	2 (2)	0	1	1	2	0	1
Lsa	2	3	0	2 (3)	0	0	0	2	0	1
Lsu	1	1	1	1 (1)	0	0	0	1	0	0
Lsi	0	1	2	2 (4)	0	0	0	2	0	2

this study using Mathematica (Wolfram Research, Inc., 1994). I simulated shell forms using CerioShell (Stone, 1995) and Mappoint (Beck, 1992), with Mathematica (Wolfram Research, Inc., 1994) as supporting software.

RESULTS

Cladogram Topologies and Measures

The cladogram obtained from the analysis of shell parameter data (Figure 4a) has *Littorina obtusata* basal, with *L. littorea*, *L. sitkana*, *L. saxatilis*, *L. scutulata* branching off sequentially, and had a length (l) of 8 steps, a consistency index (ci) of 100, and a retention index (ri) of 100. States of the characters 04, T4, and V4 for *L. obtusata* were equivocal (shown as 1), while the computer algorithm optimized H4 as 1. The bootstrap values (Figure 4a) were between 63% and 65% for all nodes. The cladogram obtained from the analysis of shell parameter data differed from the cladogram obtained from the analysis of Reid's (1990) soft body anatomical data (l = 27, ci = 85, ri = 87, Figure 4b) and the two cladograms obtained from the analysis of the "whole animal" data set (l = 31, ci = 77, ri = 61, Figure 4c, d). On the cladogram obtained from Reid's (1990) soft body anatomical data (Figure 4b), the "?" codings of character 17 were optimized as 0 by the computer algorithm, and I interpreted the state of character 20 as a reversal in the ancestor to *L. saxatilis* and *L. obtusata*, though it is equally parsimonious to optimize the latter character state as a parallelism in *L. sitkana* and *L.*

littorea. This cladogram retained Reid's (1990) original ordering of the five littorinid species used in this study. On one of the pairs of cladograms obtained from the analysis of the "whole animal" data, the state of character 32 for the hypothetical outgroup was optimized as 1 and the state of character 15 for *L. obtusata* was equivocal, either 0 (as shown) or 1, according to the computer algorithm (Figure 4c); while on the other, the state of character 32 for the hypothetical outgroup was optimized as 2, and the state of character 15 for *L. obtusata* was optimized as 1 (Figure 4d). On both cladograms, the states of characters 19, 25, 27, 30, and 42 for the hypothetical outgroup were optimized as 1, the states of characters 13, 14, and 16 for *L. obtusata* were optimized as 0, and the state of character 33 for *L. obtusata* and *L. saxatilis* was optimized as 0. The analysis of the recoded data of Boulding et al. (1993) yielded a single cladogram (l = 15, ci = 100, ri = 100, Figure 4e) when losses of alleles were coded as independent states, while the data gave four cladograms (l = 13, ci = 100, ri = 100, Figure 5) when only alleles themselves were treated as character states. One of these four latter cladograms (Figure 5a) retained the original ordering proposed by Boulding et al. (1993) for the species used in this study. All five of these cladograms differed from the cladograms obtained from the analysis of the shell form parameter, soft body anatomical, and "whole animal" data.

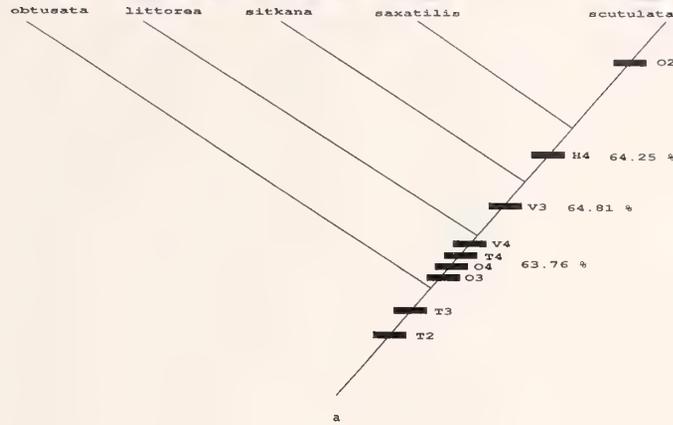
DISCUSSION

The phylogenetic tree (interpreted cladogram) based on shell parameters (Figure 4a) differs from that based on Reid's (1990) soft body anatomical characters (Figure 4b) in the positioning of two taxa—*Littorina obtusata* and *L. scutulata* switch; from the two trees resulting from the analysis of the "whole animal" data (Figure 4c, d), although the topology and ordering of taxa on one of the latter trees (Figure 4c) was identical to those of the tree based on Reid's (1990) data (Figure 4b); and from the distance-Wagner tree of Boulding et al. (1993), with *L. obtusata*, *L. scutulata*, and *L. littorea* switching positions (Figure 5a).

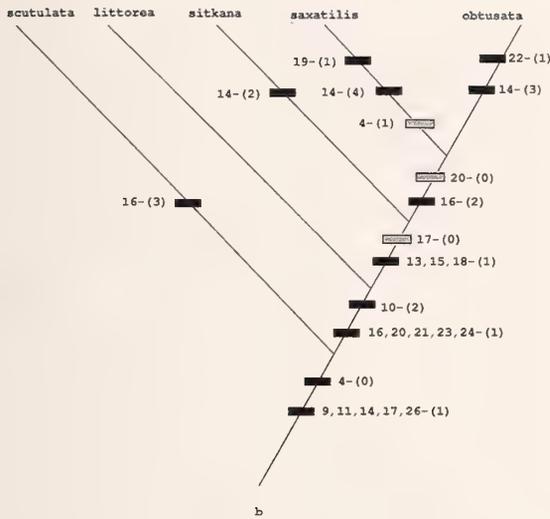
In summary, four sources of information—shell parameters, morphology, combined shell parameters and morphology ("whole animal"), and allozymes—lead to differ-

Figure 4

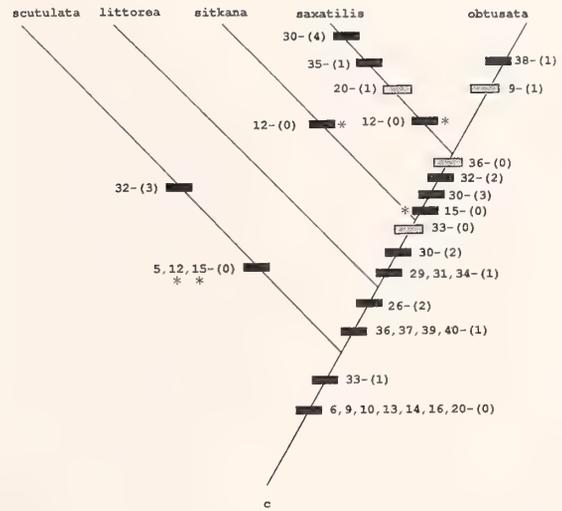
Analyses of five species of *Littorina*. 4a. Cladogram obtained from the analysis of shell parameter data, as described in this paper. Bootstrap values are placed beside the nodes they represent. 4b. Cladogram obtained from the analysis of morphological characters, as described by Reid (1990), recoded for species used in this study only. Four of the 27 steps occurred in outgroups (not shown). 4c and d. Cladograms obtained from the analysis of the combination of data sets used in a and b. 4e. Cladogram obtained from the analysis of the recoded allozyme data of Boulding et al. (1993); losses of alleles were coded as independent states. Synapomorphies indicated with black bars; parallelisms with black bars and *; reversals with gray bars. Computer-simulated forms, based on parameter values, are mapped onto the cladogram in 4a. Symbols used for species: littorina = *Littorina littorea*, obtusata = *Littorina obtusata*, saxatilis = *Littorina saxatilis*, scutulata = *Littorina scutulata*, and sitkana = *Littorina sitkana*. Characters are labeled (4a) or numbered (4b through e) as they appear in data matrices (Tables 2 through 4).



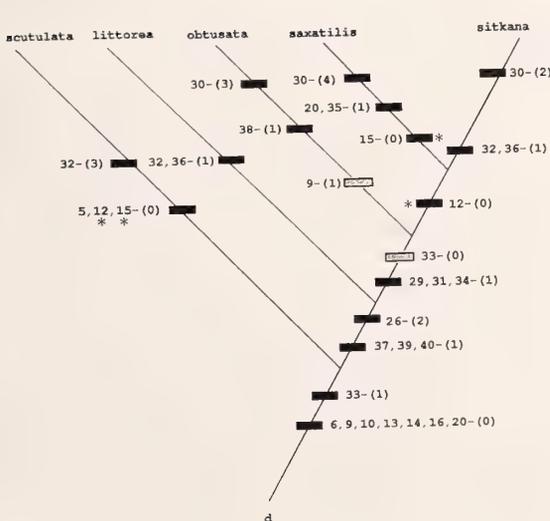
a



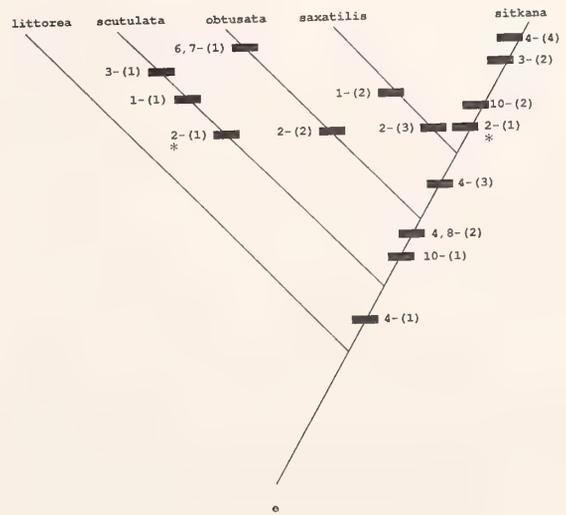
b



c



d



e

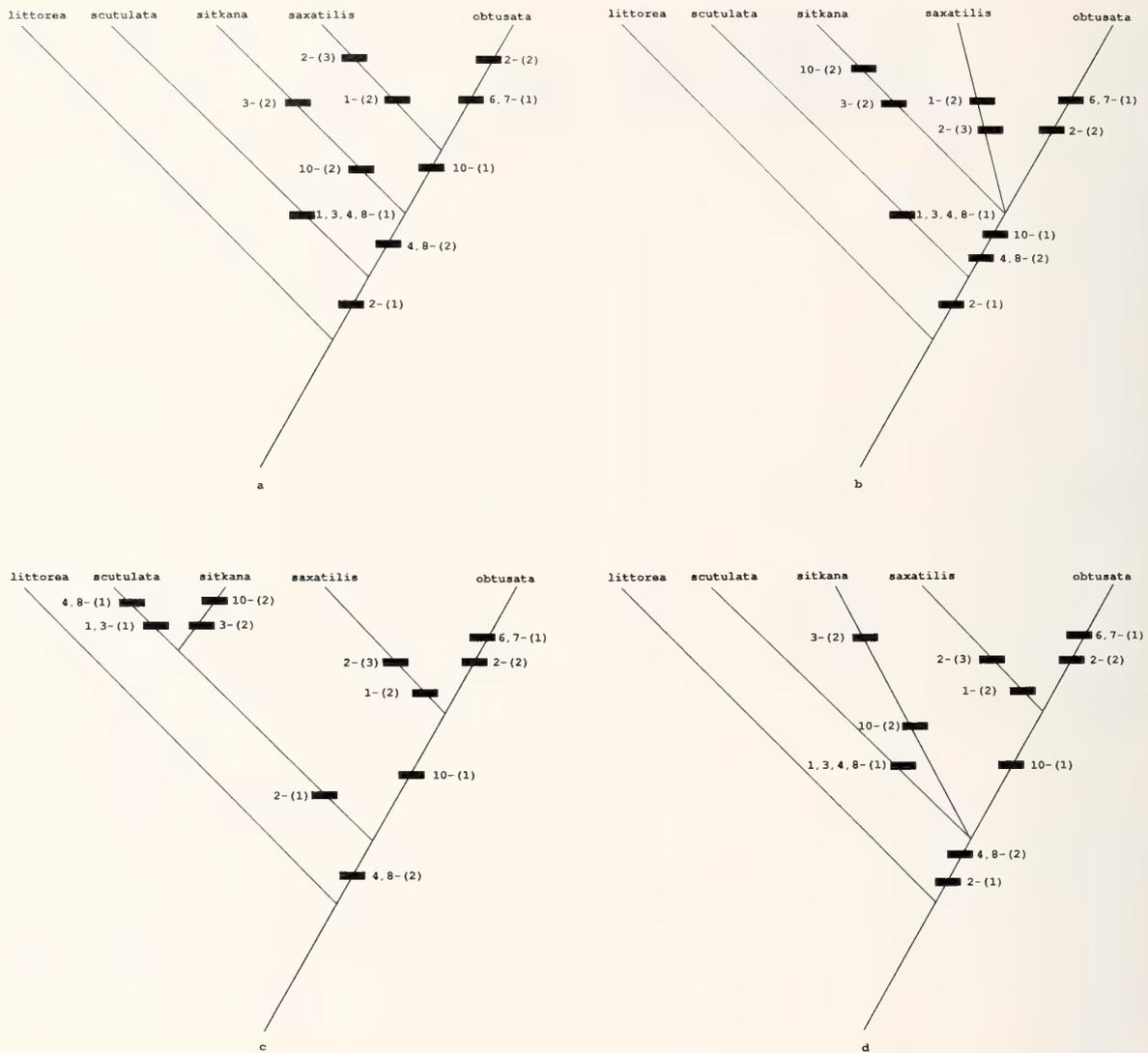


Figure 5

Topologies of cladograms resulting from recoded data of Boulding et al. (1993); loci were treated as characters and alleles as character states. The topology of the cladogram 5a retains the order proposed by Boulding et al. (1993) for the species used in this study. Species and character symbols appear as they do in Figure 4.

ent hypotheses of evolution of these five littorinid taxa. However, all agree that *L. littorea* is basal relative to *L. sitkana* and *L. saxatilis*, and that *L. saxatilis* originated late in the history of the ingroup.

The tree based on shell parameters indicates that, as a general trend, these littorinid shells have become narrower and relatively higher spired during the course of their evolution (Figure 4a). The states of characters V3 and H4 provide fine resolution for grouping clades, while the states of characters T2, O3, T3, O4, T4, and V4 group larger clades (Figure 4a). Characters V3 and H4 are features of the scaling of the aperture, while the set of characters T2, O3, T3, O4, T4, and V4 primarily consists of features of

the aperture trajectory. Given a particular aperture trajectory, the size of the aperture throughout growth determines the overall size of the shell. The shell parameter data set (Table 1) contains no 2 codings, hence, the shells of ingroup taxa have trajectories and scalings that are either insignificantly different (1) or are smaller (0) than those of the outgroups, at the 90% level of confidence. Therefore, in general, shells of ingroup species are smaller than those of the outgroups, and because horizontal aspects of shell form (parameters H and O) change to a greater extent than do vertical aspects (parameters T and V), ingroup shells are relatively higher spired.

The shape of an aperture determines, to a large extent,

the shape of the shell. Because changes in parameters only *represent* changes in growth geometries, one could explain interspecific differences in shell form, from an evolutionary perspective, in two ways: either apertures of the various ingroup species scale their apertures differently in their horizontal and vertical dimensions (as described in this study) or they rotate their apertures with respect to their coiling axes (approximately 90°—compare the orientations of apertures of the various shell forms in Figure 4a). The latter scenario would produce identical differences in shell forms as the former, but via different modes of *growth*. Of course, mapping shell forms onto a tree based on shell form parameters provides no new information, and thus, it serves simply as a visual summary of the data. No general trend in either shape or size is revealed when shell forms are mapped onto the other trees (Figure 4b–d, shell forms not shown).

Assumptions and Limitations of This Study

Throughout this analysis, I have assumed that similarities in shell forms result from genetically determined and inherited growth programs during the evolution of closely related taxa. However, littorinid shells are influenced by other (external) factors as well (Kemp & Bertness, 1984; Boulding et al., 1993; Palmer, 1990). Therefore, one must assume that ecophenotypic, external pressures influencing shell form do not confound internal, inherited growth geometries when employing this methodology. This is akin to one of the fundamental assumptions of cladistic methodology, namely that homoplasious character states are revealed against an overwhelming background of homologous character states, but at a different scale. Also, because shell forms may be plastic, the use of multiple outgroups can pose practical problems in character polarization, and, of course, the choice of outgroups itself might greatly influence the topology of the cladogram. For these reasons, I propose that shell parameters be used conservatively as a complement to other sources of data in phylogenetic systematic analyses.

It is possible that the shell parameter characters I used were partially correlated. The shape of the first aperture may have been a constraining character that effectively reduced the degrees of freedom of other characters. Nevertheless, a visual inspection of Table 1 indicates that shell parameters became more cladistically informative with an increase in whorl number. This was an artifact of the use of confidence intervals around predicted values from regression analysis: only when the values of the predicted measurements were large enough to make use of the confidence intervals as differentiating criteria were character states polarizable (see Figure 3). This artifact, in turn, may explain the intermediate bootstrap values on the cladogram (Figure 4a). Given the relatively low number of cladistically informative characters in the data set (Table 1), the sampling of an informative character was less probable than the sampling of an uninformative one but guar-

anteed that the particular node it characterized would be represented on the cladogram in the subsequent analysis.

Another possible criticism of the methodology, as I have presented it in this paper, is that I have used museum lots consisting of, at most, only 15 specimens from single localities in my analysis. Ideally, one would prefer access to larger sample sizes, representing multiple localities and a wider range of variation, in the coding and polarizing of character states.

Prospectus

Traditionally, gross features of shells have provided information for the identification and classification of snails. Contemporarily, allozyme data (e.g., Boulding et al., 1993) and gross anatomy of soft parts (e.g., Reid, 1989, 1990) have provided data for phylogenetic systematic analyses, while shell form has played a subordinate role.

But shells house an important source of information for gastropod phylogenies. Each shell is a history of that individual's ontogeny—data that can be extracted and used in a cladistic analysis. Furthermore, the shell usually is the only part of an individual that remains preserved, naturally or by museum curators. Thus, shell morphometry has much greater applicability to extensive museum collections or groups known only by holotypes than do other sources of data (Hillis, 1987). The paucity of specimens due to rarity of species, inaccessibility of collection sites, financial constraints on collecting, or extermination of habitats means that a large fraction of described species may never be collected again, thus rendering preserved museum specimens as the only source of data for the construction of evolutionary hypotheses (Hillis, 1987).

Finally, one might consider the influence that fossil specimens have on phylogenetic reconstruction. The exclusion of fossil forms can alter cladogram topologies, and thus influence inferred relationships among groups and hypotheses of character evolution within groups (Donoghue et al., 1989). Fossil taxa are most likely to exert these effects between clades separated by branches bearing many apomorphies (Donoghue et al., 1989). These apomorphically saturated internodes suggest the existence of organisms with character combinations, equivalent to growth geometries in this study, not found among extant groups (Donoghue et al., 1989). Thus, again, shells provide an important source of data that may have been overlooked. This important source of information ought to be tapped and utilized to complement other data in the construction of phylogenetic hypotheses.

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Taxonomic Remarks on Cenozoic Pseudolivid Gastropods from South America

by

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Abstract. The neogastropod family Pseudolividae was represented in the Neogene of Peru and Chile by a single genus, which we name *Testallium* to replace *Gastridium* Sowerby, 1846, non *Gastridium* Sowerby, 1842, or *Gastridium* Modeer, 1793. Besides the type species, *Testallium cepa* (Sowerby, 1846), from the Miocene of Peru and Chile, we recognize *T. voluta* (Olsson, 1932) from the early Miocene of northern Peru, and *T. escalonia*, sp. nov. from the Pliocene of Chile. *Gastridium retusum* Philippi, 1887, is assigned to *Buccinorbis* Conrad, 1865.

INTRODUCTION

The family Pseudolividae is a poorly known group of Late Cretaceous to Recent gastropod mollusks that, on the basis of shell characters as well as internal anatomy, belongs to the neogastropod superfamily Buccinoidea (see Cossmann, 1901; Squires, 1989; Kantor, 1991). Although the bathyal genus *Benthobia* Dall, 1889, is widely distributed in the Atlantic and southwestern Pacific Oceans, Recent shallow-water members of the Pseudolividae are restricted to subtropical and warm-temperate waters in western and southern Africa, the Australian region, and the west coast of North America. During the Miocene and Pliocene, however, the family was also represented on the west coast of South America by an extinct genus that has been referred to as *Gastridium* Sowerby, 1846. Unfortunately, *Gastridium* was preoccupied by *Gastridium* Sowerby, 1842, and Modeer, 1793. The distinctive South American Neogene pseudolivids therefore require a new generic name. In this paper, we (1) propose the genus *Testallium* for three Miocene and Pliocene pseudolivid species from Peru and Chile; (2) compare *Testallium* to other pseudolivid genera; (3) review the described species assigned or compared to *Gastridium* Sowerby, 1846, by previous authors; and (4) describe *Testallium escalonia*, sp. nov. from strata of probable Pliocene age in Chile.

Institutional abbreviations are as follows: BMNH, British Museum of Natural History, London, England; CAS, California Academy of Sciences, San Francisco, California, USA; PRI, Paleontological Research Institute, Ithaca, New York, USA; SGO PI, Museo Nacional de Chile, Instituto de Paleontología, Santiago, Chile; UCMP, Museum of Paleontology, University of California, Berkeley, California, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Order Neogastropoda

Superfamily BUCCINOIDEA

Family PSEUDOLIVIDAE Cossmann, 1901

Discussion: Kantor (1991) has made cogent arguments for recognizing the Pseudolividae as a family distinct from such other families as the Buccinidae and Olividae with which it had previously been associated as a subfamily. In fact, anatomical peculiarities of the group prompted him to isolate the Pseudolividae in its own suborder Pseudolividae. This taxon was characterized by the presence of

a gland and valve of Leiblein, and by having the proboscis formed by the elongation of the buccal tube rather than by the elongation of the dorsal wall of the buccal cavity as in the suborder Muricoidei (Kantor, 1991). The most obvious shell character that distinguishes Pseudolividae from the Buccinidae (*sensu lato*) is the presence of a basal external spiral groove, which ends in a more or less prominent tooth or spine at the edge of the outer lip (Cossman, 1901). Other shell features that collectively set the Pseudolividae apart from other neogastropod groups include the following: notch or sinus at posterior end of outer lip; outer lip lying in a plane; spiral sculpture consisting of cords or threads that are strongest near base and weakest near upper part of whorl; aperture narrowly elongate; columella more or less concave on upper part, smooth; siphonal canal short to almost absent. Genera are distinguished on the presence or absence of apertural lirae (spiral riblets on the inner side of the outer lip), axial sculpture, an umbilicus, and a parietal rib, as well as on shell shape. A general review of the family by Vermeij is in progress.

Genus *Testallium* Vermeij & DeVries, gen. nov.

Gastridium Sowerby, 1846: p. 261; non *Gastridium* Sowerby, 1842: p. 312 (= *Pseudoliva* Swainson, 1840) (type species, *Buccinum plumbeum* Chem., = *Buccinum crassum* Gmelin, 1791); non *Gastridium* Modeer, 1793: p. 106 (type species: *Conus geographus* Linnaeus, 1758; Gastropoda: Toxoglossa: Conidae).

Type species: *Gastridium cepa* Sowerby, 1846 (pl. 1, figs. a, b)

Diagnosis: Pseudolid characterized by deep basal external groove terminating at outer lip in blunt labral spine; last whorl basally constricted above siphonal fasciole; fasciole adapically keeled; sculpture consisting of fine spiral threads over whole surface of shell above groove, and of two to eight strong spiral cords below groove; outer lip forming notch at adapical end of aperture; inner side of outer lip smooth; columellar callus of small extent; umbilical slit narrow or absent; parietal rib at adapical end of inner lip distinct.

Etymology: *testa* (Latin: shell) and *allium* (Latin: onion), referring to the specific name *cepa* (Latin: onion) of the type species.

Discussion: Sowerby (1842, p. 312) named the genus *Gastridium* to include *Buccinum plumbeum* Chem. (= *Buccinum crassum* Gmelin, 1791). In 1846 (p. 261), he introduced the name *Gastridium* again as a new genus, this time for *Gastridium cepa* Sowerby, 1846, a Miocene species collected by Charles Darwin in 1833 at Navidad on the central coast of Chile. In his 1846 paper, Sowerby (p. 261) noted that *G. cepa* was similar to *Buccinum plumbeum*, and that Swainson (1840, p. 82, p. 306) had made the latter species the type of *Pseudoliva* Swainson, 1840. Sowerby (1846) considered the name *Pseudoliva* "absurd" because *B. plumbeum* in his mind clearly belonged to the

"Buccini" rather than to the "Olivi." In fact, Sowerby assigned *B. plumbeum* to the buccinid genus *Eburna* Lamarck, 1822 (non Lamarck, 1801), whose oldest valid name is *Babylonia* Schlüter, 1838 (see van Regteren Altena & Gittenberger, 1981). Philippi also disliked the name *Pseudoliva*, and applied *Gastridium* Sowerby, 1846, to *G. cepa* and two other species, *G. opimum* (Hupé, 1854) and *G. retusum* (Philippi, 1887). The objective synonymy of *Gastridium* Sowerby, 1842, and *Pseudoliva* Swainson, 1840, was recognized by most subsequent authors, including Sowerby (1859), Cossman (1901), Melvill (1903), and Wenz (1938–1944). Moreover, the name *Gastridium*, as used by Sowerby (1842, 1846), was preoccupied by *Gastridium* Modeer, 1793 (p. 106), a well-known Indo-Pacific Recent member of the toxoglossan gastropod family Conidae. Gray's (1847, p. 136) introduction of *Gastridia* resolved the homonymy of *Gastridium*, but his name falls as an objective synonym of *Pseudoliva* because it was based on the same type species, *Buccinum plumbeum*. Sowerby (1846), Philippi (1887), and Olsson (1932) all regarded *Gastridium* in Sowerby's (1846) sense as distinct from *Pseudoliva*, but none of these authors offered distinguishing characters for the two groups. We agree that Sowerby's (1846) *Gastridium* refers to a distinct group, and propose the new genus *Testallium* for it.

Testallium differs from *Pseudoliva* in shape, sculpture, and the development of callus. Whereas *Testallium* is constricted (that is, distinctly concave in profile) just above the base of the siphonal canal, *Pseudoliva* is weakly convex to almost straight-sided. The fasciole of *Testallium* is prominent, marked by a keel-like posterior angulation. That of *Pseudoliva* is indistinct and rounded. *Testallium* has two to eight spiral cords below the basal groove, which conspicuously crenulate the edge of the outer lip; and numerous spiral threads between the groove and the suture. Earlier whorls carry fewer, somewhat stronger cords on the upper portion of the whorl. *Pseudoliva*'s shell, by contrast, is essentially smooth except for the basal groove. The columellar callus of *Testallium* is limited in extent, whereas that in *Pseudoliva* is broad, thick, and heavy, obscuring the basal groove on the ventral half of the last whorl.

Another similar genus is *Buccinorbis* Conrad, 1865, species of which are known from the late Paleocene (Thanetian) to the late Eocene (Priabonian). Like the Miocene to Recent West and South African *Pseudoliva*, it has extensive columellar callus, and the base is not constricted; but the groove is located relatively higher on the last whorl (see also Squires, 1989). Three to five strong spiral cords below the groove form well-defined crenulations on the edge of the outer lip below the labral spine (see also Palmer, 1937). *Buccinorbis* differs from *Testallium* by the absence of basal constriction, the large, heavy columellar callus, and the absence of a parietal rib at the adapical end of the inner lip.

The western North American early Miocene to Recent genus *Macron* H. & A. Adams, 1853, differs from *Testallium* chiefly by possessing lirae on the inner side of the

outer lip. The type species, *Buccinum aethiops* Reeve, 1847, is often extremely prominently sculptured with two heavy, rounded cords below the groove and up to six spiral cords above the groove. Other species, however, such as the early Miocene *M. hartmanni* Hertlein & Jordan, 1827 and the Pleistocene to Recent *M. lividus* A. Adams, 1855, and *M. orcutti* Dall, 1918, have fine spiral threads on the last whorl between the groove and the suture, and in this respect strongly resemble species of *Testallium*.

Testallium is strongly convergent on the Miocene to Recent western South American ocenebrine muricid genus *Chorus* Gray, 1847. Both genera have a broadly fusiform, basally constricted shell with a basal spiral groove ending in a labral spine at the edge of the outer lip. *Chorus* differs from *Testallium* by the absence of a posterior sinus in the outer lip, by lacking a parietal rib, and by having an indistinct, rounded siphonal fasciole rather than a markedly angulated one. The basal groove is also shallower and less conspicuous in *Chorus* than in *Testallium*. Moreover, *Chorus* has spiral sculpture consisting of six to seven widely separated primary spiral cords on the last whorl, which do not increase in prominence basally.

Testallium cepa (Sowerby, 1846)

(Figure 1a, b)

- Gastridium cepa* Sowerby, 1846, p. 261, pl. 4, figs. 68, 69.
Monoceros labiale Hupé, 1854: pp. 199–200.
Monoceros opimum Hupé, 1854, p. 200.
Fusus labialis Hupé, 1854, pl. 3, fig. 3a.
Fusus opimus Hupé, 1854, pl. 2, figs. 6, 6a.
Gastridium cepa Sowerby, 1846: Philippi, 1887, pp. 59–60, pl. 6, fig. 2.
Monoceros labialis Hupé, 1854: Philippi, 1887, pl. 5, fig. 1; not pl. 5, fig. 6 (indeterminate species).
Gastridium opimum (Hupé, 1854): Philippi, 1887, p. 60, pl. 57, fig. 7.
Chorus aff. *C. blainvillei* (d'Orbigny, 1842): Watters & Fleming, 1972: p. 398, pl. 28, fig. 6u; non *Chorus blainvillei* (d'Orbigny, 1842) (Muricidae).
Gastridium cepa Sowerby, 1846: Tavera Jerez, 1979, p. 97, pl. 20, figs. 74, 75.

Discussion: *Testallium cepa* is a highly variable species, a fact that accounts for its long synonymy. The most variable character is the shoulder. The posterior (or anal) notch is strongly produced in the type specimen of *T. cepa*, and the shoulder is correspondingly well developed. Hupé's (1854) *Monoceros opimum* (labeled *Fusus* on his plate, and assigned to *Gastridium* by Philippi, 1887) represents an unshouldered shell in which the posterior notch is not produced. *Monoceros labiale* Hupé, 1854 (labeled *Fusus* on Hupé's plate, and assigned to *Monoceros* by Philippi, 1887) is intermediate between the *cepa* and *opimum* phenotypes. Philippi's (1887) illustration of *Gastridium opimum* (Hupé, 1854) (pl. 5, fig. 7) is indistinguishable from his illustration of *Monoceros labialis*.

Fleming (in Watters & Fleming, 1972) figured a poorly preserved specimen of *Testallium cepa* as *Chorus* aff. *C.*

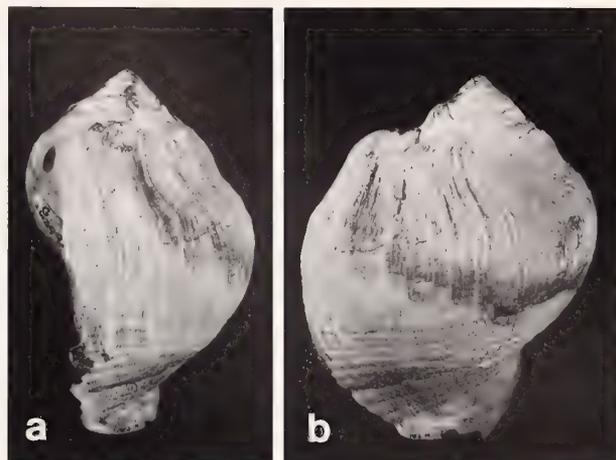


Figure 1

Testallium cepa. Holotype (BMNH G 26399); a, b. lateral and dorsal views. The shell is 5.5 cm in height.

blainvillei (d'Orbigny, 1842) from strata inferred to have been of early Pliocene age at Chepu, on Isla Chiloe, in southern Chile. They favored a Pliocene age in part because *Chorus* and several other genera in the fauna were not known from the Miocene at that time. The presence of distinctive Miocene fossils persuades us, however, that the Chepu beds are of late early Miocene age, and that they are correlated with the similarly aged strata of the Navidad Formation, from which *T. cepa* was originally collected (DeVries & Vermeij, in preparation). Fleming noted that the spiral sculpture of his specimen was weak, that the spire was higher, and that the shell was narrower than that of *Chorus blainvillei*. Moreover, his specimen lacked the nodes characteristic of *C. blainvillei*, a Pliocene species. Fleming's specimen represents a moderately shouldered form of *Testallium cepa*.

Two probably unrelated gastropods are strongly convergent in form, as well as in the expression and variability of the shoulder, to *Testallium cepa*. The Recent Panamic rapanine muricid *Vasula melones* (Duclou, 1832) often forms a keel-like ridge at the shoulder in its final stages of growth, whereas younger shells are weakly shouldered or rounded on the upper part of the last whorl. Every gradation between strongly shouldered and rounded shells can be found within populations throughout the range of the species. The "buccinid" *Triumphis distorta* (Wood, 1828), also from the Panamic Province, also shows a keeled, ridgelike shoulder in the adult stage and a rounded profile of the upper part of the body whorl in younger shells. It is striking that both *Vasula melones* and *Triumphis distorta* occur in rocky areas with intermixed sand, a habitat similar to that of the pseudolivids *Pseudoliva crassa* (Gmelin, 1791) and *Luzia zebrina* (A. Adams, 1855) in Angola (S. Gofas, personal communication to G. Vermeij, July, 1995).

Testallium occupied a similar habitat in Peru and Chile. In Chile, *T. cepa* is found in pebbly sandstones of probable

early Miocene age (DeVries & Vermeij, in preparation) near basement rocks at Punta Ahuenco on the east coast of Chiloe (Watters & Fleming, 1972); in massive sandstones at Islas Ipun and Stokes, south of Chiloe (DeVries et al., 1984); and in fine to medium-grained sandstone in the Navidad basin (Tavera Jerez, 1979), sometimes in strata with intercalations and lenses of gravel. In the Pisco Basin of southern Peru, specimens of *Testallium* are found in coarse-grained sandstones at numerous localities. At Callejon de Cerro de Piedra, near Nazca (Rivera, 1957), specimens of *T. cepa* occur with numerous specimens of *Turritella woodsi* Lisson, 1925, in probably early Miocene conglomerates and coarse-grained sandstones directly overlying basement crystalline rocks. In the Lomas Chilcatay, east of Bahía de la Independencia, specimens of *T. cepa* are found together with a diverse assemblage of early early Miocene mollusks in basal sandstones of the Chilcatay Formation and in bioclastic, balanid-rich sandstones higher in the same section that have been dated as late early Miocene (Dunbar et al., 1990).

Distribution: Early Miocene (*Rocella gelida* Zone to *Triceratium pileus* Zone, about 24–18 Ma; H. Schrader, written communication, 1987), southern Peru to southern Chile.

Testallium voluta (Olsson, 1932)

Acanthiza (*Chorus*) *voluta* Olsson, 1932: pp. 184–185, pl. 19, figs. 3, 6, 7.

Discussion: *Acanthiza* Fischer is probably a misspelling of *Acanthina* Fischer de Waldheim, 1807, another genus with a labral spine from western South America. *Chorus* Gray, 1847, is yet another genus with a labral spine from the same region. Olsson (1932) compares *T. voluta* with *Monoceros laevis* Philippi, 1887 (= *Chorus laevis*). Specimens of *T. voluta* are distinguished from those of both *Acanthina* and *Chorus* by their strong axial folds on the earliest whorls and anal notch.

Differences between *T. voluta* and *T. cepa* are more subtle. Specimens of both species show strong spiral cords on the earliest whorls, but only *T. voluta* shows any axial sculpture. What most distinguish specimens of *T. voluta* are a short siphonal canal (well under half the apertural length) and, in adult specimens, a weak to moderate sulcus on the body whorl that lies anterior to a moderately angulate, tabulate shoulder. Shouldered specimens of *T. cepa*, in contrast, have sloping shoulders, no sulci so low on the body whorls, and moderately produced siphonal canals (equal to half the apertural length).

T. voluta was considered by Olsson (1932) to be ancestral to *Clavella solida* Nelson, 1870, from the late Miocene Cardalitos Beds of northern Peru (Olsson's 1932 figure of *T. voluta* is excellent, and the reader is referred to it for illustration). Olsson (1932) assigned Nelson's species to what he called *Acanthiza* (*Chorus*). Our examination of type material of *Clavella solida* (Yale Peabody Museum YPM 00507) reveals that *C. solida* has strong axial ribs on early teleoconch whorls, as does *Testallium voluta*, but it lacks the basal groove of *T. voluta* and other species of

Testallium. Apertural features are obscured by matrix. Nelson (1870, p. 199) suggested that *Clavella solida* is related to *Triumphis distorta* (Wood, 1828). We tentatively assign it to the genus *Nicema* Woodring, 1964, which is usually included with *Triumphis* Gray, 1857, in the family Buccinidae (see Woodring, 1964).

Specimens of *T. voluta* from northern Peru are filled with a coarse-grained bioclastic matrix. Olsson (1932) proposed with some uncertainty that they were collected at the base of shales from the Heath Formation, overlying Punta Bravo "grits." Olsson (1932) believed the Heath Formation to be of Oligocene age, but subsequent work by Zuñiga & Cruzado (1979) indicates its age to be early Miocene.

Testallium escalonia Vermeij & DeVries, sp. nov.

(Figure 2a, b)

Diagnosis: *Testallium* with a relatively high spire (spire one-fourth to one-third shell height), 17 to 23 fine spiral threads on last whorl, and narrow umbilical slit.

Description: Shell relatively high-spined, consisting of five teleoconch whorls separated by shallow, appressed sutures; spire one-fourth to one-third total shell height; sculpture consisting of two cords below basal groove, and 17 to 23 fine spiral threads between the groove and the suture on the last whorl, increasing in strength toward the base; last quarter of body whorl marked with closely spaced growth lines; groove terminates in small blunt labral tooth at edge of outer lip; fasciole prominent, sharply angled posteriorly, rounded below; narrow umbilical slit on inner side, edge faintly crenulated in accordance with external spiral sculpture; columella bearing five or six low oblique ridges on lower half; weak anal notch where outer lip joins penultimate whorl posteriorly.

Holotype: CAS 66806.01, height 34.0 mm, diameter 24.2 mm, aperture height 25.4 mm.

Paratype 1: CAS 66806.02, height, 28.9 mm, diameter 19.7 mm, aperture height 21.4 mm.

Paratype 2: UCMP 39880, height 25.4 mm, diameter 15.8 mm, aperture height 20.5 mm.

Type locality: El Ganso (*ganso* = goose), 34°13'S, west of Fundo Las Damas, also known as the La Cueva Locality. La Cueva Formation of probable late Pliocene age, Chile.

Etymology: Latin noun for small onion.

Discussion: *Testallium escalonia* differs from the older *T. cepa* chiefly in having a higher spire (spire one-fourth to one-third as compared to one-seventh of shell height as in *T. cepa*) and in being less constricted at the base of the siphonal canal, which is relatively shorter. Herm (1969) did not record this or any other species of *Gastroidium* (our *Testallium*) from the Pliocene of Chile. Oddly enough, the holotype and Paratype 1 were collected by Herm. He

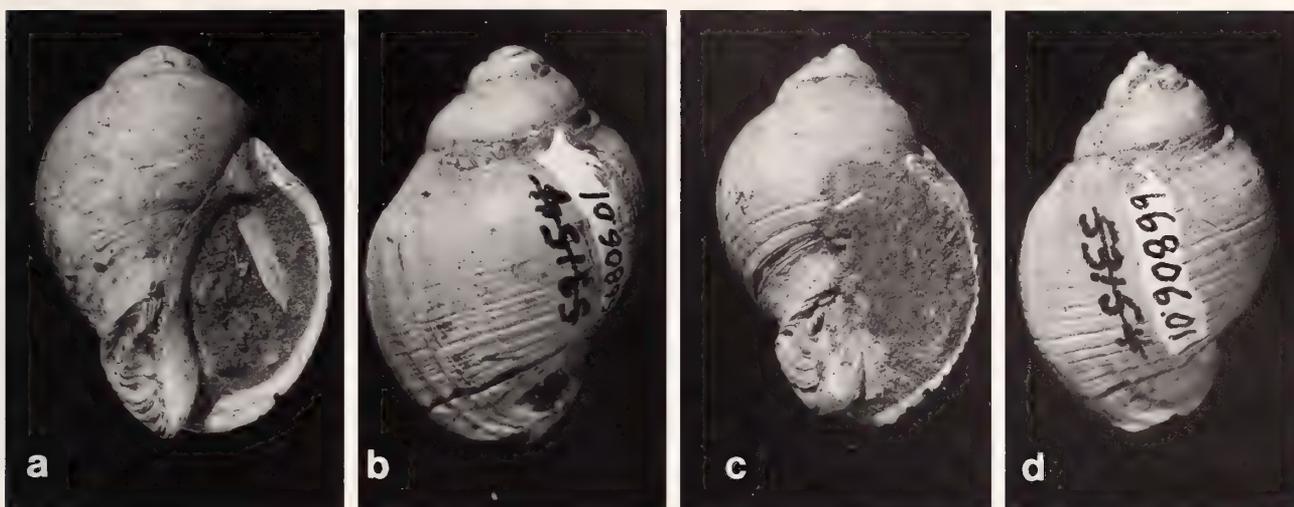


Figure 2

Testallium escalonia. Vermeij & De Vries, sp. nov. a, b. holotype (CAS 66806.01), ventral and dorsal views; c, d. paratype 1 (CAS 66806.02), ventral and dorsal views. The holotype (a, b) is 4 cm in height; the paratype (c, d) is 3.5 cm in height.

may have mistaken them for worn specimens of the muricid genus *Chorus*, which superficially resembles species of *Testallium*.

The precise age of the La Cueva fauna is not entirely clear, but it appears to be Pliocene (Herm, 1969).

Testallium escalonia is the youngest known species of its genus. Along with many other genera and species, *Testallium* evidently became extinct near the end of the Pliocene in western South America.

Genus *Buccinorbis* Conrad, 1865

Type species. *Buccinum vetustum*, Conrad, 1833

Buccinorbis retusa (Philippi, 1887)

Gastridium retusum Philippi, 1887. p. 59, pl. 6, fig. 3, 3b.

Pseudoliva parinasensis Woods, 1922, p. 93–94, pl 12, figs. 4–6.

Pseudoliva parinasensis Woods: Olsson, 1928, p. 123.

Discussion: Philippi (1887) recognized three species of *Gastridium*: *G. cepa* Sowerby, *G. opimum* (Hupé), and *G. retusum*, Philippi, 1887. Of these, the first two are referable to a single species of *Testallium* (see above), but *G. retusum* is distinct. A cast of Philippi's holotype (SGO PI 765), as well as Philippi's figures, shows that the species belongs to *Buccinorbis* Conrad, 1865. Like other species of *Buccinorbis*, *B. retusa* has the spiral groove at a relatively high position on the last whorl, and lacks basal constriction. There is a strongly developed columellar and parietal callus. None of the known specimens has the aperture exposed or the outer lip intact. Philippi (1887) thought *B. retusa* to be of Cretaceous age, but strata at the type locality (Algarrobo, Chile) are Eocene (Tavera Jerez, 1979).

Judging from the figures, *Pseudoliva parinasensis* Woods,

1922, from the early Eocene of northern Peru, is a subjective synonym of *B. retusa*. We have been unable to locate Woods's holotype to confirm this suspicion. According to Olsson (1928), *B. parinasensis* occurs in the Salina, Negritos, and Parinas Formations of early to middle Eocene age. The extent of callus formation is variable in this species, as is the strength and extent of spiral sculpture on the last whorl between the spiral groove and the suture. The specimen described from the middle Eocene of Colombia as *Pseudoliva (Buccinorbis)* cf. *P. (B.) parinasensis* by Clark & Durham (1946) differs from *B. retusum* and Woods's *P. parinasensis* from Peru by possessing an umbilicus. This feature may well have been variable in *B. retusa*, but we prefer to keep Clark & Durham's (1946) Colombian *parinasensis* form outside the limits of *B. retusa*.

Olsson's (1928) variety *samanica* from the late Eocene Talara and Saman beds (=Verdun Formation) of northern Peru is more heavily callused, larger, and less rotund than is *B. retusa*, and has a narrower anterior end. Forms questionably assigned to this variety were described from the late Eocene of Colombia (Clark & Durham, 1946) and Curaçao (Jung, 1974). Olsson's (1928) variety *mancorensis* has a laterally flattened rather than an evenly rounded last whorl and a massive callus in the columellar and parietal regions of the shell. The final stages of growth are characterized by adapical migration of the outer lip and by the increasing prominence of the shoulder. This variety was described from the Chira, Mancorá, and Heath Formations, all regarded as Oligocene by Olsson (1928). The Mancorá and Chira Formations, however, are of latest Eocene age (Zuñiga & Cruzado, 1979), and the occurrence of the *mancorensis* form in the Heath Formation, which is early Miocene, is questionable. We tentatively retain the varieties *samanica* and *mancorensis* of Olsson, 1928, as

stratigraphic subspecies of *B. retusa*, but further work and additional material may reveal that all are members of a single, long-ranging species in which whorl profile, callus development, late-stage shouldering, expression of spiral sculpture, and size are all highly variable traits. *Pseudoliva* (*Buccinorbis*) *vientoensis* Clark & Durham, 1946, from the Eocene of Colombia, may also prove to part of this variation.

ACKNOWLEDGMENTS

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First Record of a Sacoglossan
(= Ascoglossan, Opisthobranchia) from Patagonia
(Argentina): Description of a
New Species of Genus *Elysia* Risso, 1818

by

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Abstract. A new species of the genus *Elysia* Risso, 1818, is described: *Elysia patagonica* sp. nov. The material examined represents the first sacoglossan species recorded from the Argentinean coast (San Jorge Gulf, 45°58'S, 67°34'W, Patagonia). The study is based on systematic descriptions and biological information recorded during the austral summer, from 40 living specimens collected from the same locality. *Elysia patagonica* is distinguished from Atlantic *Elysia* species. The presence of *Elysia patagonica* at this latitude greatly extends the known range of the order Sacoglossa (= Ascoglossa) in South America.

INTRODUCTION

The order Sacoglossa Ihering, 1876, has never been reported among studies of the opisthobranch mollusks from Argentina. The most comprehensive studies of the Magellanic Province mollusks have been: Carcelles, 1950; Carcelles & Williamson, 1951; Scarabino, 1977; and Castellanos et al., 1987, 1993.

Marcus (1980) carried out the most recent revision for the genus *Elysia* Risso, 1818, from the western Atlantic, in which the distribution of species extended from Nova Scotia (45°N, 65°W) to Brazil (24°S, 45°W), with no existing records of its presence at any more southerly points.

The first record of a sacoglossan for the Argentinean coasts is reported in this paper, with descriptions of the

external morphology and anatomy, and comments on the ecology and biology of this new species. The species is compared with other *Elysia* species, principally those present in the Atlantic Ocean.

MATERIALS AND METHODS

Forty specimens of *Elysia* were collected at Punta Marqués (45°58'S, 67°34'W), San Jorge Gulf, in the Magellanic Province, according to Balech's (1954) biogeographic division (Figure 1). Specimens were collected by the former author on intertidal rocks, in tide pools during low tide, in the austral spring and summer (Table 1). A mean surface temperature of 16°C was measured in tide pools ($n = 30$; between 12/26/94 and 01/05/95). Total live length was measured. The animals were maintained in aquaria for several days to obtain information about their feeding and reproductive behavior. After live study, they were frozen in seawater for 3 to 5 hours to obtain totally

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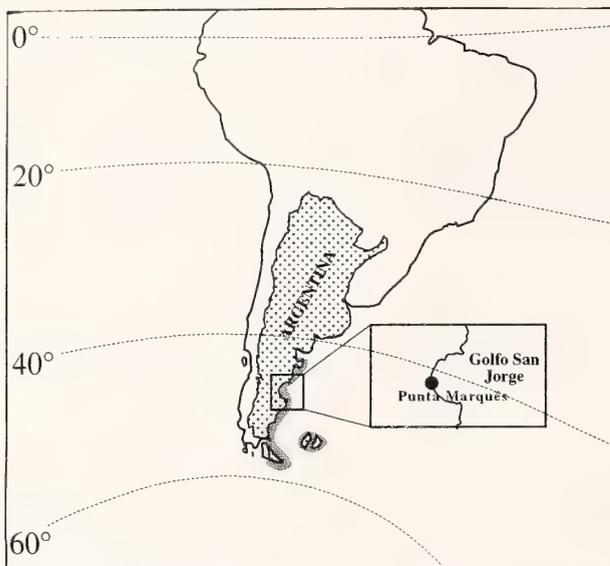


Figure 1

Map of South America, showing the Atlantic Magellanic Province (dark shadow) and the type locality of *Elysia patagonica* Muniain & Ortea, sp. nov.

opened parapodia; later they were fixed in formaldehyde seawater 4%. This technique makes it easier to obtain a detailed description of the pericardial region and to assess the dorsal vessel distribution. Several specimens were dissected and their internal organs described. The radula and penis (critical point dried) were examined by scanning electron microscope (SEM).

The material examined is deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires).

SYSTEMATICS

Elysia patagonica Muniain & Ortea, sp. nov.

(Figures 2–8)

Type material: The holotype (MACN 33780, 01/09/95, 51 mm) and four paratypes (MACN 33880, 01/09/95, 36 mm (dissected), 33 mm, 49 mm, and 38 mm).

Diagnosis: Large species. Intense dark green coloration speckled densely by silvery and bluish spots throughout the body surface. Patch of white iridescent spots over the medial dorsal region of the head. Ample parapodia with extensive folds and dorsal vessels well developed. Globular renopericardial prominence, two principal dorsal vessels and many branching lateral. Blade-shaped teeth with blunt tips and finely denticulate cutting edges.

External morphology: The specimens collected are between 9 and 70 mm (total length alive). Intense dark green

Table 1

Examined material of *Elysia patagonica* from Punta Marqués (Patagonia). Date: collection date, *n*: sample size, Size: length range (mm), Alga: seaweed where the animals were collected.

Date	<i>n</i>	Size	Alga
11 Jan. 92	9	28–50	<i>Bryopsis plumosa</i>
26 Oct. 92	3	18–26	<i>Bryopsis plumosa</i>
20 Dec. 93	1	36	<i>Bryopsis plumosa</i>
31 Dec. 94	12	17–43	<i>Bryopsis plumosa</i>
4 Jan. 95	1	9	<i>Codium</i> sp.
9 Jan. 95	14	32–70	<i>Bryopsis plumosa</i>

coloration like the host algae, speckled with silvery and bluish spots densely distributed throughout the parapodial surface. The size of spots varies, appearing as white iridescent blotches on the parapodial edges (Figure 2A). A conspicuous aggregation of white spots is present over the medial dorsal region of the head, constituting a patch (Figure 2B). This patch varies among animals, but it is always conspicuous (Figure 3). The expanded parapodia and edges exhibit extensive folds, giving them a leaflike appearance. The maximum parapodial width is between 20 and 38 mm. The renopericardial prominence is situated behind the head, and it has a marked globular aspect with small branching veins on the anterior portion. Over the rest of it, cream coloration can be observed through the "translucent" mantle. Around the heart region, there is a smooth ring, with spots as noted over the rest of the body. The dorsal vessels are well developed. The branching of the lateral dorsal vessels begins from two parallel trunks that start in the pericardial area and end at the posterior parapodial region. In some large animals, this vessel distribution forms a dark smooth band around the parapodia. The dark appearance of this band is due to the fact that the vessel distribution does not reach the parapodial edge (Figure 4).

Ventrally, the parapodia are completely smooth, without vessels, but with identical coloration to the dorsal surface. The foot is light yellow in color, dorsally visible only in the anterior portion, projecting beyond the sides of the head (propodium) (Figure 2D). The sole foot has an anterior transverse groove, situated below the neck end. The size of the metapodium coincides with the head and neck length. The head and rhinophores are the same color as the rest of the body, but the end of the rhinophores is lighter. In the largest specimens, the head is often covered by folds of the large parapodia. The eyes are located laterally, behind the rhinophores. The rhinophores are long and rolled, with a wide groove. The anal papilla is prominent on the right side, just anterior to the renopericardial prominence.

Anatomy: Internal organs are situated between the head and pericardial region, occupying one-third of the body

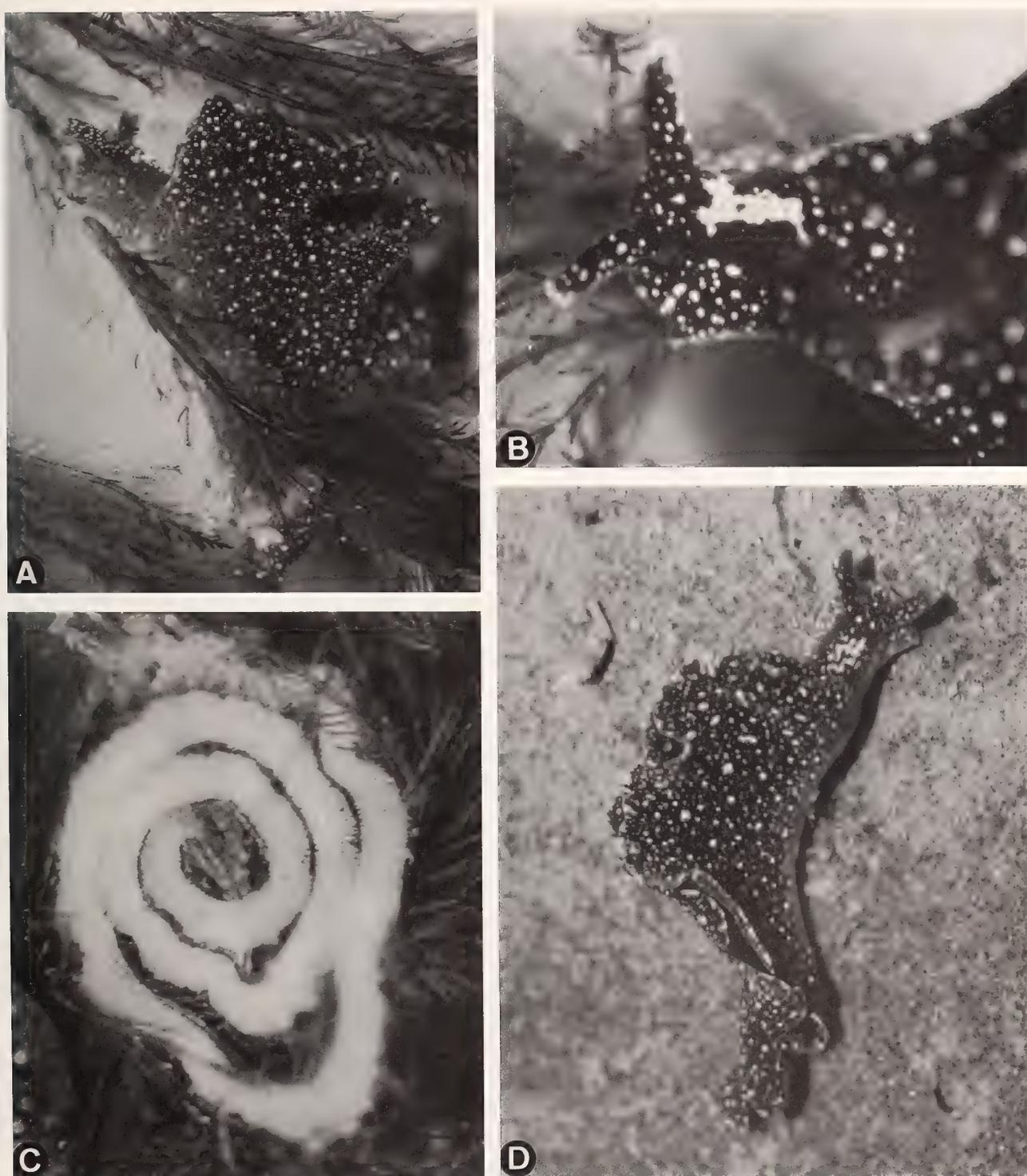


Figure 2 (A-D)

Living animals of *Elysia patagonica* Muniain & Ortea, sp. nov. A. Animal feeding on *Bryopsis plumosa*. B. Dorsolateral view of the head showing the patch of white spots. C. Spawn eggs on the host algae. D. Specimen (35 mm) with closed parapodia, projecting the foot beyond the sides of the head.



Figure 3

Dorsal view of three different heads showing variations in the patch of white spots.

length. The rest of the body is represented by parapodial extension, where the digestive vessels and some reproductive follicles are situated throughout the surface.

Digestive tract. The pharynx is 1.2 mm (length) with a well-developed dorsal septate muscle and a short ascus muscle. At the beginning of the esophagus, there is a nerve ring with the main ganglia (two pedal, two cerebral). At both sides of the esophagus, there are two long and narrow salivary glands. At the end of the esophagus, a muscular esophageal pouch opens. The stomach is ample in its first section (ventral); from it, a long main duct of the digestive gland extends in the parapodial caudal direction. The second section (dorsal) is elongated, muscular, and thinwalled.

The intestine is expanded; the epithelium is strongly muscular (Figure 5A).

Radula. The ascending limb of the radula in the 40 mm individual (length alive) contains seven fully formed teeth, one partially formed tooth at the beginning, nine in the descending limb, and many discarded teeth in the ascus (Figure 6A). The teeth are blade-shaped and finely denticulate in the cutting edges. The longest tooth is the first in the descending limb (approx. 230 μm). Each tooth shows a developed "hooked-base" (Figure 6B-F).

Reproductive system. The reproductive system is complex, as in the rest of the family Elysiidae. The penial opening is situated at the base of the right rhinophore.

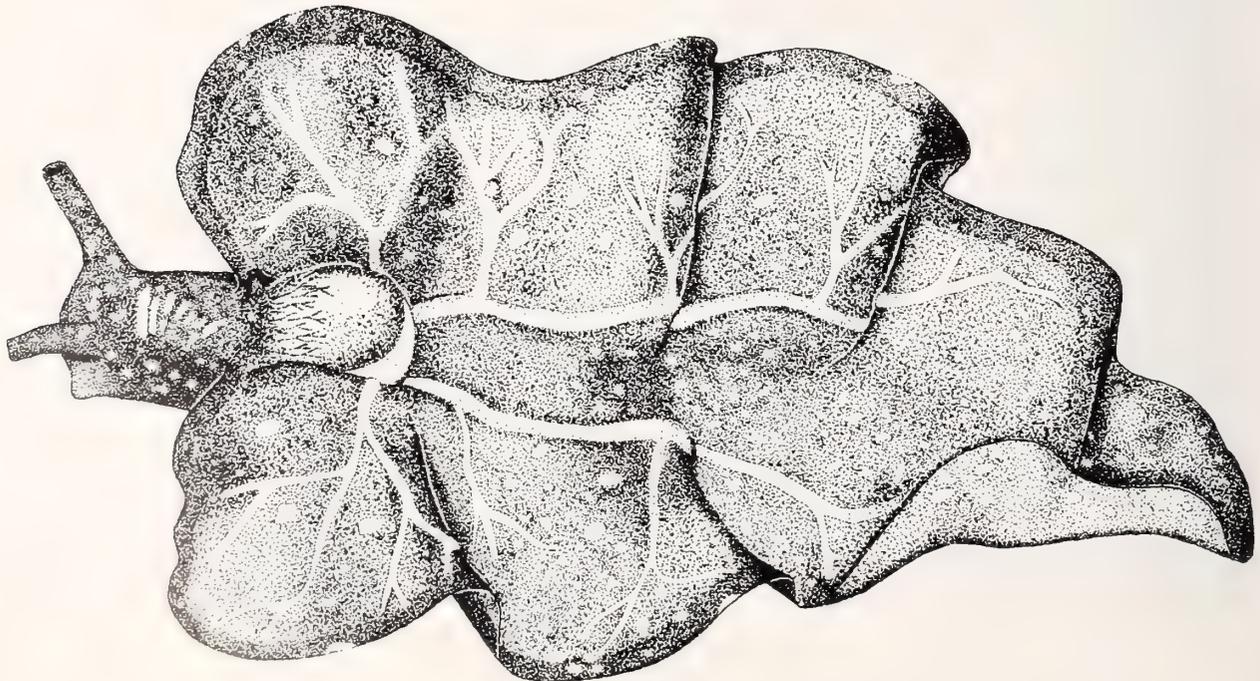


Figure 4

Dorsal view of live animal (40 mm) showing the expanded parapodia with the renopericardial prominence, anal papilla, and dorsal vessel distribution.

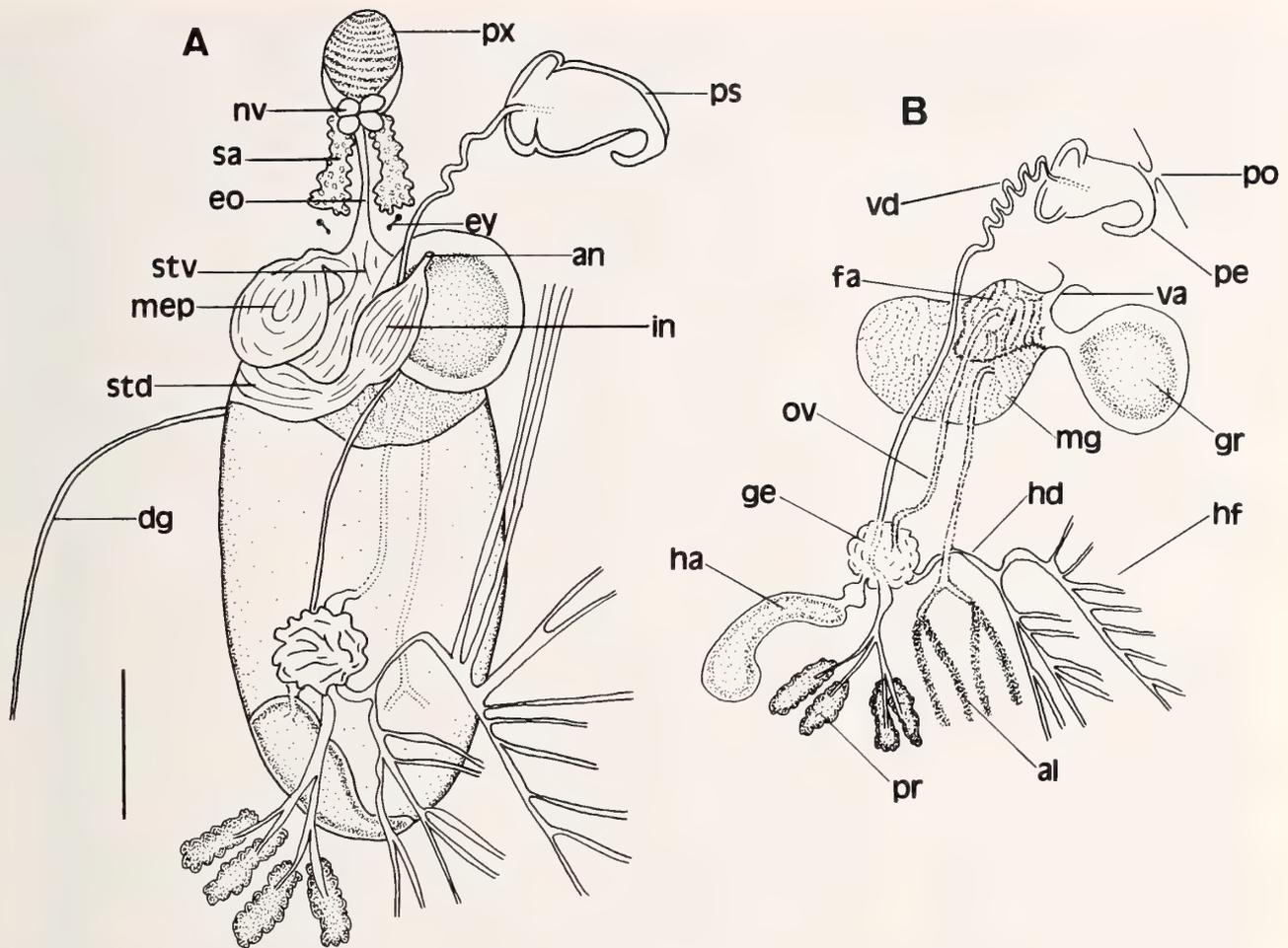


Figure 5

Anatomy of *Elysia patagonica* Muniain & Ortea, sp. nov. (paratype MNBR: 33880, 36 mm). A. Dorsal view of the internal organs, digestive tract, scale bar: 2 mm. Key: **an**, anus; **dg**, duct digestive; **eo**, esophagus; **ey**, eyes; **in**, intestine; **mep**, muscular esophageal pouch; **nv**, nerve ring; **px**, pharynx; **sa**, salivary glands; **std**, dorsal portion of stomach; **stv**, ventral portion of stomach. B. Reproductive system. Key: **al**, albumen glands; **fa**, fertilization area; **ge**, globular structure; **gr**, genital receptacle; **ha**, hermaphrodite ampulla; **hd**, hermaphrodite duct; **hf**, hermaphrodite follicles; **mu**, mucus gland; **ov**, oviduct; **pe**, penis; **po**, penial opening; **pr**, prostate; **ps**, penial sheath; **va**, vagina; **vd**, vas deferens.

The penis is large (approx. 500 μm expanded), naked, and drawn into a penial sheath (in all dissected specimens). A wide and thick base is visible when the penis is expanded, although it terminates in an unarmed tip. The vas deferens at the beginning of the penial base is convoluted (Figure 7), and subsequently very long, running from the penis into a globular structure, which also receives separately the ducts from the hermaphrodite follicles and the large hermaphrodite ampulla. The hermaphrodite follicles are densely distributed throughout the parapodia, and cream ovate structures are seen in all the extension. The prostate gland is branched and separated to the hermaphrodite follicles. The vaginal opening cannot be observed exter-

nally, but the vagina lies at the lateral wall in the transverse groove. A large and spherical genital receptacle (bursa copulatrix) is connected by a wide duct to the female reproductive system. Two inner ducts connect with the fertilization area and the mucus gland apparently, one of them (oviduct) from the globular structure, and the second from the albumen glands (Figure 5B).

Biology and ecology: *Elysia patagonica* sp. nov. lives mainly on the green alga *Bryopsis plumosa*, where it feeds and spawns. Only one specimen occurred on *Codium* sp. The egg mass consists of a yellow jelly ribbon, with a spiral shape of concentric loops (Figure 2C). The largest



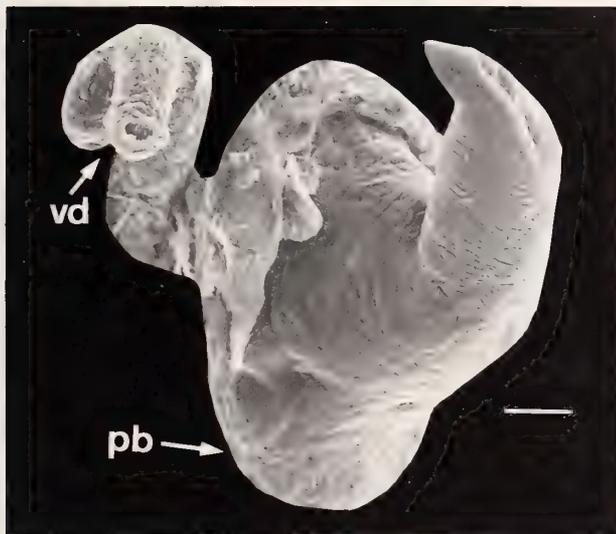


Figure 7

Scanning electron micrograph of the penis (paratype). Key: **pb**, penial base; **vd**, vas deferens. Scale bar: 100 μm .

spawn can have up to seven loops. Inside every capsule there is normally more than one embryo (Figure 8). The capsules range from 250–300 μm in diameter.

Etymology: The name describes the most austral zone of Argentina: Patagonia, where the species was collected.

DISCUSSION

Marcus (1980) completed the last revision of *Elysia* from the western Atlantic Ocean and discussed the geographical distribution of species from Florida to Brazil. None of them approximate the characteristics of our specimens. To compare them, we have taken into account coloration (no preserved), size, vessel distribution, teeth and penial morphology, and the algae in their diet. Features of the reproductive system can often be important when comparing descriptions of some species; however, in many studies such descriptions are absent, owing to the complexity of the reproductive system. On other occasions, differences in terminology made comparisons difficult (Marcus, 1980; Jensen, 1992). *Elysia ornata* Swainson, 1840, lives on *Bryopsis plumosa* (Jensen, 1993a and our data) and reaches a maximum size of 50 mm. However, *E. ornata* has a conspicuous black and orange band that borders the parapodia, and the dorsal vessel distribution and radula differ

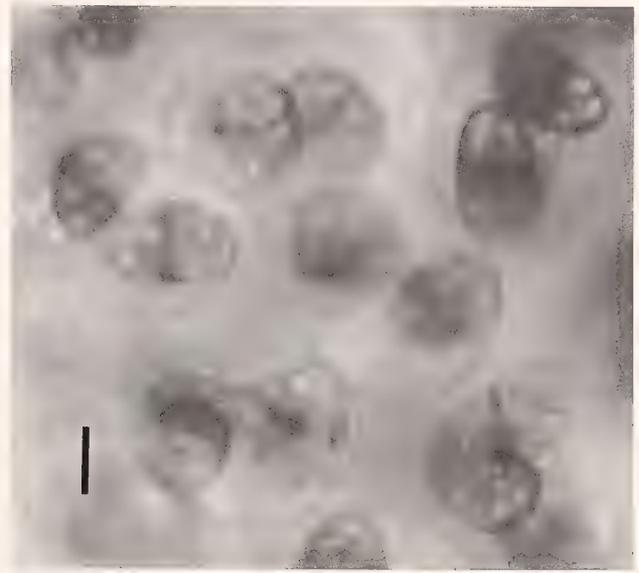


Figure 8

Twin embryos from the egg mass of *Elysia patagonica* Muniain & Ortea, sp. nov. Scale bar: 100 μm .

from *E. patagonica*. Other important distinctive features present in *E. ornata* are the male and female separate follicles, a large, muscular penis, and the anterior follicles functioning as ampulla. Literature describing the egg mass in *Elysia* species is very scarce. Jensen (1992) mentioned the common occurrence of twin embryos egg masses from Atlantic specimens (Canary Islands) of *E. ornata*, in agreement with our observations in *E. patagonica*.

Another large tropical Atlantic species (maximum 40 mm) is *Elysia subornata* Verril, 1901. It can be distinguished by its general green coloration, with fine grayish white mottling, minutely papillose parapodia, and a renopericardial prominence which forms a long ridge along the body length. Another distinctive characteristic is the morphology of the radular teeth, which is very different from that of *E. patagonica*, since *E. subornata* is a caulerpivorous species (Marcus & Marcus, 1957; Clark & De Frees, 1987), showing teeth with broad tips.

The white patch on the head is present in all of our specimens, and we consider it a distinctive systematic feature for the species. Verril, 1900 indicated in *Elysia crispa* (Mörch, 1863) (misspelling name) from Bermuda, a squarish white spot on the back of the head and neck, with

Figure 6 (A–F)

Scanning electron micrograph of some elements of the radula of *Elysia patagonica* Muniain & Ortea, sp. nov. A. Entire radula, scale bar: 100 μm . B. Teeth of ascending limb, scale bar: 10 μm . C. Tooth: blade-shaped, blunt tip, and hooked base, scale bar: 10 μm . D. Longest tooth: the first in the descending limb, scale bar: 10 μm . E. Tip of tooth showing, finely denticulate, cutting edge, scale bar: 10 μm . F. Details of discarded teeth in the ascus, scale bar: 10 μm .

prolongations into the rhinophores. Marcus (1980) and Marcus & Marcus (1967) indicated that *E. tuca*, from Curaçao, has a white crosslike figure on the back of the head and a white triangle on the neck. Clark, 1984 commented on Verrill's mistake in identifying the species *Elysia tuca* Marcus, 1967. However, in *E. patagonica*, the white patch is only situated on the medial dorsal region of the head. Other distinctive features present in *E. tuca* are an armed penis, an elongate renopericardial prominence, and the distribution of anterior and posterior dorsal vessels (Marcus, 1980).

Elysia viridis (Montagu, 1804) is a species from the east Atlantic and Mediterranean coasts. This species is widely distributed from north of Europe to the South African coast (Eland's Bay, west Atlantic coast) (Gosliner, 1987a). The external appearances of *E. viridis* and *E. patagonica* are easily distinguished; *E. viridis* presents triangular parapodia, showing a long neck and short rhinophores with a violet edge. Other species of the genus *Elysia* cited from the South African coast (Macnae, 1954; Marcus & Marcus, 1966; Barnard, 1974; Gosliner, 1987a, b) have Indo-Pacific distribution and vivid bright colors. Another African green species, except *E. viridis*, is *Elysia halimeda* Macnae, 1954, and it is characterized by a stout body and subrectangular and short parapodia, distinguishable from *E. patagonica*.

Jensen (1980, 1983, 1993b) correlated morphological adaptations of sacoglossan radular teeth to the characteristics of the algae upon which they feed. According to Jensen, the dental morphology of *E. patagonica* shows the "blade-shaped cusp" type, with denticles along the cutting edges. This morphology is present in species which feed upon *Bryopsis* and *Chaetomorpha*. Atlantic species that feed on *Bryopsis* sp. are *E. ornata* and *E. viridis*. *Elysia viridis* is one of the few species which has a wide diet including filamentous algae (*Bryopsis*, *Chaetomorpha*) and pseudoparenchymatous (*Codium*) (Jensen, 1994). However, we have found all our specimens on *Bryopsis plumosa*, except one animal on *Codium*.

Gosliner (personal communication) suggests a similarity of *E. patagonica* to the Pacific species *E. hedgpethi* Marcus, 1961 (= *E. bedeckta* MacFarland, 1966), in general morphology, coloration, and use of the same algae (*Bryopsis*). However, MacFarland (1966) mentioned bright spots of different colors—blue, emerald green, bright red, and orange-yellow—which are absent in our specimens. Also, the long, narrow body with triangular parapodia ending in a point described for *E. hedgpethi* does not occur even in juvenile Patagonian specimens. In addition, the white patch on the head of our specimens is absent in Marcus & Marcus' (1961) and MacFarland's (1966) descriptions of *E. hedgpethi*. Both papers lack illustrations of the reproductive system, and only Marcus & Marcus partially analyzed it. A large hermaphrodite ampulla and receptacle genital observed in *E. patagonica* were not indicated in Marcus & Marcus' description.

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Range Extensions of Magellanic Nudibranchs (Opisthobranchia) into the Peruvian Faunal Province

by

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Abstract. Extensive nudibranch collections using SCUBA were made in central and northern Chile. Of a total of 17 species identified, the known ranges of 12 species are extended, three within the Peruvian faunal province, and an additional nine species from the Magellanic into the Peruvian faunal province. This study confirms an earlier suggestion that the sudden disappearance of Magellanic nudibranch species north of Chiloé Island indicated by former data was not due to real distributional barriers, but to sporadic collecting and poor knowledge of the central and northern Chilean nudibranch fauna.

INTRODUCTION

Since the last century, little effort has been spent investigating the nudibranch fauna of the central and northern Chilean coast, which is part of the Peruvian faunal province. Eleven species have been reported from this area north of the 41°S boundary with the Magellanic faunal province by Lesson (1831), d'Orbigny (1835-1846), and Gould (1852), all of whom described external features only. Bergh (1873, 1898) added nine valid species with more complete descriptions. *Doris peruviana* d'Orbigny, 1837, already known from Peru (d'Orbigny, 1835-1846) and the Galapagos Islands (Pilsbry & Vanatta, 1902), was recorded from Valparaíso, central Chile by Dall (1909). Recently, *Okenia luna* Millen, Schrödl, Vargas & Indacochea, 1994, was described ranging from the Bahía de Coliumo, central Chile to southern Peru (Millen et al., 1994). Many of the older species descriptions remain incomplete and based on one or very few specimens from their type locality or from a limited area. It is remarkable that only two typical Magellanic species common on the Chilean coast south of 41°S, *Anisodoris fontaini* (d'Orbigny, 1837) and *Diaulula hispida* (d'Orbigny, 1837), are reported from the central Chilean coast (Marcus, 1959). For other Magellanic species, the area just north of Chiloé Island appears to be an abrupt distributional barrier, although Marcus suggested that this barrier could be artificial due to the sparse collecting in central and northern Chile.

This study gives new distributional data on 17 nudibranch species found in several localities on the central and northern Chilean coast and evaluates the status of

Chiloé Island as the northern limit of Magellanic nudibranchs.

COLLECTING SITES AND METHODS

From 1991-95, extensive nudibranch collections were made by SCUBA in the Bahía de Coliumo, central Chile, at 0-20 m depth during approximately 60 hours of total search time. During February and March 1994, five additional localities were searched for nudibranchs in central and northern Chile, diving within the same depth range for up to 5 hours in each site. The locations of the collecting sites are shown in Figure 1, and their geographic coordinates given in Table 1. Voucher specimens of each species were deposited in the Zoologische Staatssammlung München (ZSM); additional specimens are in the private collection of the author.

RESULTS

During this study, 17 species of nudibranchs found in the Bahía de Coliumo, central Chile, were positively identified. Several of these species were also found in localities farther north (Table 1). An alphabetical list of these 17 nudibranch species with their known distributional ranges follows. Ranges extended by this study are marked by an asterisk. Collecting data and locality where specimens were found are given for each species.

**Acanthodoris falklandica* Eliot, 1907—Falkland Islands and Hope Harbour (Eliot, 1907; Odhner, 1926), Chiloé Island (Marcus, 1959) to the Bahía de Coliumo. Bahía de

Table 1
Nudibranchs collected from central and northern Chile.

Species collected	Collecting sites and coordinates:					
	Bahía de Coliumo 36°32'S, 72°57'W	Pichidangui 32°08'S, 71°33'W	Los Hornos 29°38'S, 71°20'W	Bahía Inglesa 27°07'S, 70°53'W	Juan López 23°30'S, 70°32'W	Caleta Buena 22°25'S, 70°15'W
<i>Aeolidia papillosa</i> var. <i>serotina</i>	X					
<i>Acanthodoris falklandica</i>	X					
<i>Anisodoris punctuolata</i>	X					
<i>Anisodoris rudbergi</i>	X	X	X	X		
<i>Anisodoris fontaini</i>	X		X			
<i>Cadlina sparsa</i>	X					
<i>Diaulula hispida</i>	X					
<i>Doto uva</i>	X					
<i>Gargamella immaculata</i>	X					
<i>Holoplocamus papposus</i>	X	X				
<i>Neocorambe lucea</i>	X					X
<i>Okenia luna</i>	X					
<i>Phidiana lottini</i>	X		X			
<i>Rostanga pulchra</i>	X					
<i>Thecatera darwini</i>	X	X	X	X	X	
<i>Tritonia odhneri</i>	X					
<i>Tyrinna nobilis</i>	X		X			

Coliumo: 3 specimens collected by J. Sanchez, C. Pérez & S. Millen, 17 December 1994, at depths of 8–15 m (ZSM No. 1899; 1 specimen, dissected).

Aeolidia papillosa var. *serotina* Bergh, 1873—Falkland Islands (Eliot, 1907; Odhner, 1926) to Valparaíso (Bergh, 1873). Bahía de Coliumo: 1 specimen collected by J. Sanchez & C. Pérez, 17 December 1994, at a depth between 4 and 15 m (ZSM No. 1900).

**Anisodoris fontaini* (d'Orbigny, 1837)—Cabo San Antonio, Argentina; Melinka, southern Chile (Odhner, 1926). Valparaíso (d'Orbigny, 1835–1846) to Los Hornos. Los Hornos: 1 specimen collected by M. Schrödl, 14 March 1994, at 8 m depth on bare rocks (ZSM No. 1901). Bahía de Coliumo: 11 specimens collected by M. Schrödl, 12–26 April 1992, at depths of 0–11 m on bare rocks except for the smallest specimen which was on *Gigartina* sp. (ZSM No. 1902; 1 specimen).

Anisodoris punctuolata (d'Orbigny, 1837)—Guaitecas Islands (Odhner, 1926) to Callao, Peru (Dall, 1909). Bahía de Coliumo: 5 specimens collected by M. Schrödl, 17 April 1992, at depths of 0–2 m on rocks next to sponges (ZSM No. 1903; 1 specimen).

**Anisodoris rudbergi* Marcus & Marcus, 1967—San Vicente, central Chile (Marcus, 1959) to Bahía Inglesa, northern Chile. Bahía Inglesa: 4 specimens collected by K. Salger & M. Schrödl, 16 March 1994, at depths of 6–12 m on bare rocks (ZSM No. 1904; 1 specimen, dissected). Los Hornos: 2 specimens collected by M. Schrödl, 14 March 1994, at depths between 15–20 m on bare rocks. Pichidangui: 3 specimens collected by M. Schrödl, 12 March 1994, at depths of 10–14 m on rocks next to yellowish sponges. Bahía de Coliumo: 25 specimens collected by M.

Schrödl, 31 March–17 April 1992, at depths of 0–9 m, 1 specimen on sand and 24 specimens on rocks (2 specimens were feeding on *Haliclona* sp.) (ZSM No. 1905; 1 specimen, dissected).

**Cadlina sparsa* (Odhner, 1921)—Northern Chiloé (Marcus, 1959) to the Bahía de Coliumo. Juan Fernández Islands (Odhner, 1921). California (see Behrens, 1991). Bahía de Coliumo: 4 specimens collected by M. Schrödl, 27 February 1995, at depths of 5–6 m on cave walls (ZSM No. 1906; 1 specimen).

Diaulula hispida (d'Orbigny, 1837)—Isthmus Bay, Smyth Channel, Patagonia (Odhner, 1926) to Valparaíso (d'Orbigny, 1835–1846). Bahía de Coliumo: 7 specimens collected by M. Schrödl, 31 March–17 April 1992, at depths of 1–7 m on rocks, 2 specimens in a small cave (ZSM No. 1907; 2 specimens).

**Doto uva* Marcus, 1955—Brazil. Chiloé Island (Marcus, 1959) to the Bahía de Coliumo. Bahía de Coliumo: 7 specimens collected by M. Schrödl, 08 April 1992, at depths of 6–7 m on hydrozoans (ZSM No. 1908; 2 specimens).

**Gargamella immaculata* Bergh, 1894—Cabo San Antonio, Argentina; Burdwood Bank (Odhner, 1926). Patagonia and Chiloé Island (Marcus, 1959) to the Bahía de Coliumo. Bahía de Coliumo: 5 specimens collected by M. Schrödl, 17–26 April 1992, at depths of 1–11 m, on rocks. 2 specimens collected by M. Schrödl, 27 February 1995, at depths of 9–10 m, on rocks (ZSM No. 1909; 2 specimens).

**Holoplocamus papposus* Odhner, 1926—Bahía Blanca, Argentina; Magellan Strait (Marcus & Marcus, 1969) to Pichidangui, central Chile. Pichidangui: 1 specimen collected by M. Schrödl, 12 March 1994, at 10 m depth on



Figure 1
Collecting sites.

a vertical rock wall (ZMS No. 1910). Bahía de Coliumo: 26 specimens collected by M. Schrödl, 18–28 January 1994, at depths of 1–9 m, most specimens on rocks, some on algae (ZSM No. 1911; 2 specimens).

**Neocorambe lucea* (Marcus, 1959)—Golfo Corcovado (Marcus, 1959) to Caleta Buena. Caleta Buena: 2 specimens collected by M. Schrödl, 17 March 1994, at 7 m depth on *Macrocytis pyrifer*a encrusted with its bryozoan prey *Membranipora isabelleana* (d'Orbigny) (ZSM No. 1912; 1 specimen). Bahía de Coliumo: 4 specimens collected by M. Schrödl, 31 January 1994, at depths of 0–5 m on *M. pyrifer*a encrusted with *M. isabelleana* (ZSM No. 1913; 1 specimen).

Okenia luna Millen, Schrödl, Vargas & Indacochea, 1994—Bahía de Coliumo, central Chile to Ancón, Peru (Millen et al., 1994). Bahía de Coliumo: 10 specimens collected by M. Schrödl, 25 January 1994, at depths of 10–12 m on *Tegula* shells encrusted with the bryozoan species *Alcyonidium nodosum* O'Donoghue & de Waterville, 1944 (ZSM No. 1914; 2 specimens).

Phidiana lottini (Lesson, 1831) (valid name for *Phidiana inca* (d'Orbigny, 1837), see Schrödl, 1996).—Gulf of Ancud, southern Chile (Bergh, 1898; Marcus, 1959) to Callao, Peru (d'Orbigny, 1835–1846). Los Hornos: 1 specimen collected by M. Schrödl, 14 March 1994, at 2 m depth on algae. Bay of Coliumo: 108 specimens collected by M. Schrödl, March to June 1992, at depths of 0–15 m on different substrates, several specimens on floating algae (ZSM No. 1915; 2 specimens).

**Rostanga pulchra* MacFarland, 1905—Argentina (Marcus & Marcus, 1969). Chiloé Island (Marcus, 1959) to the Bahía de Coliumo. Gulf of California to Alaska (see Behrens, 1991). Bahía de Coliumo: 1 specimen collected by C. Pérez & J. Sanchez, 17 December 1994, at a depth between 10 and 15 m (ZSM No. 1916).

**Thecatera darwini* Pruvot-Fol, 1950—Orange Bai, Hoste Island (Pruvot-Fol, 1950) to Juan López, northern Chile. Juan López: 18 specimens collected by K. Salger & M. Schrödl, 17 March 1994, at depths of 3–12 m, most specimens on vertical rock walls (ZSM No. 1917; 2 specimens). Bahía Inglesa: 61 specimens observed by K. Salger & M. Schrödl, 16 March 1994, at depths of 2–12 m in groups on rocks encrusted with bryozoans and small algae. Los Hornos: 6 specimens collected by K. Salger & M. Schrödl, 14 March 1994, at depths of 3–20 m on bare rocks. Pichidangui: About 150 specimens observed by K. Salger & M. Schrödl, 12 March 1995, at depths of 2–16 m, often in groups on rocks encrusted with bryozoans and small algae. Bahía de Coliumo: 76 specimens collected by M. Schrödl, 03 May 1992, at depths of 0–9 m, often in groups on rock walls encrusted with bryozoans and small algae (ZSM No. 1918; 2 specimens).

**Tritonia odhneri* Marcus, 1959—Chiloé Island (Marcus, 1959) to the Bahía de Coliumo. Bahía de Coliumo: 22 specimens collected by M. Schrödl, 26 April 1992, at depths of 9–15 m on or next to their gorgonian prey *Lo-*

phogorgia platyclados (Philippi) (ZSM No. 1919; 1 specimen).

**Tyrinna nobilis* Bergh, 1898—Chiloé Island (Bergh, 1898; Marcus, 1959) to Los Hornos, northern Chile. Los Hornos: 1 specimen collected by K. Salger, 14 March 1994, at 15 m depth on rocks (ZSM No. 1920; dissected). Bahía de Coliumo: 3 specimens collected by S. Millen, S. Gigglinger, C. Pérez & J. Sanchez, 17 December 1994, at depths between 0 and 10 m on rocks (ZSM No. 1921; 1 specimen).

DISCUSSION

The Bahía de Coliumo represents a new collecting locality within the previously known ranges of *Aeolidia papillosa* var. *serotina*, *Anisodoris punctuolata*, *Diaulula hispida*, and *Phidiana lottini*; these species already were known from central Chile (Marcus, 1959). The range of the central Chilean species *Anisodoris rudberghi* is extended north to Bahía Inglesa, that of *A. fontaini* to Los Hornos.

Cadlina sparsa has a disjunct distribution. It is known from Chiloé Island (Marcus, 1959), Juan Fernández Islands (Odhner, 1921), and California (see Behrens, 1991). In this study, *C. sparsa* is reported for the first time from the central Chilean coast. *Rostanga pulchra* has a similar disjunct distribution known from Argentinian Patagonia (Marcus & Marcus, 1969) and Chiloé Island (Marcus, 1959), as well as from the Gulf of California and the west coast of North America (see Behrens, 1991). *Doto uva*, reported from Brazil and Chiloé (Marcus, 1959), also shows an unusual wide and disjunct distribution. Both species were found in the Bahía de Coliumo, the first records of *Rostanga pulchra* and *Doto uva* from the Peruvian Faunal Province. To this province, an additional seven species previously only reported from Magellanic waters south of 41°S are added by the present study.

The total number of nudibranch species known from the central and northern Chilean coast increases to 35, and in the entire Peruvian faunal province, including the Juan Fernández Islands, to 39 from a previous total of 29 (Dall, 1909; Marcus, 1959; Millen et al., 1994). Approximately half of these species appear to be endemic to the Peruvian province. However, this figure is probably artificially high because: (1) several species descriptions of Lesson (1831), d'Orbigny (1835–1846), Gould (1852), and Bergh (1898) do not allow proper identification (Marcus, 1959); and (2) several species pairs are probably one variable species, so a number of synonymies will be necessary (Schrödl, in preparation).

Nevertheless, one zoogeographic conclusion can be drawn from this study: Formerly only two species with typical Magellanic distributions, *Anisodoris fontaini* and *Diaulula hispida*, had their geographical limit on the central Chilean coast north of Chiloé Island at Valparaíso. *Tritonia australis*, which is known from Argentina (Marcus & Marcus, 1969), Patagonia, Chiloé (Marcus, 1959), and the Juan

Fernandez Islands (Bergh, 1898), is a problematic species which should be revised (Wägele, 1995), and the Magellanic *Aeolidia serotina* Bergh, 1873, which occurs north to Valparaíso (Bergh, 1873), was regarded as just a variety of the cosmopolitan *Aeolidia papillosa* (Linnaeus, 1761) by Marcus (1959). Since several Magellanic nudibranch species had their northern limits at Chiloé Island, Marcus (1959) had to regard Chiloé as a distributional boundary between Magellanic and Peruvian nudibranchs, but he pointed out that the Chilean and Peruvian coast north of Chiloé was poorly known. As a result of the present study, only the northern limit of *Flabellina falklandica* (Eliot, 1907) still terminates at Chiloé. The other species considered by Marcus (1959) to be Magellanic with a northern distributional limit at Chiloé are *Acanthodoris falklandica*, *Thecacera darwini*, and the two Chilean species of the genus *Gargamella*, *G. immaculata* and *G. latior*, which will be synonymized (Schrödl, in preparation). All now have their ranges extended farther north. In addition, the southern Magellanic species, *Holoplocamus papposus*, as well as *Neocorambe lucea* and *Tyrinna nobilis*, known from Chiloé Island, have their ranges extended into the Peruvian faunal province. Consequently, the area near Chiloé Island need no longer be considered as an important distributional barrier for Magellanic nudibranchs; as Marcus (1959) suggested, the sudden disappearance of Magellanic nudibranch species north of Chiloé was an artifact of limited collecting in central and northern Chile. The increased faunal overlap of Magellanic nudibranch species into the Peruvian faunal province, as shown in this study, suggests that they follow the general pattern of Magellanic benthic organisms invading a transition zone of central Chile (Brattström & Johanssen, 1983).

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Karyotype of the Nudibranch, *Phidiana inca* (Mollusca: Opisthobranchia)

by

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Abstract. The chromosomes of the nudibranch *Phidiana inca* (d'Orbigny, 1837) were obtained from early embryos, and studied using karyometric analysis. The karyotype consists of nine metacentric, one submetacentric, and five telocentric chromosome pairs, being the first nudibranch species, out of 46 species studied, with a different chromosome number, $n = 15$ instead of $n = 13$. This study is also the first contribution to the cytogenetics of Chilean nudibranchs and gastropods.

INTRODUCTION

Chromosome number and/or karyotype are known for most commercially important bivalve mollusks (Insua & Thiriot-Quévieux, 1991) and some aquatic gastropods, but many species have not yet been studied from a cytogenetic point of view. Thiriot-Quévieux et al. (1988) indicate that chromosomes are described for 125 bivalve species, 73 belonging to Mytilidae, Pectinidae, Ostreidae, and Unionacea. The other studied species are distributed between Pteriomorpha and Heterodonta.

In the order Nudibranchia, the haploid chromosome number is known for 45 species and subspecies, belonging to the four suborders and 16 families (Patterson, 1969; Thiriot-Quévieux, 1994).

In Chile few native mollusk species have been studied cytogenetically, and all of those are bivalves: *Argopecten purpuratus* (von Brand et al., 1990), *Choromytilus chorus* (Palma-Rojas, 1980), *Semele solida* (Guerra & Campos, 1991), and *Tiostrea chilensis* (Ladrón de Guevara et al., 1994).

Four species of nudibranchs are found in the Coquimbo Region (30°17'S, 71°34'W) belonging to the suborders Doridacea and Aeolidacea (Guisado, personal communication), and none of them is known cytogenetically. This

work is the first contribution to the cytogenetics of Chilean nudibranchs, and also to Chilean gastropods.

Phidiana inca (Opisthobranchia: Aeolidacea), reproduces throughout the year. These animals are functional hermaphrodites with internal cross fertilization involving two animals. The ovotestis is located in the posterior portion of the animal, close to the anus. Hermaphroditic ducts connect the gonad with the anterior reproductive organs, where the endogenous and exogenous male gametes are stored in different structures (Rivest, 1984).

Phidiana inca shows repeated copulation and lays its zygotes in a spiral-like band, embedded in a gelatinous matrix, with one to three eggs per capsule. The egg diameter is $97.1 \pm 3.3 \mu\text{m}$. The zygotes stay attached to each other after spawning through a double constriction (Brokordt, 1995). The first polar body is expelled 1 hour after the egg lay, and the second polar body about an hour later. Twenty-four hours after spawning, they reach the gastrula stage. The following development varies from one species to another. The intracapsular development is completed in *Phidiana inca* in 6 days at 18–20°C, and in 12 days at 14–16°C (Brokordt, 1995). The purpose of this work is to determine the diploid chromosome number and construct the karyotype, using the centromeric position (Levan et al., 1964), and a karyo-idiogram (Spotorno, 1985).

MATERIALS AND METHODS

Fixation and Yolk Extraction

Adult specimens of *Phidiana inca* were collected from La Herradura Bay and transported to facilities belonging to the Universidad Católica del Norte, Coquimbo, Chile. The specimens were held in tanks with running seawater and air and food supply. The fixation and yolk extraction is a modification of the technique described by von Brand et al. (1990) for *Argopecten purpuratus* embryos. Twenty-four hours after the egg lay, the bandlike spiral was taken out of the culture tank; the embryos were mechanically separated from the gelatinous matrix and incubated in a colchicine: seawater solution (0.2%) for 2 hours, then changed to a mixture of seawater: distilled water (70–80%), and incubated for 30 minutes. Then two changes with the modified Carnoy's fixative (methanol: acetic acid, 1:3) were performed. To extract the yolk, three changes with methanol: chloroform (1:1), 30 minutes each, were used. Then they were held in acetic acid: distilled water (50%) for 30 minutes. This step was repeated twice. Then they were changed into Carnoy for 10 minutes, and stored in fresh Carnoy at 4°C. All steps were performed at room temperature.

Staining Procedure

The Feulgen reaction described by Navarrete et al. (1983) was applied. In this procedure, centrifugation was used for each step. The eggs were hydrolized in HCl (1 N) for 7 minutes at 60°C, then washed in sulphurous water at 4°C, and stained with Schiff's reagent for 60 minutes at room temperature. The samples were then washed with distilled water (three times), and once with acetic acid (50%). The treated samples were kept in acetic acid (50%).



Figure 1

Mitotic metaphase plate of *Phidiana inca*.

Table 1

Chromosome number and mitotic metaphase plate frequencies of *Phidiana inca*.

Chromosome number	Metaphase plates
26	1
27	0
28	9
29	11
30	49
31	1

Chromosome Preparations and Karyotype

Slides were prepared using "squash" technique, where a small amount of sample, stained as described above, was deposited on a clean, warm glass slide, covered with a cover glass and pressed with the thumb. The preparations were observed using a Nikon Biophot Microscope. Seventy-one metaphase plates were counted to determine the diploid chromosome number. The 15 best metaphase plates were photographed, and the chromosomes were cut out and measured to obtain the total length and arm lengths. The mean karyotype was arranged according to chromosome sizes (from larger to smaller). A karyo-idiogram (Spotorno, 1985) was made using percentage arm values (long and short arm) over the total length of the haploid chromosome set obtained for each chromosome. These data

Table 2

Measurements, including mean (\bar{x}), standard deviation (SD) of relative length, arm ratio, centromeric index and classification of the chromosomes of *Phidiana inca*, where M = metacentric, SM = submetacentric, and T = telocentric chromosome pair.

No. of chromosome pair	Relative length	Arm ratio	Centromeric index	Classification
1	12.83 ± 0.57	0.94 ± 0.07	48.49 ± 1.77	M
2	11.70 ± 0.73	0.94 ± 0.07	48.25 ± 1.92	M
3	10.37 ± 0.34	0.63 ± 0.07	38.57 ± 2.50	M
4	9.05 ± 0.23	0	0	T
5	7.71 ± 0.26	0.43 ± 0.10	29.75 ± 5.19	SM
6	6.66 ± 0.63	0.69 ± 0.13	40.41 ± 4.87	M
7	5.98 ± 0.24	0.75 ± 0.08	42.81 ± 2.89	M
8	5.36 ± 0.30	0	0	T
9	4.88 ± 0.27	0	0	T
10	4.55 ± 0.43	0.69 ± 0.07	40.83 ± 2.45	M
11	4.54 ± 0.35	0.68 ± 0.16	40.10 ± 5.32	M
12	4.41 ± 0.21	0	0	T
13	4.12 ± 0.27	0.67 ± 0.05	40.11 ± 1.67	M
14	3.94 ± 0.48	0.74 ± 0.13	42.18 ± 3.99	M
15	3.90 ± 0.36	0	0	T

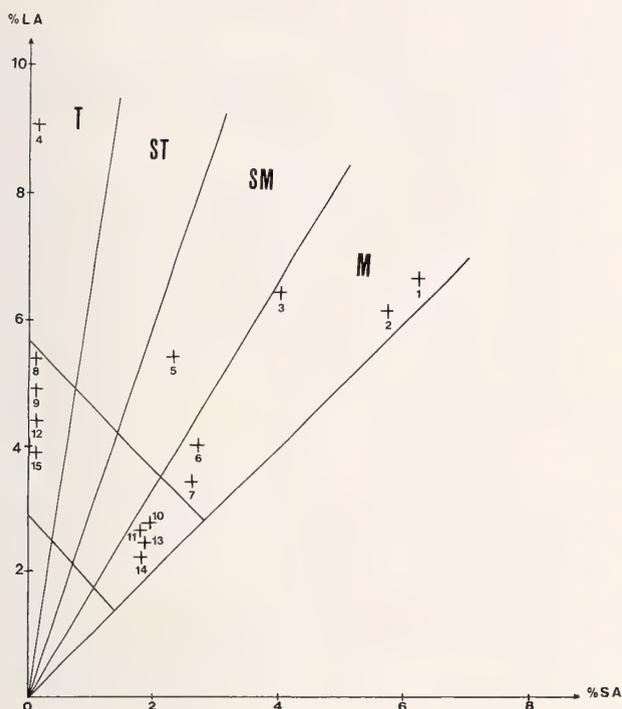


Figure 2
Karyo-idiogram of *Phidiana inca*.

were represented in a bivariate graph. Also, the centromeric index (Levan et al., 1964) was obtained by $([\text{short arm}/\text{total length}] \times 100)$.

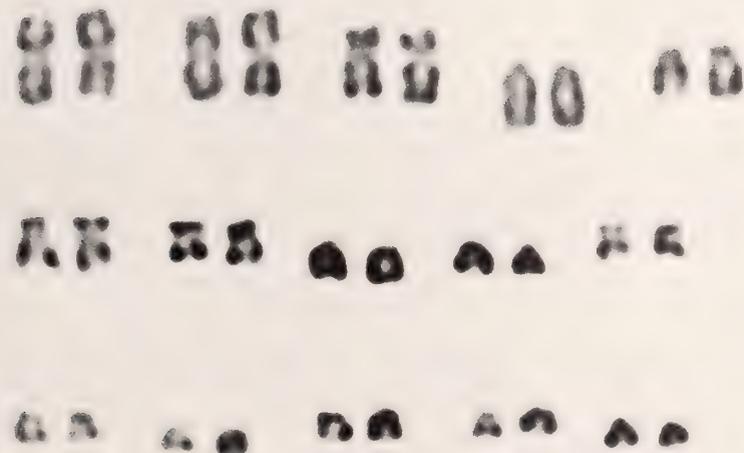
RESULTS

The frequencies of diploid chromosome numbers obtained by counting metaphase plates (Figure 1) are shown in Table 1. The chromosome number counted was between 26 and 31, with one metaphase each, and the modal number of metaphase plates showed 30 chromosomes.

Table 2 gives the chromosome measurements, their mean (\bar{x}) and standard deviation (SD), and classification obtained for each chromosome pair, measuring chromosomes from 15 metaphase plates. The mean chromosome relative length ranged between 12.83 and 3.90. The real lengths for the largest and shortest chromosomes were 3.92μ and 1.13μ , respectively.

The karyo-idiogram is shown in Figure 2, where LA stands for long arm, and SA for short arm, where each chromosome is represented by a cross, and its location in this graph is given by the length of their arms. The results of this grouping were nine metacentric chromosome pairs (M), one submetacentric chromosome pair (SM), and five telocentric chromosome pairs (T).

The karyotype obtained for *Phidiana inca* is shown in Figure 3. No evidence was obtained of the presence of secondary constrictions that could be associated with nucleolar organizer regions (NOR).



2.13 μ

Figure 3
Karyotype mount of the diploid complement of *Phidiana inca*.

DISCUSSION

The results obtained indicate that *Phidiana inca* has a diploid chromosome number of $2n = 30$, and the karyotype is composed of 9 M + 1 SM + 5 T chromosome pairs. This value differs from those chromosome numbers given for the studied nudibranchs, including two species belonging to the suborder Aeolidacea, *Spurilla neapolitana* and *Limenandra fusiformis*, as described by Patterson (1969) and Thiriôt-Quiévreux (1994). All studied species show a haploid chromosome number of $n = 13$. Therefore, *Phidiana inca* is the first nudibranch having a different chromosome number $2n = 30$ ($n = 15$). The taxonomic status of the order Nudibranchia has often been questioned, but using the occurrence of the same chromosome number ($n = 13$) in all species studied, Schmekel (1985) considers the nudibranchs as a unique, natural order among the gastropods, with an early Cephalaspidea as a possible ancestor. Our results raise an interesting question regarding the possibility of the existence of more than one ancestral organism, or an early differentiation between nudibranchs located in geographically distant areas. *Phidiana inca* is the first southern Pacific nudibranch studied. To be able to discuss this problem in greater depth, it is necessary to study cytogenetically more nudibranch species from the Pacific coast.

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The Role of the Follicular Epithelium in the Oosorption Process in *Eupera platensis* Doello Jurado, 1921 (Bivalvia: Sphaeriidae): A Light Microscopic Approach

by

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Abstract. *Eupera platensis* Doello Jurado, 1921, is a simultaneously hermaphroditic freshwater bivalve. The gonad produces a small number of large, yolky eggs and few sperm simultaneously. Eggs are incubated within both inner demibranchs, and embryos (45 to 90) are retained until released as fully developed juveniles.

At the light microscope level, the oosorption process implies: 1) breakage of the egg cell membrane and consequent liberation of vitellinic material to the alveolar lumen, 2) phagocytosis of the vitellinic droplets by the follicle cells, and 3) reaction of blood amoebocytes that invade the acinus lumen to phagocytose the remnants of the degenerated oocytes.

Oosorption is frequently found in gonads which have recently spawned; however, it has been also detected in unspawned ones. Phagocytosis by the follicle cells affects oocytes in a late stage of vitellogenesis as well as ripe and unspawned ova.

Although in other mollusks (mainly in gastropods), the follicle cells are involved in the phagocytosis of degenerative oocytes, the process is not as extensive as reported here in *E. platensis*.

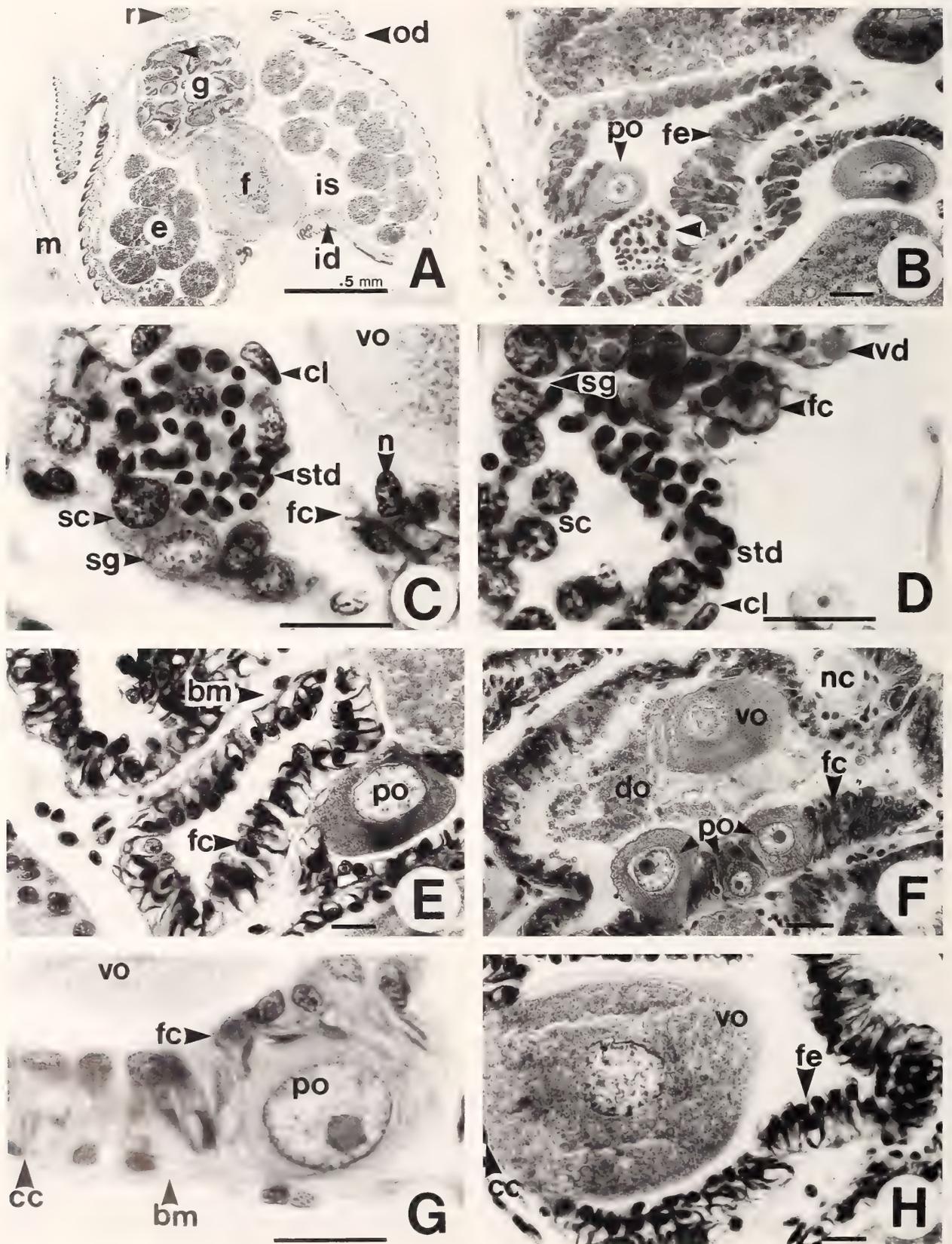
Assuming that parent energy devoted to reproduction is a finite and limited resource, and taking into account the reduced number of large ova susceptible to being retained within inner demibranchs, the oocyte breakdown and subsequent phagocytosis of degenerated oocytes by follicle cells are here considered as processes which, integrated with the set of life history traits that constitutes the reproductive strategy of the species, leads to prevention of important energy loss that would imply the development of surplus gametes with no chance of success.

INTRODUCTION

Oocyte degeneration and oosorption are little known processes among mollusks (de Jong Brink et al., 1983). These processes have been described in bivalves as either the result of an autolytic phenomenon characterized by vacuolization and liquefaction of the oocyte cytoplasm, or as a reaction process carried out by amoebocytes that invade the acinar lumen to phagocytose aborted or unspawned ova (Christiansen & Brodsky, 1971; Vinuesa, 1981; Ituarte, 1986). In other cases, such as in *Pecten maximus* (Linnaeus, 1758), and *Neororbicula limosa* (Maton, 1809), the two processes of oosorption described above are considered as integrated into a sequential process in which the autolytic phase is followed by the reaction of blood amoebocytes to phagocytose the remnants of the degenerated oocytes (Dorange, et al., 1989; Ituarte, 1986).

The phagocytic activity of follicle cells has been reported or suggested in mollusks (Griffond & Gomot, 1979; Hill, 1977; Huebner & Anderson, 1976; Bottke, 1972; de Jong Brink et al., 1983; Dorange et al., 1989). However, little is known about the details of the phagocytosis process, and, in general, about the role of follicle cells in bivalve oogenesis and oosorption. Bivalve follicular cells are reported as being capable of phagocytosing and digesting materials derived from degenerating oocytes (Dorange et al., 1989). The result of this process has been described as globular acidophilic inclusions in the follicular cell cytoplasm (Coe & Turner, 1938; Christiansen, 1971; Pujals, 1985). Superfluous male gametes or residuals of atypical spermatogenesis have been also described as engulfed by follicular cells (Pujals, 1985; Coe & Turner, 1938).

In the present paper, the gonadal structure of *Eupera platensis* Doello Jurado, 1921, is briefly re-examined, and



the role of the follicle cells in the oosorption process is described at the light microscope level.

MATERIALS AND METHODS

Specimens of *E. platensis* were collected from a small stream close to the Río de La Plata estuary at La Plata, Buenos Aires, Argentina (voucher specimens at the Department of Invertebrates, Museo de La Plata, MLP 5155).

Whole specimens ranging from 2 to 8 mm in shell length (maximum shell length for the species is about 10 mm) were fixed in Zenker's fluid added with formalin (10% in the mixture volume) (Gabe, 1968). Anterior and posterior adductors were sectioned prior to rinsing the whole specimens in the fixative in order to facilitate the fixative action. Inner and outer demibranchs were retained to determine the pre- or post-spawning condition of individuals from the presence or absence of either ova or embryos in incubation.

Tissues were fixed for 4 hr (by this time, valves were decalcified by the corrosive action of the fixative), rinsed in tap water for 24 hr, and dehydrated in ethanol 96% (three washes of 2 hr each) and n-Butanol (three washes of 24 hr each). Tissues were embedded in paraffin wax, and sections (5 μm thick) were stained with Mayer's hematoxylin and eosin (a series of 25 histological preparations was deposited at the Invertebrate Department MLP no. 5156).

RESULTS

Gonad Structure

E. platensis is a functional (simultaneous) hermaphrodite in which the female tissues are more extensive than male ones (Figure 1A, B). Spermatogenic tissues are mainly developed in the postero-dorsal region of the gonadal mass. Eggs and sperm develop within common acini (Figure 1A–D), although the male germinal cells are separated from the female cells by a thin one-cell layer conjunctive wall (Figure 1C, D). The hermaphrodite gonad is composed of two lateral pairs of tubules that arise from the posterior end of the visceral mass and develop forward in a scarcely branched tubular system. In the early stages of gonadal

development, the follicular cells are the predominant elements in the structure of the acinus (Figure 1E). Germ cells are scattered along the base of the epithelium. The follicular layer is supported by a thin connective basement membrane (Figure 1E–G). The follicular epithelium consists of cylindrical cells of variable height with a middle or distal nucleus and basophilic cytoplasm (Figure 1E, G).

During this study, early and late vitellogenic oocytes and sperm were observed in recently spawned individuals (the spawned condition can be identified by the presence of brooding eggs or embryos within inner demibranchs) (Figure 1A).

Oocyte–Follicle Cell Relationship

At the early stages of their development, germ cells become surrounded by follicle cells, which are largely in contact with the wall of the acinus. Later, the follicle cells become detached from the apex of the oocyte, which protrudes toward the lumen of the acinus, keeping in contact with the connective wall of the acinus by a stalk (Figure 1F–H).

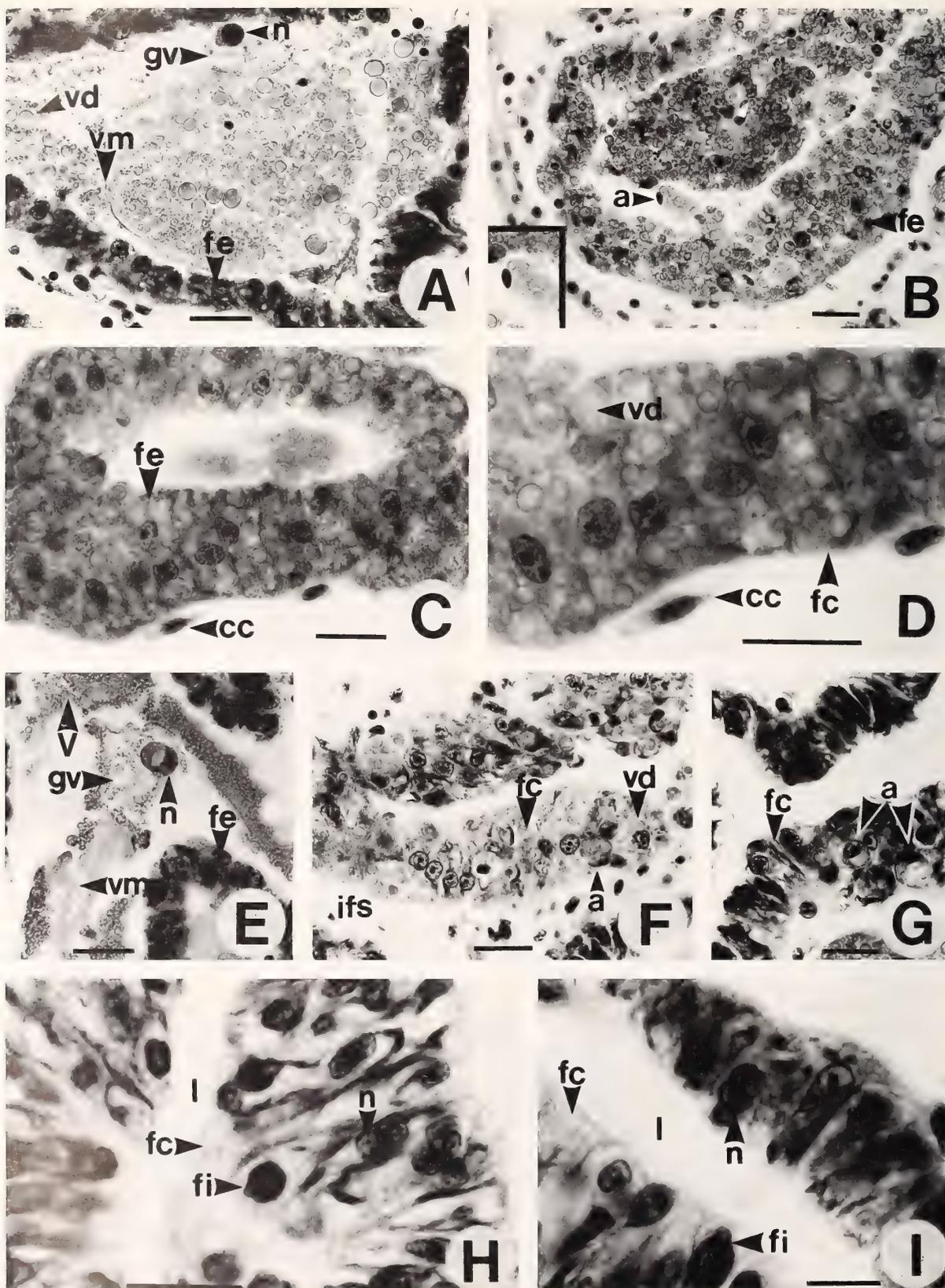
The follicle cells undergo morphological changes that are in accordance with different functional phases. During the early development of the gonad, the follicle cells are nearly cubic in shape (height: 14 μm) with a strongly basophilic cytoplasm. As oogenesis progresses, follicular epithelium increases in height, becoming cylindrical (height: 23 μm) with the nuclei of cells located distally (Figure 1E, G, H). During the phagocytic phase, the follicle cells vary in shape and size according to the degree of cytoplasm repletion by engulfed material (cell height increases from 27 to 46 μm) (Figure 2A–D). The post-phagocytic stage is characterized by the shrinkage of the follicular cell cytoplasm (cell height: 23–27 μm) (Figure 2H, I).

Oosorption

In *E. platensis* oosorption involves both the follicle cells and amoebocytes. Phagocytosis by the follicle cells has been observed as a common after-spawning process affecting late vitellogenic stage oocytes and/or ripe and un-

Figure 1

Gonadal structure in *Eupera platensis*. **A.** Cross section through the visceral mass showing the gonad and inner demibranchs containing brooding embryos. **B.** Location of male germinal tissues (arrow) within a hermaphrodite acinus. **C.** Cross section through a hermaphrodite acinus showing the male germinal cells separated from the female ones by a thin conjunctive one-cell layer. **D.** Detail of a hermaphrodite acinus showing the simultaneous occurrence of spermatogenesis beside follicular cells in active phagocytosis of vitellinic droplets. **E.** Cross section through a gonad from a juvenile showing the arrangement of follicular cells in the follicular wall. **F.** Cross section through a female acinus showing different stages of the oocyte-follicle cell relationship. **G.** Light micrograph showing the close relationship between an early previtellogenic oocyte and the surrounding follicle cells. **H.** A vitellogenic oocyte widely attached to the acinus wall. Scale bars for all figures (except A) = 20 μm . Abbreviations: bm, basement membrane; cc, conjunctive cell; cl, conjunctive layer; do, degenerated oocyte; e, embryos; f, foot; fc, follicle cell; fe, follicular epithelium; g, gonad; id, inner demibranch; is, interlamellar space; m, mantle; n, nucleus; po, previtellogenic oocyte; od, outer demibranch; r, rectum; sc, spermatocytes; sg, spermatogonia; std, spermatids; vd, vitellinic droplet; vo, vitellogenic oocyte.



spawned ova. However, oosorption also takes place during pre-reproductive periods (these conditions may be easily determined in *Eupera* by the presence or absence of ova or embryos within brood pouches of the inner demi-branches). At the light microscope level, there was no evidence that might indicate the further oocyte breakdown.

The oosorption process begins with the breakup of the oocyte cell membrane and vitelline membrane. The liberated ooplasm, formed of acidophilic granules, fills the acinus lumen (Figure 2A). The follicular cells adjacent to the broken oocyte engulf the vitellinic granules, which become densely packed in the cell cytoplasm (Figure 2B-D). The phagocytosed material does not seem to immediately undergo chemical changes in the follicle cells, or, if any transformations takes place, it is not evidenced by stainability changes. At the end of the oosorption process, relics of phagocytosed and metabolized materials appear at the distal end of the follicle cell cytoplasm as rounded dense or filamentous basophilic corps (Figure 2H-I).

The vitellinic membrane and germinal vesicle of degenerative oocytes are not phagocytosed by the follicle cells, but remain in the lumen of the acinus until amoebocytic activity (Figure 2E). Then, their further destiny is unknown.

As the oosorption by follicle cells proceeds, amoebocyte activity increases. Amoebocyte cells are round in shape, with a translucent cytoplasm, and an excentric oval nucleus (Figure 2B). Invading the lumen of the acinus, amoebocytes begin the phagocytosis of the remaining yolk granules. Amoebocytes are also visible at the base of the follicular epithelium and among follicle cells (Figure 2F-G). Their cytoplasm is full of vitellin droplets (insert in Figure 2B) or, in certain cases, by a more finely granulated acidophilic material, suggesting that these cells have begun the digestion of engulfed particles (Figure 2F-G).

Phagocytic activity of amoebocytes never takes place before the reaction of the follicular epithelium, and only after the breakdown of the oocyte membrane and vitelline envelope.

As described above, the follicular epithelium of *E. platensis* undergoes important morphological transformations during oosorption; moreover, an important metabolic activity is required in order to metabolize the phagocytosed material. However, degenerative changes in follicular cells have not been observed after these processes.

After spawning, and when resorption of the residual ova is completed, the acinus collapses. Follicle shrinkage is followed by the ingression of blood cells to the interfollicular space originated by the acinus shrinkage (Figure 3). Loss of follicle cells was not observed.

Oosorption by follicle cells does not involve early vitellogenic or previtellogenic ova, although occasionally, they may undergo autolysis. This process is difficult to detect at the light microscope level. It is characterized by the vacuolization of the oocyte cytoplasm and alteration of their stainability (staining stronger than healthy oocytes). The ultimate destiny for the debris resulting from oocyte autolytic breakage has not been determined.

DISCUSSION

Gonad Structure and Oosorption

The gonad structure of *E. platensis* corresponds to the type described for bivalves such as species of the genera *Bankia*, *Mya*, *Teredo*, among others (Coe, 1943; Sastry, 1979). In these species, at the early stages of gonad development, follicular cells are the relevant elements in the acinar wall. Germinal cells are reduced in number and scattered along the base of the acinus between the conjunctive basement membrane and follicle cells. As oogenesis progresses, a reduced number of follicle cells completely surround the early developing oocytes, which keep in contact with the basement membrane. The arrangement of follicle cells is similar to that described in other Sphaerids such as *Sphaerium striatinum* (Lamarck, 1818) (Woods, 1931). Griffond (1977) and Griffond & Gomot (1979) described, in the freshwater gastropod *Viviparus*, a comparable follicular cell arrangement.

Figure 2

Oosorption process in *Eupera platensis*. **A.** Micrograph of a late vitellogenic oocyte just after its breakdown, showing the broken vitelline membrane and the vitellinic droplets occurring freely in the acinus lumen. **B.** Early phase of the resorption process. The follicular epithelium has begun phagocytosis of the vitellus derived from a degenerated oocyte. Blood amoebocytes, having come into the acinus, show their cytoplasm filled with phagocytosed vitellinic droplets (insert: detail of the amoebocyte cytoplasm full of yolk granules). **C.** Later steps of phagocytosis: the follicle cells show their cytoplasm swollen after vitellus ingestion. **D.** detail of the previous micrograph showing densely packed vitellinic droplets within the follicle cell cytoplasm. **E.** The phagocytosis of the vitellinic content of a degenerated oocyte has been completed (only a small amount of vitellus remains in the lumen of the acinus). Even so, the germinal vesicle and the vitelline membrane still remain in the acinar lumen without being involved in the phagocytic activity of the follicular epithelium. **F-G.** Two final steps in the resorption process: the follicle cells show their cytoplasm nearly free or free (in G) of ingested vitellinic droplets, but with a slightly visible filamentous content. **H-I.** The follicular epithelium after oosorption. The follicle cell cytoplasm shows several residual corps with a filamentous concentric structure. Scale bars for all figures = 20 μm . Abbreviations: a, amoebocyte; cc, conjunctive cell; gv, germinal vesicle; fc, follicle cell; fe, follicular epithelium; fi, residual corp with filamentous concentric structure; l, lumen of the acinus; n, nucleus; vd, vitellinic droplets; vm, vitelline membrane.

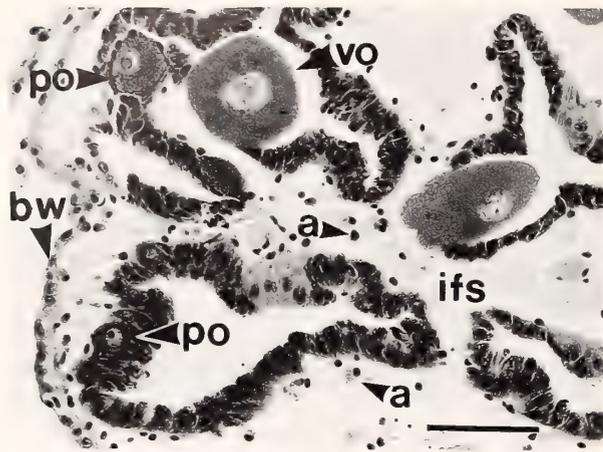


Figure 3

A post-spawning gonad (as determined by the presence of embryos in the inner demibranchs) showing the collapse of the follicles, the accumulation of blood amoebocytes, and residual (?) oocytes. Scale bar = 100 μm . Abbreviations: a, amoebocyte; bw, body wall; ifs, interfollicular space; po, previtellogenic oocyte; vo, vitellogenic oocyte.

Oocyte degeneration may take place in all stages of development; however, it is more frequent in advanced developmental stages (i.e., late vitellogenic or ripe and unspawned oocytes). Similar facts have been described in young *Viviparus* (Griffond, 1977), but it is in contrast to that described in *Biomphalaria glabrata* (Say, 1818) and *Lymnaea*, in which only ripe oocytes, that is to say those oocytes surrounded by a follicular cavity, degenerate (de Jong Brink et al., 1983).

The oosorption process carried out by the follicular epithelium in *E. platensis* has an unusual extent. The direct involvement of the follicular epithelium in the phagocytosis of the bulk of the important amount of vitellus resulting from degenerated large, yolky oocytes is a distinctive characteristic of the resorption process in this species. Such intense phagocytic activity of the follicle cells constitutes a unique phenomenon in Mollusca.

Follicular cells in *Pecten maximus* have been reported to phagocytose relics of degenerated oocytes, and the possibility of re-use of the valuable components of the phagocytosed material has been suggested (Dorange et al., 1989). Huebner & Anderson (1976) for the nudibranch *Cratena*, and Bottke (1972) for *Viviparus* also suggest, from histochemical and ultrastructural evidence, that the follicle cells seem to function in oocyte resorption. According to Griffond & Gomot (1979), the presence of lysosomes and residual bodies in the follicle cells of *Viviparus* indicates that these are active in absorbing degenerative material from the lumen of the gonad. Similar facts are reported by Hill (1977) for the follicle cells of *Agriolimax reticulatus* (Müller, 1774). However, none of the reviewed cases showed phagocytic activity of the follicle cells as extensive as that reported here in *Eupera*.

The phagocytic activity of the follicle cells in *E. platensis* only affects degenerated secondary or late vitellogenic oocytes and unspawned ova. Phagocytic activity never takes place before the oocyte breakdown. The same facts have been described for other invertebrates such as Nemertina (Bierne, 1983) and Sipunculida (Rice, 1983).

In other bivalves, particularly in those with a follicular epithelium arrangement similar to that of *E. platensis*, the loss of part of the follicular epithelium and its regeneration before a new gametogenetic cycle has been described. Coe & Turner (1938) described in *Mya arenaria* Linnaeus, 1758, that "... nearly all the follicular cells are eventually eliminated during spermiogenesis of well-nourished individuals. . . ." Pujals (1985) described the destruction of part of the follicular epithelium during oogenesis in *Erodona mactroides* Daudin, 1802. In spite of the high morphological transformations which take place during oosorption, degenerative changes in follicle cells have never been observed in *E. platensis*.

Litter Size, Egg Size and Oosorption

The existence of a trade-off between egg size and egg number has been largely recognized among invertebrates (Thorson, 1950; Lloyd, 1987; Olive, 1985; Calow, 1978, 1983; Bridges, 1993). This trade-off is determined by the fact that the energy available for reproduction is finite (Stearns, 1976). In *E. platensis*, spawned ova (200–250 μm diameter) are retained within both inner demibranchs where, after fertilization, the embryos develop to an advanced stage, being released as juveniles (≈ 1 mm shell length). As in other Sphaeriidae, the number of brooding embryos correlates with parental shell size (Vincent & Lafontaine, 1984; Meier-Brook, 1977); in general, individuals with size between 6 and 7.5 mm in shell length incubates 45–90 embryos. The minimum parental size at which brooding takes place was reported to be 4.3 mm in shell length (Ituarte, 1988). In the latter case, the litter size can be reduced to only 20 embryos (Ituarte, 1988).

In *E. platensis*, the occurrence of abortive ovocytes and the consequent resorption process takes place at any time in the reproductive cycle. A similar fact has been observed in *Pecten maximus* (Dorange et al., 1989). This fact suggests that the oocyte breakdown and subsequent resorption process are determined by different factors, originating in different functional requirements, but in every case, leading to prevent the inefficient energy budget that would imply a surplus production of gametes and/or the release of a number of large, yolky eggs which cannot be brooded. Two alternatives may be considered:

- In pre-reproductive individuals (as determined by the lack of brooding ova or embryos in inner demibranchs), breakdown of oocytes and consequent phagocytosis by follicle cells could originate as a response to space requirements. Space, in the restricted gonad volume within the visceral mass, may constitute a limiting factor for the development of large, yolky eggs.

– In recently spawned gonads (as determined by the presence of eggs or early embryos in inner demibranchs), the reduced sustainable litter size determined by the restricted space in the incubatory organs may be a limiting factor to induce the resorption of surplus female gametes whose release would imply (due to the impossibility of being incubated) an important energy loss. Beauchamp (1986) has suggested the physical space for brooded young as one of the limiting factors which controls brood size in *Lasaea subviridis* Dall, 1899. In Polychaeta, oosorption has been suggested as a process which may play a role in the oocyte output from the germinal epithelia, and then as a regulatory fecundity factor (Olive, 1983).

In mollusks, the internal factors controlling the resorption process are not known, but a neuroendocrine mechanism of control has been suggested in pectinids (Motavkine & Varaksine, 1983 *vide* Dorange et al., 1989). In some other cases such as in *Mytilus edulis* Linnaeus, 1758, this fact has been demonstrated (Lubet et al., 1986).

Calow (1978, 1983) stressed that in restrictive environments, reproductive effort is directed toward the reduction of egg number, increasing egg size, and the development of some parental care to the embryos, which are released in a more advanced developmental stage. This seems to be the case in *E. platensis*. The constraints imposed by the unpredictable freshwater environment have determined the development of a reproductive strategy directed toward the production of an extremely reduced litter size, and the development of large, yolky eggs, which are incubated for a long period of time, being released as fully developed juveniles, increasing the success of the offspring. These life history traits can be regarded, according to Olive (1985), as the set of co-variable reproductive traits with which *E. platensis* has adjusted its life history to an unpredictable environment. Many of the reproductive traits recognized by Olive (1985) as co-variables in the reproductive strategy of species, are determined by the particular characteristics of gametogenesis (i.e., egg size, fecundity, type of spermatozoa, etc). Also related to gametogenesis, follicular epithelium in *Eupera* develop an intense activity, phagocytosing degenerated oocytes. Then, a question arises: does the massive resorption process carried out by follicular cells constitute, in this particular case, a reproductive trait *per se*? If this is so, it can be suggested that the resorption process (due to its adaptive significance) has been added (evolutionary) to the suite of co-variable reproductive traits of the species according to the adjustment model favored in evolution.

If energy is a limited resource for parents, oogenesis implies an important metabolic effort to supply the energy required in vitellus synthesis, particularly in species such as *E. platensis* in which a great amount of vitellus is accumulated by the ripe oocyte. Then, the particular characteristics of the gamete resorption process carried out by the follicular epithelium may be regarded as one of the fitting elements of adaptive significance in order to avoid

a superfluous energy budget. These statements are in accordance with Olive's (1983) opinion, that oosorption plays an important role in the coordination of the reproductive cycle, particularly in those iteroparous species in which the resorptive process returns the ovary to a resting condition.

The activity of the follicle cells in the oosorption process here described constitutes an interesting phenomenon not known for other bivalves, and it deserves further analysis at the electron microscopic level in order to describe the characteristics of the endocytosis process. Moreover, investigations on enzymatic activity (peroxidases and acid phosphatase) will help to elucidate the ways in which the follicular epithelium digests the phagocytosed material, and whether the resulting products are stored *in situ* or elsewhere to allow the re-use of the valuable components of broken down oocytes, as suggested in *Pecten maximus* (Dorange et al., 1989) and *Mytilus edulis* (Lubet et al., 1986; Pipe, 1987).

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A Revision of Three Maghrebian Hygromiid Genera: *Numidia* Issel, 1885, *Xerofalsa* Monterosato, 1892, and *Xeroplana* Monterosato, 1892 (Pulmonata: Helicoidea)

by

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Abstract. The taxonomic status of the following nominal genera of the xerophilous hygromiids is revised: *Numidia* Issel, 1885, *Xerofalsa* Monterosato, 1892, and *Xeroplana* Monterosato, 1892. *Numidia* and *Xerofalsa* are objective synonyms, but the senior name is not available because of the existence of two senior homonyms. Examination of the type species of *Xerofalsa* (*Helix idia* Issel, 1885) and *Xeroplana* (*Helix doumeti* Bourguignat, 1876) shows that they are identical in anatomical organization. *Xerofalsa* and *Xeroplana*, therefore, cannot be regarded as distinct taxa, but are synonymous. Since they were published at the same time, according the principle of the first revisor, it is established that *Xerofalsa* is a junior synonym of *Xeroplana*.

Xeroplana seems close to the group of *Cernuella* Schütler, 1838 (*Cernuella*, *Xeroamanda* Monterosato, 1892, and *Xerocincta* Monterosato, 1892) with which it shares the following characters: (1) penial nerve from pedal ganglion, (2) right ommatophore retractor independent of genitalia, (3) mantle border with long left lateral lobe, (4) 0 + 2 dart-sac complex, and (5) penial complex joining vaginal complex at level of dart-sac complex. It differs from the group of *Cernuella* by virtue of: (1) dart-gun open as far as tip, (2) openings of two stylophores very close to each other, and (3) section of dart.

INTRODUCTION

In the last 20 years, research into the taxonomy and systematics of the helicoid snails has gathered impetus from the study of the internal structure of the distal genitalia (dart-sac complex and penis). This research was innovative and produced many revisions of taxa established in the past and many descriptions of new taxa. Nevertheless, many nominal taxa of the genus and the species groups, especially from southern Europe and northwestern Africa, remain uncertain. This is true of the three genera introduced by Issel (1885) and Monterosato (1892) for Tunisian (and also western Mediterranean) xerophilous hygromiids having a very depressed shell with a sharp peripheral keel. They are: *Numidia* Issel, 1885, *Xerofalsa* Monterosato, 1892, and *Xeroplana* Monterosato, 1892.

Numidia Issel, 1885 (p. 9; in the reprint: p. 5) was established to include "quelle elici della costa settentrionale d'Affrica e dell'Europa meridionale, le quali . . . hanno l'ultimo giro della spira acutamente carenato, l'ombelico aperto e profondo, il peristoma acuto e la spira depressa

o pianeggiante" [those hygromiids of the northern coast of Africa and southern Europe having the last whorl of the spire acutely carinate, the umbilicus open and deep, the peristome acute and the spire depressed or flat], such as *Helix idia* Issel, 1885, *H. doumeti* Bourguignat, 1876, *H. depressula* Rossmässler, 1839, *H. maroccana* Morelet, 1876, and *H. explanata* Müller, 1774. A few years later, *H. idia* was selected as type species by Pilsbry (1895: 258).

Numidia was regarded by Pilsbry (1895) and Gude & Woodward (1921), and as *Numidica* [sic] by Hesse (1926, 1934) and Thiele (1931), as a junior synonym of *Jacosta* Gray, 1821 (type species: *Helix albella* Draparnaud, 1891 [= *Helix explanata*]). Kobelt (1904) also disregarded it, listing some of the originally included species in *Numidia*, e.g., *H. doumeti*, *H. idia*, in *Xeroamanda* Monterosato, 1892 (type species: *Helix amanda* Rossmässler, 1838), and others in *Jacosta*, e.g., *H. depressula*, *H. explanata*. When *Jacosta* was suppressed under the law of priority to ensure that the generic name *Helicella* Férussac, 1821, remained available for use in its accustomed sense (ICZN, 1956), Zilch (1960) replaced it with *Leucochroa* Beck, 1837 (type spe-

cies: *Helix albella* Draparnaud, 1801 [= *Helix explanata*]), and considered *Numidia* as a junior synonym of the latter. Subsequently, Forcart (1965) demonstrated that *Leucochroa* was not available to replace *Jacosta* because its type species is not *Helix albella* Draparnaud, 1801, but *Helix albella* Linnaeus, 1758 [= *Helix pisana* Müller, 1774, cf. Forcart, 1965: 255–256; Gittenberger & Ripken, 1987: 37]. Forcart proposed *Xerosecta* Monterosato, 1892 (type species: *Helix explanata* Müller, 1774) as a replacement name. At this point, one might conclude that *Numidia* is a senior synonym of *Xerosecta*.

However *Numidia* Issel, 1885, is a junior homonym of *Numidia* Forster, 1817 (Aves) and *Numidia* Cocco, 1832 (Crustacea) (Neave, 1940: 361) and cannot be used as a valid name (ICZN, 1985: Art. 52a). A junior homonym which is not rejected as a junior synonym must be replaced (ICZN, 1985: Art. 60a) by an available junior synonym, if one exists (ICZN, 1985: Art. 60b) or by a new name (ICZN, 1985: Art. 60c). *Xerofalsa*, junior objective synonym of *Numidia*, is available to replace the senior synonym.

Numidica Hesse, 1926 (error pro *Numidia*, Issel, 1885) is an incorrect subsequent spelling and, as such, has no status in the zoological nomenclature (ICZN, 1985: Art. 33c).

Xerofalsa was introduced by Monterosato (1892: 21) for a “gruppo di specie Tunisine, depresso da un lato, con segni di accrescimento verrucosi; ombelico infundibuliforme con l’orlo molto rialzato [group of Tunisian species, depressed on one side, with verrucose growth lines, funnel-shaped umbilicus with very raised edge],” comprising *Helix idia*, *H. enica* Letourneux & Bourguignat, 1887, and *H. zeugitana* Letourneux & Bourguignat, 1887. In the same year, *H. idia* was designated as the type species in an anonymous comment on Monterosato’s paper, believed to be written by Kobelt (1892: 152), editor of *Nachrichtsblatt der deutschen malakozoologischen Gesellschaft*.

Pilsbry (1895) and Gude & Woodward (1921) regarded *Xerofalsa* as being, like *Numidia*, a junior synonym of *Jacosta*. Kobelt (1904) did not comment on the status of the genus but listed the three species originally included in the genus by Monterosato under *Xeroamanda*. Hesse (1926), followed by Thiele (1931), took a more prudent position, regarding *Xerofalsa* as a taxon of uncertain status lacking anatomical data. Finally, Zilch (1960) tentatively placed *Xerofalsa* among the synonyms of *Xeroplexa* Monterosato, 1892 (type species: *Helix setubalensis* Pfeiffer, 1850). He was probably induced to do this by Kobelt who had listed the species originally included in *Xerofalsa* under *Xeroamanda*, since Zilch considered the latter to be a junior synonym of *Xeroplexa*.

Ktari & Rezig (1976) published the first anatomical report of the type species. The structure of the distal genitalia they found coincided with that of the subfamily Hygromiinae *sensu* Schileyko (1978, 1991) (dart sac complex with 0 + 2 stylophores) and particularly with the group

of genera with 0 + 2 stylophores and right ommatophore retractor free from the genitalia (*Cernuella* Schütler, 1838, *Xerosecta*, *Polloneriella* Alzona & Alzona Bisacchi, 1940, *Microxeromagna* Ortiz de Zárate López, 1950, *Xeromunda* Monterosato, 1892). It was therefore similar but different from that of *Candidula* Kobelt, 1871 of which *Xeroplexa* is a junior synonym (Gittenberger, 1985). According to Manganelli & Giusti (1988), some features of *H. idia* (e.g., the enlarged base of the digitiform glands) revealed by Ktari & Rezig (1976) suggested that *Xerofalsa* was a genus endemic to North Africa distinct from, but close to *Cernuella*, and possibly close to *Alteniella* Clerx & Gittenberger, 1977 (type species: *Cernuella zilchi* Brandt, 1959), introduced as subgenus of *Cernuella*.

Finally, *Xeroplana* was established by Monterosato (1892:21–22) for a “gruppo Tunisino a specie nummuliformi, a carena tagliente, a colorazione sbiadita e di sostanza quasi cornea; ombelico patulo [Tunisian group of nummuliform species with a sharp keel, faded coloring, almost corneous consistency and a wide umbilicus],” consisting of *Helix doumeti* and *H. depressula*. *Helix doumeti* was designated type species by Kobelt (1892).

Like *Xerofalsa*, *Xeroplana* was considered a junior synonym of *Jacosta* by most authors involved in the revision of western Mediterranean hygromiids (Pilsbry, 1895; Gude & Woodward, 1921; Hesse, 1926, 1934; Thiele, 1931) with the sole exception of Kobelt (1904) who listed the species originally included in this genus under *Xeroamanda*. When *Jacosta* was suppressed and replaced with *Leucochroa*, *Xeroplana* became a junior synonym of the latter (e.g., Zilch, 1960). Subsequently, Forcart (1965) demonstrated that *Leucochroa* was not available to replace *Jacosta* and proposed *Xerosecta* as replacement name. At this point, one might conclude that *Xeroplana* and *Xerosecta* are synonyms.

This hypothesis could be corroborated by the anatomical study of the type species published by Hesse (1934), who, examining specimens of *Helix doumeti* collected at “Redeyef im südlichen Tunis” (Hesse, 1934:21, pl. 5, fig. 35a–f) demonstrated that this species had a scheme of the distal genitalia similar to that of the species that he assigned to *Jacosta* (*H. explanata* and *H. depressula*). However, a more recent study of specimens assigned to *H. lacosteana* Morlet, 1881, an entity usually considered close to or a synonym of *H. doumeti*, excluded this interpretation (Manganelli & Giusti, 1988). Though finding that the outline of genitalia delineated by Hesse (1934) was very similar, Manganelli & Giusti (1988) demonstrated that the internal structure of the distal genitalia (not studied by Hesse) was completely different from that of *Xerosecta*. Manganelli & Giusti (1988) did not confirm *Xeroplana* as a distinct genus because they lacked complete evidence of the synonymy between *H. lacosteana* and *H. doumeti*.

The aim of the present paper is to revise *Xerofalsa* and *Xeroplana* by studying their respective type species and to ascertain their taxonomic and nomenclatural status.

MATERIALS AND METHODS

Whole shells were photographed under the light microscope (Wild M5A). All dimensional parameters (shell height, maximum shell diameter, aperture height, and aperture diameter) were measured using calipers.

Living specimens were drowned in water, then fixed and preserved in 75% ethanol, buffered with NaHCO_3 . The bodies were isolated after crushing the shells and dissected under the light microscope (Wild M5A) using very thin, pointed watchmaker's tweezers. Anatomical details were drawn using a Wild camera lucida. Anatomical parts were measured using a millimetric lens on the same microscope.

Radulae were manually extracted from the buccal bulbs, washed in pure 75% ethanol, mounted on copper blocks with electronconductive glue, sputter-coated with gold, and photographed using a Philips 505 SEM.

The material examined is listed as follows: locality, geographical references, collector(s), date, number of specimens in parenthesis. Locality names were according to the map Algérie-Tunisie 1/1,000,000, Michelin no. 972, 1988, and geographical references according to Tactical Pilotage Chart 1:500,000, sheets G-2A 354 and G-2D 422.

Unless otherwise indicated, all the examined specimens illustrated are kept in the Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy).

THE TYPE SPECIES OF *XEROFALSA* AND *XEROPLANA*

Xeroplana idia (Issel, 1885)

(Figures 1–12)

Helix (Numidia) idia Issel, 1885: 8–9, fig. at p. 8. Type locality: "Hammam-el-Lif presso Tunisi," Tunisia. Type series: Issel claimed to have examined six specimens, but in what remains of his collection at the Museo di Storia Naturale in Genoa (Italy), there is no syntype of the species (M. Bodon, personal communication). The original type series is considered lost, and the specimen illustrated on p. 8 is designated as the lectotype of the species (ICZN, 1985: Art. 74a, 74c).

H[elix]. idia Letourneux & Bourguignat, 1887: 89, junior primary homonym and junior subjective synonym of *Helix (Numidia) idia* Issel, 1885. Type locality: "Sous les pierres au Djebel Reças [Djebel Ressay] (Let.) et sur les collines près d'Hammam-el-Lif [Hammam Lif] (Berthier)," Tunisia. Type series: Six syntypes from Djebel Reças and one from Hammam Lif are kept in the Bourguignat Collection at the Muséum d'Histoire Naturelle in Geneva (Switzerland).

Material examined: Tunisia: Djebel Zaghouan, 10°8'E, 36°23'N, F. Giusti leg. 5.11.89 (11 preserved specimens + 45 shells).

Diagnosis: A species belonging to *Xeroplana* (a genus of the Hygromiidae with penial nerve from pedal ganglion,



Helix (Numidia) idia, Bourg. e Let.

Figure 1

The lectotype of *Xeroplana idia* (Issel, 1885).

right ommatophore retractor independent of genitalia, mantle border with long left lateral lobe, 0 + 2 dart-sac complex, penial complex joining vaginal complex at level of dart-sac complex, dart-gun open as far as tip, openings of stylophores very close to each other and peculiar section of dart). *X. idia* is easily distinguished from the other known species of the genus, *X. doumeti* (Bourguignat, 1876) by virtue of its smaller shell (maximum shell diameter: 15.6–18.0 mm) with a wide, deep, open, funnel-like umbilicus bordered by a sort of raised, crenulated and keeled edge. Anatomically it is distinguished by the digitiform glands, which are subdivided into two opposite groups of non-numerous and branched units and by the epiphallus, which is almost twice the length of the penis.

Shell (Figures 1–3): Shell dextral, medium-sized, markedly lenticular and keeled, rather thin and fragile, uniformly yellowish-white, with pale brown speckling near carina, frequently with traces of pale brown bands fragmented into rows of small, pale brown spots; bands occasionally quite continuous and darker brown in lower half; shell surface opaque, with fine, closely spaced, slightly raised ribs; ribs thicker and more raised near keel, which thus appears crenulated; spire flat or very slightly raised, consisting of 5–5 $\frac{2}{3}$ whorls, regularly and rather rapidly expanding; last whorl large, dilated, descending slightly or not at all near aperture, with evident, crenulated and frequently undulating keel at periphery; sutures superficial, shouldered by keel of preceding whorl; umbilicus wide (about $\frac{1}{4}$ of maximum shell diameter), deep, open and funnel-shaped, bordered by sort of raised, crenulated and keeled edge; aperture oblique, droplike in outline, its external margin well angled at peripheral keel, its lower margin (at border with columellar margin) slightly angled at periumbilical keel; peristome interrupted, simple and with sharp edge, very slightly reflected only at its columellar margin, with upper margin sometimes starting at keel, sometimes below keel of preceding whorl.

Dimensions of the shell are given in Table 1. The dimensions of the specimens utilized for the original descriptions by Issel (1885) and Letourneux & Bourguignat (1887) are slightly smaller than those of the specimens examined by us, possibly because the former were not yet adult. The diameter of the shell, according to Issel, is 14 mm, and the height 4.5 mm; the diameter of the shell, according to



Figures 2-3

Two shells of *Xeroplana idia* (Issel, 1885) from Djebel Zaghouan (Tunisia). Giusti. Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). All $\times 3.5$.

Letourneux & Bourguignat, is 13 mm, and the height 4 mm.

General anatomy: Mantle border (Figure 4) with five lobes: right lateral, subpneumostomal, right dorsal, left dorsal, and left lateral; right dorsal and left dorsal lobes border upper margin of pneumostome; left lateral lobe in form of long, thin lamina, upper vertex of which ends close to left vertex of left dorsal lobe; subpneumostomal lobe, variable in shape, usually triangular; right lateral lobe, elongated triangular, its upper vertex situated just below anal opening. Near peripheral keel of shell, mantle border

has triangular, pointed projection resembling mantle tentacle. Foot with non-partite sole, of holopod type. Retractor of right ommatophore independent of penis and vagina. Kidney sigmurethrous. Jaw odontognathous. Penial nerve from right pedal ganglion. Data on color of body available only from preserves specimens, which are yellowish-pink with walls of pallial cavity greyish with black pigment bordering blood vessels and brownish-black spots close to mantle border near pneumostome and anus.

Genitalia (Figures 5-12): General scheme of the semi-diaulic monotrematic type. Large hermaphrodite gonad

Table 1

Number of whorls and dimensions (in mm) of the shell of *Xeroplana idia* and *X. doumeti*. For each dimension mean, standard deviation (above) and range (below) are given.

Species	Locality	Number of whorls	Shell diameter	Shell height	Aperture diameter	Aperture height	Number of specimens
<i>Xeroplana idia</i>	Djebel	5-5½	17.0±0.66	6.0±0.61	7.6±0.38	5.2±0.37	20
	Zaghouan		15.6-18.0	4.9-7.4	6.8-8.3	4.7-5.8	
<i>Xeroplana doumeti</i>	Djebel	5½-6	21.3±1.47	7.9±0.93	10.1±0.97	5.5±0.62	8
	Bou-Hedma		19.0-24.0	7.2-10.0	8.4-11.3	4.4-6.6	
<i>Xeroplana doumeti</i>	Djebel Ech	5¾-6½	24.2±1.17	8.8±0.72	11.0±0.59	6.0±0.42	6
	Cherichira		23.0-26.4	7.8-9.7	10.3-12.2	5.3-6.5	
<i>Xeroplana doumeti</i>	Sbeitla	5¾-6	23.0-25.5	8.0-9.9	9.5-11.3	5.5-7.5	3

(ovotestis) consisting of bunch of acini, the ducts of which converge into first hermaphrodite duct, its initial portion very slender, then widening to function as seminal vesicle; first hermaphrodite duct ending in clublike "talon" adhering to internal side of large, beanlike albumen gland; talon (Figure 10) consisting of seminal receptacles (a tree-like system of tubules, ending in about, six to seven branches) and fertilization chamber; second hermaphrodite duct (ovispermiduct) arising from base of albumen gland and consisting of female channel with seminal groove (corresponding to uterine ovispermiduct) and prostate gland with sperm groove (corresponding to prostatic ovispermiduct), fused to define single lumen; rather long (2.9-3.0 mm; n:2) free oviduct following female channel; duct of bursa copulatrix arising from where proximal vagina follows free oviduct, rather long (11.2-11.3 mm; n:2) and slender, initially slightly flared, ending in large, ovoid bursa copulatrix (gametolytic gland); proximal vagina medium in length; two tufts of slightly branched digitiform glands situated at half proximal vagina length, arising from opposite sides of vagina (Figure 7); dart-sac complex 0 + 2 i.e., consisting of one pair of stylophores, fused to vagina walls for most of its length; stylophores of equal size fused in single massive structure with only their apices free of each other; outer stylophore containing dart; inner stylophore with small, empty cavity; cavities of stylophores opening independently one above other into groove of conical structure named "dart-gun," projecting into distal vagina lumen, similar to that described in other hygromiids (cf. Manganelli & Giusti, 1988) but simpler and shorter and open to tip (Figure 9); vaginal pleats, variable in number, along internal surface of vagina walls on both sides of dart-gun; dart slightly curved, slender, pointed, with only one lateral wing which arises at ½ of its length to end at tip (transverse section polygonal with lateral, hooklike projection); long slender vas deferens following sperm groove (which runs inside prostate gland of ovispermiduct) and ending in penial complex; penial complex composed of flagellum, epiphallus, and penis; flagellum rather long (6.7-7.3 mm; n:2), ending level with where

vas deferens enters penial complex and epiphallus begins; epiphallus rather long (5.1-7.9 mm; n:2), ending where penial retractor muscle joins penial complex wall; penis short (2.6-3.7 mm; n:2) containing penial papilla (glans); proximal penis ⅓-¼ of penis length; penial papilla long and slender, cylindro-conical, with wrinkled sides and apical opening bordered by two or three "lips," its base not connected to penial walls by frenula (Figure 11); penial

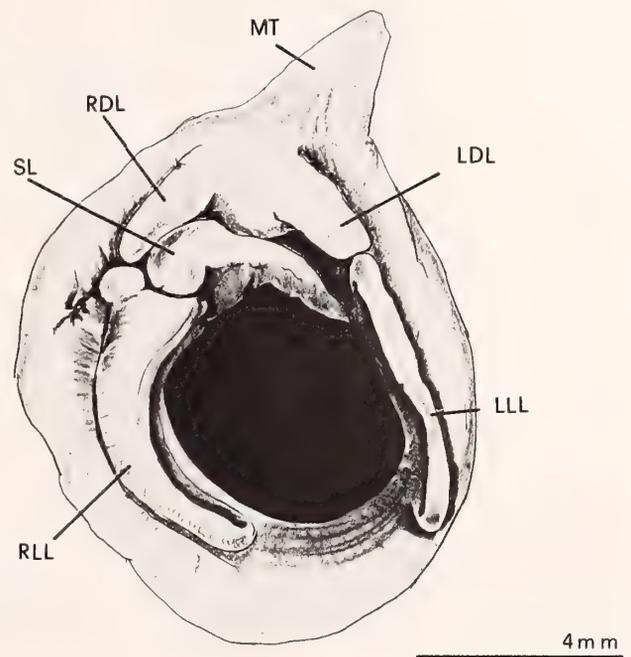
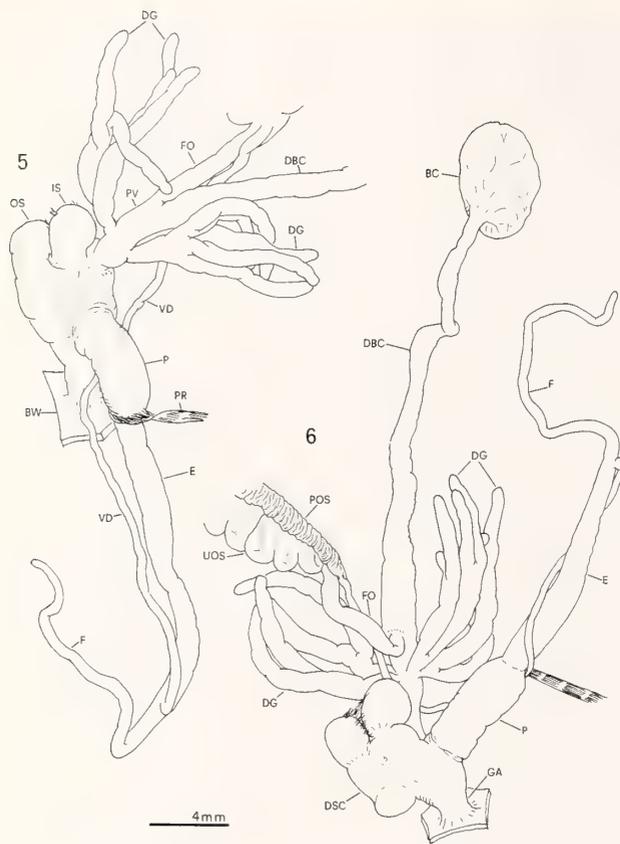


Figure 4

The mantle collar of a specimen of *Xeroplana idia* (Issel, 1885) from Djebel Zaghouan (Tunisia). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4; I-53100 Siena, Italy). Key: LDL, left dorsal lobe; LLL, left lateral lobe; MT, mantle "tentacle"; RDL, right dorsal lobe; RLL, right lateral lobe; SL, subpneumostomal lobe.

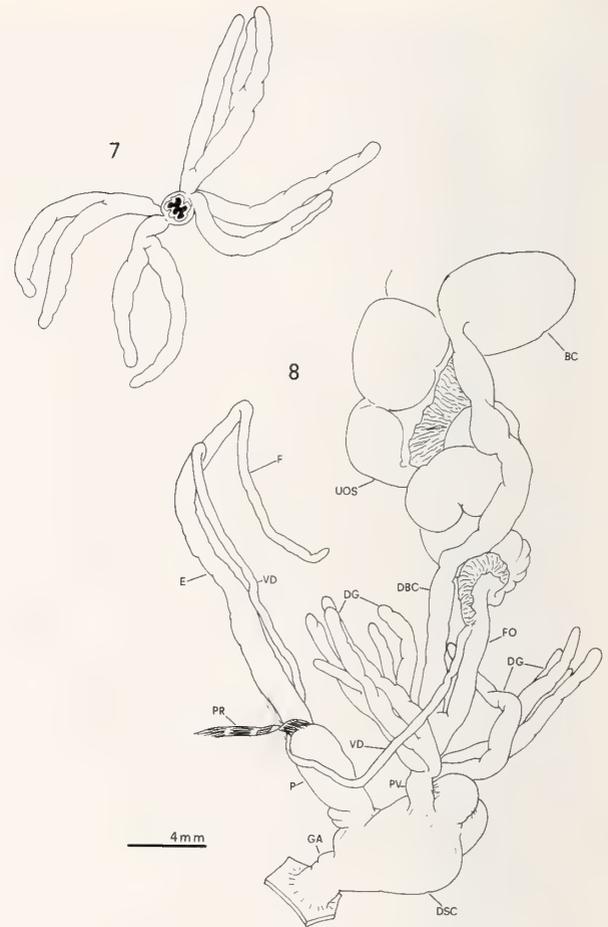


Figures 5-6

Two different views of the distal genitalia of a specimen of *Xeroplana idia* (Issel, 1885) from Djebel Zaghouan (Tunisia). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: BC, bursa copulatrix; BW, body wall; DBC, duct of bursa copulatrix; DG, digitiform glands; DSC, dart sac complex; E, epiphallus; F, flagellum; FO, free oviduct; GA, genital atrium; IS, inner stylophore; OS, outer stylophore; P, penis; POS, prostatic portion of ovispermiduct; PR, penial retractor muscle; PV, proximal vagina; UOS, uterine portion of ovispermiduct; VD, vas deferens.

papilla walls compact, transverse section revealing ring of small lacunae at center of space between ejaculatory duct and external wall (Figure 12); ejaculatory duct continuing directly from proximal penis and epiphallus lumen; penis entering distal vagina level with apex of dart-gun and with opening into vagina, bordered by sort of annular pleat, possibly a sphincter; genital atrium rather short, opening on right side of body, a short distance from right ommatophore.

Radula: Radula consisting of many rows each of about 71-75 teeth; central tooth with large tricuspid crown, mesocone long, more than twice ectocone height; first lateral teeth with bicuspid crown, its mesocone long and robust, and its ectocone small (about $\frac{1}{2}$ mesocone height); last lateral and latero-marginal teeth with bicuspid crown, their



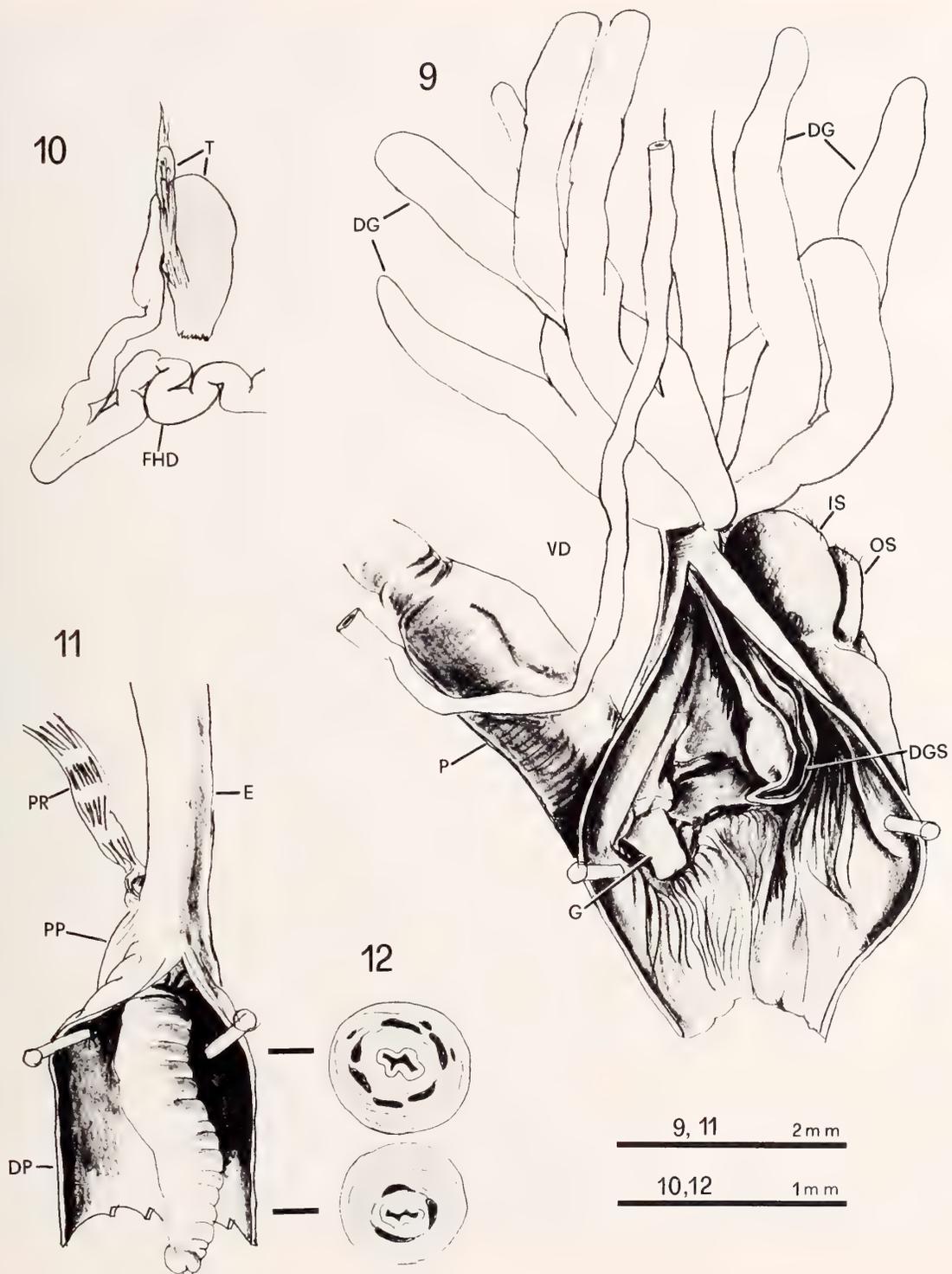
Figures 7-8

Digitiform glands and distal genitalia of a second specimen of *Xeroplana idia* (Issel, 1885) from Djebel Zaghouan (Tunisia). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: BC, bursa copulatrix; DBC, duct of bursa copulatrix; DG, digitiform glands; DSC, dart sac complex; E, epiphallus; F, flagellum; FO, free oviduct; GA, genital atrium; P, penis; PR, penial retractor muscle; PV, proximal vagina; UOS, uterine portion of ovispermiduct; VD, vas deferens.

mesocones long, with very small protuberance on inner side about $\frac{2}{3}$ up mesocone (exceptionally, some latero-marginal teeth without trace of this small protuberance) and their ectocones small, slender, and pointed; extreme marginal teeth with crown composed of long, very slender mesocone, its tip usually with small protuberance on its inner side, only occasionally split into two points, and very reduced ectocone, frequently split into two small, sharp points.

Habitat: The species lives on calcareous substrates, under stones or litter under bushes, occasionally on bare rocks in areas not directly exposed to sunlight.

Distribution: The species is recorded from northeastern Tunisia, and specifically from the hills of Hammam-el-



Figures 9–12

Internal structure of the distal genitalia (9), talon (10), and penial papilla (11) with two transverse sections (12) of *Xeroplana idia* (Issel, 1885) from Djebel Zaghouan (Tunisia). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: DG, digitiform glands; DGS, dart gun; DP, distal penis; E, epiphallus; FHD first hermaphrodite duct; G, penial papilla (glans); IS, inner stylophore; OS, outer stylophore; P, penis; PP, proximal penis; PR, penial retractor muscle; T, talon; VD, vas deferens.

Lif near Tunis (Issel, 1885; Letourneux & Bourguignat, 1887), Djebel Recas (Letourneux & Bourguignat, 1887), Djebel Bou Karnine (Ktari & Rezig, 1976), Djebel Ressas (Ktari & Rezig, 1976) and the limestone formation at Djebel Zhagouan, south of Tunis.

Remarks: Many authors agree in attributing the authorship of the species to Letourneux & Bourguignat (1887) (Kobelt, 1888, 1904; Westerlund, 1889; Pilsbry, 1895). Issel stated that the species "fu rinvenuta quasi simultaneamente ad Hammam-el-Lif presso Tunisi, dal Marchese Doria e dal consigliere Letourneux [was found almost simultaneously at Hammam-el-Lif near Tunis, by the Marquis Doria and counsellor Letourneux]." Marquis Doria sent Issel six specimens, only one of which seemed adult. Issel described the species from the latter and measured the shell.

Issel probably communicated his discovery to Bourguignat who was writing the *Prodrome de la Malacologie Terrestre et Fluviale de la Tunisie* in collaboration with A. Letourneux. Issel presumably learned from Bourguignat that he was publishing the species under the name *Helix idia* and cited the species as *Helix (Numidia) idia*, ascribing its authorship to "Bourguignat and Letourneux." This can be deduced from the fact that Issel added: "*Helix idia*, Bourguignat in littera" after the species name.

However, Letourneux & Bourguignat did not publish a valid description of *H. idia* until 2 years after that of Issel (1885). It is evident that Issel did not obtain anything more than the species name from Bourguignat, as his description is based on the six specimens (or on the only adult specimen) received from Marquis Doria. The author of *H. idia* is therefore Issel (1885), not Letourneux & Bourguignat (1887) (ICZN, 1985: Art. 50a).

Xeroplana doumeti (Bourguignat, 1876)

(Figures 13–18)

Helix doumeti Bourguignat, 1876: 39–40. Type locality: "Djebel Hedmar, près Gabès, au sud de la régence de Tunis"; corresponding to "Djebel Bou-Hedma, entre Gafsa et Sfax" (Letourneux & Bourguignat, 1887: 88), Tunisia. Type series: eight syntypes are kept in the Bourguignat Collection, at the Muséum d'Histoire Naturelle in Geneva (Switzerland), one designated as lectotype (Figure 13).

Helix lacosteana Morlet, 1881: 394–395, pl. 6, figs. 1, 2. Type locality: "Chott-Djerid, djebel Aïdoudi," Tunisia. Type series: unknown.

Material examined: Tunisia: Djebel Bou-Hedma, between 9°30' and 9°35'N, 34°26' and 34°33'E (eight syntypes), Bourguignat Collection, at the Muséum d'Histoire Naturelle in Geneva (Switzerland); Djebel Ech Chericira, 9°7'E, 35°13'N, I. Sparacio leg. 8.5.92 (six preserved specimens); Sbeitla, 10°43'E, 35°36'N, G. Selmi leg. 3-4.11.76 (four preserved specimens + one shell).

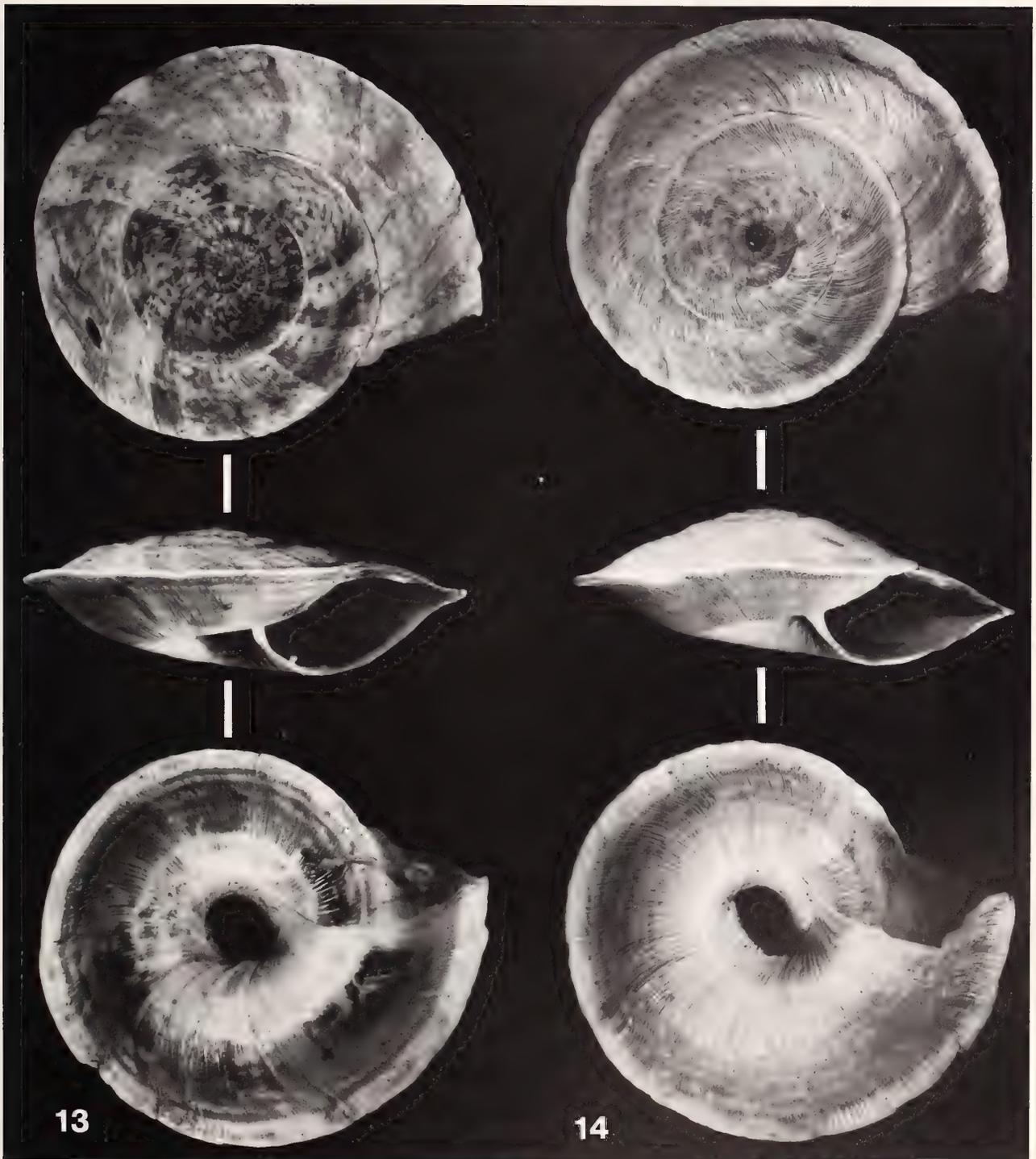
Diagnosis: A species belonging to *Xeroplana* (a genus of the Hygromiidae with penial nerve from pedal ganglion, right ommatophore retractor independent of genitalia, mantle border with long left lateral lobe, 0 + 2 dart-sac complex, penial complex joining vaginal complex at level of dart-sac complex, dart-gun open as far as tip, openings of stylophores which are very close to each other and peculiar section of dart). *X. doumeti* is easily distinguished from the other known species of the genus, *X. idia* (Issel, 1885) by virtue of its larger shell (maximum shell diameter: 19.0–26.4 mm) with a wide, deep, open, funnel-shaped umbilicus, which is not bordered by any sort of raised, crenulated or keeled edge. Anatomically it is distinguished by the digitiform glands, which are divided into two opposite groups of more numerous and branched units, and by the epiphallus which has almost the same length as the penis.

Shell (Figures 13–18): Shell dextral, medium-sized, markedly lenticular and keeled, thin but rather robust, uniformly yellowish-white, frequently with traces of pale brown bands or bands fragmented into rows of small, pale brown spots on upper half, immediately above keel, and on lower half, between keel and umbilicus rim; shell surface opaque, striated by very fine, close, slightly raised ribs; ribs slightly thicker and more raised near keel; spire conical, more or less raised, consisting of 5½–6⅞ whorls, regularly and rather rapidly expanding; last whorl large, dilated, slightly or not descending near aperture, with markedly pronounced, fringed, and often undulating keel at periphery; sutures superficial, shouldered by keel of preceding whorl; umbilicus open, wide (about ¼ of maximum shell diameter), funnel-like and deep; aperture oblique, oval to droplike in outline, its external margin angled at peripheral keel; peristome interrupted (its upper and lower margins united by thin callosity on last whorl wall), simple and with sharp edge, slightly reflected only at its columellar margin, with upper margin sometimes starting at keel, sometimes immediately below keel of preceding whorl.

Dimensions of the shell are given in Table 1.

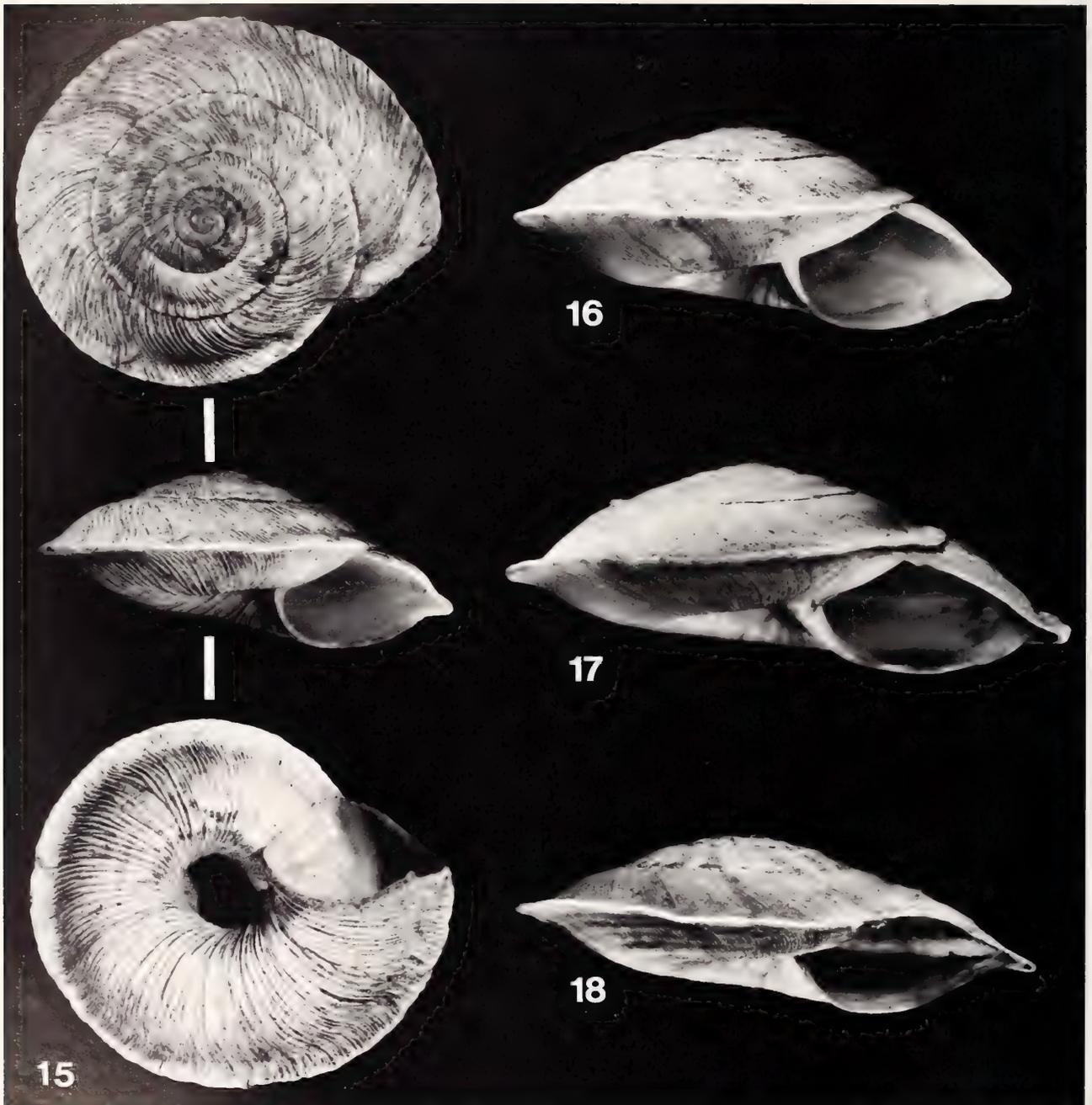
General anatomy: Body morphology agrees with that of *X. idia*. Dextral dorsal and left dorsal lobes of the mantle border less elongated. Mantle border has shorter and less pointed projection where shell aperture is angled (at peripheral keel of shell).

Genitalia: General scheme and details similar to those described in *X. idia*. Study of four adult specimens revealed in respect to *X. idia*: longer penial flagellum (7.9–10.9 mm), epiphallus same length or slightly longer (6.8–9.2 mm), penis slightly longer (5.0–5.7 mm), bursa copulatrix duct same length or slightly longer (11.2–15.6 mm) and free oviduct longer (4.9–5.1) (larger dimensions are in proportion to larger body size); the digitiform glands are divided into two opposite groups of units which are more numerous and branched; bases of units cover larger portion



Figures 13–14

The lectotype (13) and a paralectotype (14) of *Xeroplana doumeti* (Bourguignat, 1876) from Djebel Bou-Hedma (Tunisia). Bourguignat Collection, Muséum d'Histoire Naturelle in Geneva (Switzerland). All $\times 3.5$.



Explanation of Figures 15 to 18

Figure 15. Another paralectotype of *Xeroplana doumeti* (Bourguignat, 1876) from Djebel Bou-Hedma (Tunisia). Bourguignat Collection, at the Muséum d'Histoire Naturelle in Geneva (Switzerland). All $\times 3.5$.

Figures 16–18. Shells of *Xeroplana doumeti* (Bourguignat, 1876) from Djebel Ech Cherichira (Tunisia). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). All $\times 3.5$.

of the vagina perimeter (smaller portion of vagina perimeter is left free between the two groups); epiphallus almost the same length as penis (see Manganelli & Giusti, 1988: fig. 12, as *X. lacosteana*).

Radula: Radula almost identical in number and shape of teeth to that described for *X. idia*.

Habitat: No personal data available. G. Selmi (personal communication) reported observing specimens in open fields on grass.

Distribution: Central southern Tunisia. Bourguignat (1876: 40) reported it from Djebel Edmar, near Gabes. Letourneux & Bourguignat (1887: 88, note 2) corrected this, stating that "Le type de l'*Helix doumeti* a été trouvé, en 1874, par M. Doumet-Adanson dans le Djebel Bou-Hedma, entre Gafsa et Sfax" and that the species was collected in many localities of the hilly regions of southern Tunisia.

Remarks: The discovery of the type series of *Helix doumeti* in the Bourguignat collection at the Muséum d'Histoire Naturelle in Geneva (Switzerland) and a careful review of the literature allowed us to clarify the relationships between this nominal species and *H. lacosteana*. Kobelt (1888:17) regarded *H. lacosteana* Morlet, 1881 (type locality: "Chott-Djérid, Djébel Aidoudi") and *H. doumeti* Bourguignat, 1876 (type locality: "Djebel Hedmar, près Gabés, au sud de la régence de Tunis"; corresponding to "Bou-Hedma, entre Gafsa et Sfax" cf. Letourneux & Bourguignat, 1887:88) as synonyms, but since he was unable to study Bourguignat's (1876) paper, he could not ascertain whether *H. doumeti* was validly described. He therefore preferred to use Morlet's name. His action may seem incomprehensible outside the context of his controversy with the authors of the Nouvelle Ecole (cf. Dance, 1970). Manganelli & Giusti (1988) determined their specimens from Sbeitla as *Xeroplana lacosteana* on the basis of the description and figures of Kobelt (1888:16–17, pl. 96, fig. 531). Hence their specimens are also identical to *X. doumeti*, and this was fully confirmed by the finding of the syntypes of the latter species in the Bourguignat Collection at the Muséum d'Histoire Naturelle in Geneva (Switzerland) (Figures 13–15).

DISCUSSION

Examination of the type species of *Xerofalsa* (*Helix idia*) and *Xeroplana* (*Helix doumeti*) permitted us to ascertain that they are identical in anatomical organization. *Xerofalsa* and *Xeroplana*, therefore, cannot be regarded as distinct taxa, but are synonymous.

Since the names *Xerofalsa* and *Xeroplana* were published at the same time, precedence between them is determined by the first revisor (ICZN, 1985: Art. 24), who should choose the name that will best serve the stability and universality of the nomenclature (ICZN, 1985: Recommendation 24A). As no author, acting as first revisor, has yet

determined the precedence between *Xeroplana* and *Xerofalsa*, we establish *Xerofalsa* as junior synonym of *Xeroplana*. Unlike *Xeroplana* (cf. Manganelli & Giusti, 1988; Nordsieck, 1993), *Xerofalsa* has never been used as a valid genus.

At present, *Xeroplana* includes two species from Maghrebian Africa: *X. doumeti* (Bourguignat, 1876) and *X. idia* (Issel, 1885). Other nominal species which may belong to this genus are: *Helix henoniana* Bourguignat, 1870 (type locality: "en Kabylie, au Chabet-el-Akra"; Algeria) and *H. enica* Letourneux & Bourguignat, 1887 (type locality: "Oued-el-Hammam au sud du Djebel Zaghouan"; Algeria). The latter are conchologically very similar to the former (see Kobelt, 1888:pl. 96) and live in the same geographical area inhabited by the *Xeroplana* species.

Xeroplana seems close to the group of *Cerneuella* (*Cerneuella*, *Xeroamanda*, and *Xerocincta*) with which it shares the following characters: (1) penial nerve from pedal ganglion, (2) mantle border with long left lateral lobe, (3) penial complex joining vaginal complex at level of dart-sac complex. It differs from the group of *Cerneuella* by virtue of: (1) dart-gun open as far as tip, (2) openings of stylophores close to each other, and (3) particular section of dart.

A cladistic analysis is in preparation to verify the relationships between *Xeroplana* and the allied genera of the hygromiids.

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Comparative Survivorship of Sympatric
Native North American Gastropods
(*Anguispira*, *Mesodon*, *Physella*, *Pleurocera*)
and an Introduced Bivalve (*Dreissena*)
Exposed to Freezing Temperatures

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Abstract. Seventy-four specimens from four genera of native gastropods were cooled from 2.0°C to -3.3°C over a 3 hour period under laboratory conditions. The taxa examined included two terrestrial pulmonates (*Anguispira alternata* and *Mesodon inflecta*), a pulmonate known to occupy both permanent and ephemeral aquatic habitats (*Physella integra*), and an aquatic prosobranch (*Pleurocera canaliculatum*). There was no mortality in the pulmonates, but 39% mortality occurred in the prosobranch *Pleurocera*. Additionally, a sample of 43 zebra mussels (*Dreissena polymorpha*), a non-native but recently introduced species, were aurally exposed to the same temperature cycle. Of the 43 mussels, 20 had been acclimated to 2°C, and 23 acclimated to 15°C. Mortality occurred in both treatments (35% mortality in the 15°C acclimated and 25% in the 2°C acclimated) and did not differ significantly between the two groups. No mortality occurred among controls.

INTRODUCTION

The most common ways in which organisms survive in a subfreezing environment are avoidance (including supercooling) and/or freeze tolerance. Supercooling, the extension of the liquid phase below the equilibrium freezing point of tissue fluids, has been documented in a diversity of animal groups including various mollusks and intertidal

invertebrates, terrestrial arthropods, and both terrestrial and aquatic vertebrates (Storey & Storey, 1988). Freeze tolerance, although less common, has also been reported for such animals as some marine invertebrates and some vertebrates (Storey & Storey, 1988).

Illinois gastropods occur in a wide variety of habitats and include terrestrial, aquatic, and semi-aquatic species. These forms may all be periodically exposed to subfreezing

temperatures, particularly during the spring and fall months when ambient temperatures can vary widely within a 24 hour period. However, there is little information available on how these species tolerate periodic and short-term exposure to subfreezing temperatures. The purposes of this study were twofold: (1) to examine the effects of a temperature cycle that would expose four species of native mollusks to freezing temperatures, and (2) to determine whether an introduced mollusk is more or less able to withstand exposure to subfreezing temperatures compared to the native mollusks we studied. Our study was not intended to determine mortality curves or to investigate the efficacy of freezing as a control method for the zebra mussel *Dreissena polymorpha*.

We selected a prosobranch, *Pleurocera canaliculatum* (Say, 1821), which is strictly aquatic and occupies large rivers (Burch, 1982). We also included three pulmonates. One, *Physella integra* (Haldeman, 1841), Family Physidae, is a basommatophoran pulmonate that occupies both permanent and ephemeral aquatic habitats (Te, 1978). Additionally, two terrestrial stylomatophoran species, *Anguispira alternata* (Say, 1816), Family Endodontidae, and *Mesodon inflecta* (Say, 1821), Family Polygyridae, were included. The two terrestrial species are active during spring and fall months and are readily obtained during these seasons. As such, individuals are likely to encounter subfreezing temperatures under natural conditions.

We also included specimens of an introduced bivalve, the zebra mussel *Dreissena polymorpha* (Pallas, 1771), in this study. Zebra mussels attach themselves with a byssus to firm substrates. Included among these substrates are the shells of various species of native unionid bivalves (Nalepa & Schloesser, 1993; Tucker et al., 1993) and species of native gastropods including *P. canaliculatum* (Tucker, 1994).

MATERIALS AND METHODS

Gastropods were collected in October and November 1993 in Madison County, Illinois at the following locations: *P. integra* were collected on 1 November from bullrush stems exposed to air and in water (13°C) of a ditch near the junction of Old Poag Road and Wanda Road, SW¼ Sec. 12, T. 4 N, R. 9 W, 0.3 km W of Poag; *P. canaliculatum* were collected on 3 November crawling on or partially buried in silt-clay substrate in 2 to 8 cm of water (11°C) along the main stem of the Mississippi River at Clifton Terrace Road, NW¼ Sec. 32, T. 6 N, R. 10 W, 0.6 km S of Clifton Terrace; *M. inflecta* and *A. alternata* were collected on 1 November from under debris near Old Poag Road, SW¼ Sec. 12, T. 4 N, R. 9 W, 0.3 km W of Poag; additional specimens of *M. inflecta* were collected on 22 October from the base of bluffs along Illinois Route 100, SE¼ Sec. 4, T. 5 N, R. 10 W, 0.6 km W of Alton. *D. polymorpha* were collected on 8 November from 2 to 20 cm of water (12°C) in clumps or druzes at the boat ramp at Grafton, Jersey County, Illinois. Voucher specimens of

all species used in this experiment are deposited in the collections of the Illinois Natural History Survey.

Gastropods were refrigerated at 4°C until 8 November and then kept at 15°C until 20 November. The bivalves were placed in aerated river water and maintained at 15°C until 20 November. On 20 November, 20 of the bivalves were transferred in fresh river water from the collection site to an environmental chamber and gradually cooled to 2°C.

On 20 November, animals were placed in dry, 13 × 18 cm plastic containers, with each species being maintained in a separate container. All animals were gently tamped dry before being placed into the containers. Containers were covered and allowed to equilibrate at 2°C in the environmental chamber for 48 hours. Chamber temperature and the temperature within one of the experimental containers were recorded at 15 minute intervals. Chamber temperature was reduced 1°C after 30 minute intervals until temperatures in the container and the chamber reached -3.1° to -3.3°C. Animals were maintained at this temperature for 30 minutes, gradually warmed to 2°C over a 30 minute interval, and then were transferred to 15°C. *D. polymorpha*, *P. canaliculatum*, and *P. integra* were covered with fresh river water. An additional sample of 20 *P. canaliculatum* were aerially exposed at 5°C for 12 and 24 hours to examine the potential effects of aerial exposure versus the cooling cycle on survivorship. Control samples ($n = 20$) of *D. polymorpha* and *P. integra* were also exposed aerially for periods of at least 24 hours at 5°C. All controls were handled in the same manner as experimental animals excepting exposure to the experimental cooling cycle.

Mortality of mollusks was assessed approximately 12 hours after transfer to 15°C. We believed 12 hr to be adequate time to permit mollusks either to recover from or succumb to the effects of the treatment. Bivalves were considered dead if they continued to gape even after being touched. Gastropods were considered dead if they did not crawl or failed to retract the operculum when it was touched.

Mortality data were analyzed with two-way *G* tests (Sokal & Rohlf, 1981). Similar to the chi-square test, the *G* test evaluates the goodness of fit of the observed data relative to expected results. For the experiment we conducted, the *G* test is the most appropriate statistical test to apply to mortality data (Sokal & Rohlf, 1981) which has but two outcomes (i.e., lived or died). Values for *P* reported herein were obtained by substituting the *G* values into a computer chi-square function program (SAS Institute, 1988). All statistically significant *P* values were sufficient to exclude type I errors at the 0.05 level for these multiple *G* tests (Rice, 1989).

RESULTS

Ninety-seven of the 117 animals survived the cooling cycle (Table 1). Among gastropods, only *P. canaliculatum* suffered mortality, and this decreased survivorship was significantly different from the other gastropods ($G = 22.273$,

$P < 0.001$, $df = 4$). Mortality also occurred among *D. polymorpha*, but did not differ significantly between individuals acclimated at 2°C or 15°C ($G = 0.489$, $P > 0.40$, $df = 1$). The mortality that we observed for *P. canaliculatum* was not significantly different from *D. polymorpha* acclimated at 2° and 15°C ($G = 0.425$, $P > 0.50$, $df = 1$). Control samples of *D. polymorpha*, *P. integra*, and *P. canaliculatum* showed no mortality when aerially exposed at 5°C for 24 hours.

At the time that the gastropods were transferred to 15°C, following the cooling cycle, and after being gradually warmed to 2 C, it was noted that almost all of the *M. inflecta* were actively crawling in the experimental containers. Within several minutes after being transferred to 15°C, at least some individuals of *A. alternata* and *P. integra* were also actively crawling in the containers.

DISCUSSION

Our results suggest that both the terrestrial and aquatic species of pulmonates that we studied are much better able to withstand exposure to subfreezing temperatures for short durations than are either the prosobranch or the bivalve that we studied. However, we hesitate to generalize these results to all pulmonates and prosobranchs making up Illinois' diverse molluscan fauna (i.e., Cummings, 1991). Since the former are much more likely to experience such conditions in nature than are the latter, which occupy more predictable aquatic habitats, our results are consistent with the natural histories of these species. There is some evidence, however, that these aquatic species may also occasionally encounter subfreezing temperatures in nature (*Pleurocera*—Dazo, 1965; *Physella*—Cheatum, 1934). *Dreissena polymorpha* may also be exposed to subfreezing temperatures due to fluctuations in water levels during winter months. We observed living individuals of *D. polymorpha* and *P. canaliculatum* exposed during winter drawdowns at the collecting sites in Pool 26 of the Mississippi River, clearly indicating that exposure to subfreezing temperatures occurs in nature.

Because our study was not designed to determine the maximum duration of exposure to subfreezing temperatures that could be tolerated, we do not know if the three pulmonates we studied vary in this trait. However, all three species appeared to recover completely from the cooling cycle once warmed. Therefore, *M. inflecta*, a species near the northern limit of its range in Illinois, was able to tolerate short exposure to subfreezing temperatures as well as the widely distributed *A. alternata*. Likewise, the aquatic pulmonate, *P. integra*, withstood these conditions as well as the two terrestrial pulmonate species. *P. gyrina*, a species closely related to *P. integra*, is known to be active in winter months and has been observed crawling on the underside of the ice in frozen lakes in Illinois (Zetek, 1918).

Although our experiments were not designed to determine freezing kill curves or LT_{50} for differing temperature

Table 1

Survivorship of four species of native gastropods and an introduced bivalve to exposure to subfreezing temperatures. Animals were cooled from +2.0° to -3.1°C to -3.3°C over a period of 3 hours.

	Dead	Alive	Total
Gastropoda			
<i>Anguispira alternata</i>	0	21	21
<i>Mesodon inflecta</i>	0	18	18
<i>Physella integra</i>	0	17	17
<i>Pleurocera canaliculatum</i>	7	11	18
Bivalvia			
<i>Dreissena polymorpha</i> 2°C Acclimated	8	15	23
<i>Dreissena polymorpha</i> 15°C Acclimated	5	15	20
Controls			
<i>Physella integra</i>	0	20	20
<i>Pleurocera canaliculatum</i>	0	20	20
<i>Dreissena polymorpha</i>	0	20	20

regimens (e.g., Clarke et al., 1993), our results are remarkably consistent with the LT_{50} at -3°C of 3.2 h determined by Clarke et al. (1993) for *D. polymorpha*. Our cooling cycle exposed this bivalve to subfreezing temperatures averaging -1.7°C for 2.5 h. Not surprisingly, the mortality we observed (35%) was slightly lower than the mortality for the cooling cycle used by Clarke et al. (1993) to arrive at the LT_{50} for -3°C.

Our results suggest that the exotic species, *D. polymorpha*, is able to withstand short-term exposure to subfreezing temperatures as well as the native prosobranch *P. canaliculatum*. Therefore, exposure of *D. polymorpha* to freezing temperatures through river drawdowns, as is practiced in early spring along navigable rivers (Sparks, 1992), will probably not result in greater mortality rates in *D. polymorpha* than in *P. canaliculatum* and provides no relative advantage to either species. Dewatering during the winter months has been suggested as a method to control *D. polymorpha* populations (Claudi & Mackie, 1994). Our results indicate that this technique would likely result in similar levels of mortality in native aquatic gastropods such as *P. canaliculatum*.

The possible effects of aerial exposure may complicate the interpretation of the results of our study for the mollusks that are normally aquatic. Since these animals are usually submerged in water, the mortality we observed may be due to aerial exposure rather than to freezing temperatures. However, *P. canaliculatum* controls that were aerially exposed for 12 and 24 hours at 5°C showed no mortality in this study. Additionally, in other experiments designed to determine effects of aerial exposure on *D. polymorpha* and *P. integra*, we found no mortality among individuals of either species exposed at 5°C for 60 hours (Paukstis et al., unpublished observations; Tucker et al., in press). Thus, we believe that the mortality we observed

in this study was due to low temperatures and not to desiccation.

The ability of *M. inflecta*, *A. alternata*, and *P. integra* to tolerate exposure to subfreezing temperatures and to become active at low temperatures following exposure to subfreezing temperatures may be of considerable advantage to these species in areas such as central Illinois where passages of spring and fall cold fronts can result in widely varying ambient temperatures. For *M. inflecta* and *A. alternata*, this may allow active feeding late into the fall and early in the spring, resulting in faster growth and ability to put additional resources into reproductive tissue.

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The Distribution of Five Species of *Septaria* (Gastropoda: Neritoidea) in Fijian Streams

by

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Abstract. Five species of the limpetlike neritid *Septaria* were sampled in different regions along streams on the Fijian islands of Ovalau and Taveuni. *Septaria lineata* lived on loose pebbles and cobbles in the slow-flowing tidal regions, *S. bougainvillei* on boulders and rocks in faster flow, while *S. macrocephala* and *S. sanguisuga* were most abundant on inland bedrock slopes. *S. suffreni* was thinly distributed in all habitats. *S. lineata*, which inhabited the tidal regions, had a higher and wider shell than the other species, while *S. macrocephala* and *S. sanguisuga*, which lived on the steep rock faces, had narrow lower shells enabling them to fit into rock crevices when the streams were in flood. The factors, ion content of the water, current flow, substrate type, and shell shape, all helped to determine the distribution of each *Septaria* species along the streams.

INTRODUCTION

Starmühlner (1979) described the distribution of gastropods in mountain streams of the tropical Indo-Pacific islands of Madagascar, Ceylon (Sri Lanka), and New Caledonia. He found that the headwaters and upper courses of the streams were dominated by genera of the families Thiaridae and Hydrobiidae. In the lower courses (below 100 m elevation), there were many species of Neritidae e.g., *Septaria borbonica*, *Neritina gagates* (Madagascar), *Septaria tessellata* (Ceylon), and *Neritina pulligera* and *Septaria porcellana depressa* (New Caledonia). In the less mountainous Andaman Islands, Starmühlner (1982) found neritid gastropods extended above 100 m, and on the Samoan islands of Upolu and Tutuila, neritids, including three species of *Septaria*, continued to an elevation of 250 m (Starmühlner, 1993).

When Haynes (1988a) sampled streams on the Fijian islands of Ovalau, Gau, Kadavu, and Taveuni, she found that neritids, including some species of the limpetlike *Septaria*, extended above 300 m. Neritids were the most abundant gastropods at all elevations in the streams.

The present investigation studied the distribution of five species of *Septaria*—*Septaria lineata* (Lamarck, 1816), *Septaria suffreni* (Récluz, 1841), *Septaria macrocephala* (Guilou in Récluz, 1841), *Septaria bougainvillei* (Récluz, 1841), and *Septaria sanguisuga* (Reeve, 1856)—from the mouth

to the headwaters of Fijian streams. It also considered whether the distribution of a species was correlated with any of the factors: water temperature, pH, conductivity, type of substrate, or shell shape.

Species of the genus *Septaria* become flat and limpetlike when the veliger larvae settle. The shell shape of specimens 2 mm in length is like that of the adult shells shown in Figure 1A–E. However, it is difficult to separate the species at this small size. In all *Septaria* species, the operculum is imbedded in the foot, and so, the animal cannot be enclosed within the shell. *Septaria* species differ in this way from the freshwater Hawaiian limpet, *Neritina granosa*, which has an external operculum and also passes through a conical stage before it becomes limpetlike in shape.

Way et al. (1993) investigated how the distribution of differing morphs (conical, intermediate, and winged) within the species *N. granosa* was related to microhabitat current flow. They found winged morphs (more flattened shape) mainly below the terminal waterfall, and that intermediate and conical morphs predominated above the falls. However, as they found no significant difference in lift or drag between the different morphs, they were of the opinion that microhabitat flow had little or no effect on the shell morphology of *N. granosa*.

As the shell shapes of the five Fijian *Septaria* showed no obvious intraspecific variation at different sizes or in different regions of a stream, one of the aims of this in-

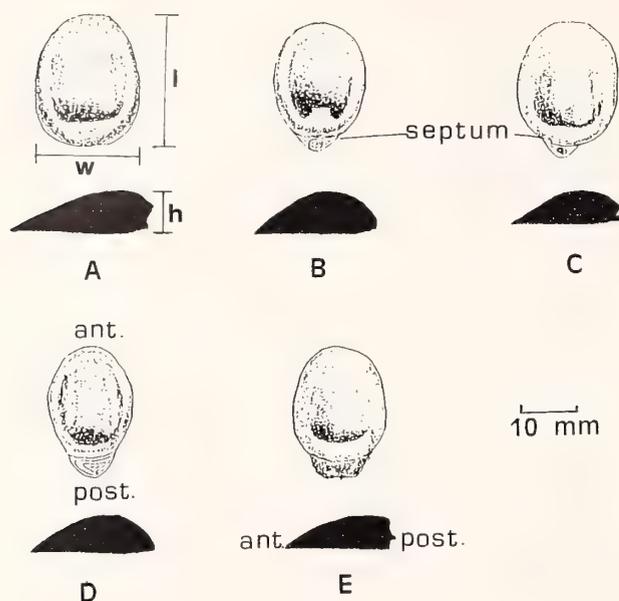


Figure 1

Diagrams of the ventral and side views of the shells of five *Septaria* species. A. *S. lineata*, B. *S. suffreni*, C. *S. bougainvillei*, D. *S. sanguisuga*, E. *S. macrocephala*. ant., anterior; h, height; l, length; post, posterior; w, width.

investigation was to find if the shell shape differences between species affected the way each species was distributed within a stream.

STUDY AREAS

Two similar streams on different islands were sampled for comparison. These were the Naisogo Creek, Ovalau, and the Naivika Creek, Taveuni (Figure 2). The islands of Ovalau and Taveuni are small volcanic islands rising to 626 m and 864 m, respectively, above sea level. Both islands have heavy rain storms that cause the streams to suddenly flood and become turbulent. The high central regions of both islands are covered in rain forest, while village gardens border the coastal areas. Along the complete length of the streams, the main benthic invertebrates were neritid gastropods which feed on periphyton (Haynes, 1991). The Naisogo Creek, Ovalau, and Naiviki Creek, Taveuni, flowed over similar terrain (Figure 3). Upstream from the sea, a brackish and tidal region extended for about 200 m (Figure 3d). The bottom was composed of pebbles and cobbles, diameter 16–256 mm, and it rose to 6 m elevation. A steeper region of riffles, small cascades, and pools with a substrate of boulders and rocks, diameter > 256 mm (Wentworth classification [Minshall, 1984]) rose from 6–200 m above sea level (Figure 3c). Farther inland, 1000–1200 m from the sea at 200–350 m elevation, the streams flowed swiftly over bedrock slopes (Figure 3a, b).

MATERIALS AND METHODS

Septaria species were identified and counted from 10 quadrats (0.5 × 0.5 m) in each of the three regions of the streams during each sampling. The Naisogo Creek was sampled seven times (27/8/88, 18/11/88, 8/3/89, 28/11/89, 9/3/90, 12/3/91, and 28/6/91), and the Naiviki Creek three times (9/10/90, 19/4/92, and 14/2/92). The tidal regions of the Lami and Nasekawa Rivers (Figure 2) were also sampled five times, as few *S. lineata* were found in the Naisogo and none in the Naivika Creek. No other *Septaria* species were found farther upstream in these two larger rivers.

Current speed, temperature, conductivity (total ions), and pH of the water were determined at the times of sampling in all four streams. Current speed was measured with a Jens Current Measuring Stick, pH and temperature with a Philip Harris sensorimeter, and conductivity with a Philip Harris conductivity sensorimeter.

The length, width, and height (Figure 1A) of 60 shells of each species from the smallest identifiable (6–10 mm long) to the longest found (21–29 mm long) were measured with calipers to an accuracy of 0.5 mm (Figure 1A–E). *S. macrocephala* shells were not measured, as many were eroded at the apex, and the length could not be measured accurately (Figure 1E). However, their shell dimensions were so similar to those of *S. sanguisuga* that, until 1989, the two species were considered to be synonymous (Haynes & Wawra, 1989).

The width/length and height/length ratios of each species were tested using the Mann-Whitney U-test against shell ratios of the same species from different streams and against each of the other species to find if the ratios of each pair tested had the same distribution and medians. In the case of *S. bougainvillei*, where sufficient specimens from both the boulder region and the bedrock region were available, the ratios from each habitat were also tested (Table 2).

To verify that the growth rate was similar throughout the life of the limpets, shell width was plotted against length (Figure 4) for *S. lineata*, *S. bougainvillei*, and *S. sanguisuga*, and the shell height/length ratio against the width/length ratios for *S. lineata* and *S. sanguisuga* (Figure 5).

RESULTS

Table 1 shows that the distribution of *Septaria* species in the streams was not random and that distribution follows a definite pattern. *S. lineata* and *S. suffreni* were the only species present in the region influenced by the tide in the Lami and Nasekawa Rivers and the Naisogo Creek (Table 1). *S. lineata* was confined to the brackish and tidal region where the substrate was pebbles and cobbles, while *S. suffreni*, which was not abundant anywhere, was distributed on all substrates along the length of the streams (Table 1).

S. bougainvillei was the most abundant species above the



Figure 2

Map of the main islands of Fiji showing the locations of the streams and rivers investigated. 1. Lami River, 2. Naisogo Creek. 3. Naivika Creek. 4. Nasekawa River.

influence of the tide (Figure 3c) in the steep, swift region with stones and boulders as substrate. It was less abundant on the rock slopes where *S. macrocephala* and *S. sanguisuga* reached their greatest densities (Figure 3a, b). The variance to mean ratios (Table 1) were generally more than one, indicating aggregated distribution. *Septaria* species reached their greatest densities on bedrock slopes in both streams (48.4–48.9 m⁻² compared with 24.1–31.8 m⁻² on boulders).

The total ions (measured by conductivity) in the water were higher in the tidal part of the streams (Table 1). Ion content in the Naivika Creek was less than in the Naisogo Creek (Table 1), but the distribution of *Septaria* species was similar. pH varied little from region to region, while water temperature was cooler at higher elevation. Water velocity depended to a large extent on recent rainfall, but, in general, the velocity in the tidal region was 10–50 cm sec⁻¹, the middle region was 30–60 cm sec⁻¹, and the rock slope 30–100 cm sec⁻¹ (Table 1).

The Mann-Whitney U-test showed that when the shell dimensions of each species were compared with specimens of the same species from different streams there was no

significant difference (at 5% level) ($U = 70$, U_1 and U_2 were greater than 70). The Mann-Whitney U-test confirmed that *S. lineata* shells were wider than the shells of other species (at 5% level) ($U = 75$, $U_1 = 9-14$) and that *S. bougainvillei* shells were similar within the Naisogo Creek ($U = 86$, U_1 and U_2 greater than 86) (Table 2).

The growth in length and width increased at a constant rate in the three species, *S. lineata*, *S. bougainvillei*, and *S. sanguisuga* (Figure 4), and the width of *S. lineata* was consistently greater than *S. sanguisuga* at all sizes. *S. bougainvillei* shell width lay between the other two species (Figure 4). Figure 5 shows that the young (<15 mm) of the two species, *S. lineata* and *S. sanguisuga*, whose widths differ most, have the greatest shell length/height ratios i.e., they are relatively low and long. It also confirms that *S. lineata* shells are wider and higher than *S. sanguisuga*.

DISCUSSION

Septaria species were distributed within the streams so that each species reached peak abundance in a distinct region and on a particular substrate of a stream. Current speed

Table 1

The mean abundance, variance, and variance/mean ratio of *Septaria* m⁻² on different substrates in the three regions along Fijian streams/rivers. The chemical and physical conditions in each region are included.

	Stones & cobbles influenced by the tide						Boulders & rocks 200-1000 m from sea						Bedrock slope 1000-1200 m from sea					
	Naisogo Ck.		Lami R.		Nasekawa R.		Naisogo Ck.		Naivika Ck.		Naisogo Ck.		Naivika Ck.		Naisogo Ck.		Naivika Ck.	
	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2
<i>S. macrocephala</i>	0	—	0	—	0	—	3.3	18.5	5.6	—	—	29.6	86.5	2.9	15.4	37.2	2.4	
<i>S. sanguisuga</i>	0	—	0	—	—	—	0	—	—	—	—	5.0	27.0	5.4	27.6	96.0	3.5	
<i>S. bougainvillei</i>	0	—	0	—	—	—	19.4	350	18.0	27.7	47.6	12.1	121	10.0	2.4	19.4	8.1	
<i>S. suffreni</i>	0.8	0.6	2.0	3.6	1.8	1.1	1.4	2.3	1.6	3.0	17.6	5.9	4.8	2.2	3.0	2.3	0.8	
<i>S. lineata</i>	0.5	0.4	0.8	20.8	136.9	6.6	6.3	10.2	1.6	0	—	0	—	0	0	—	—	
Total	1.3	—	22.8	—	7.6	—	24.1	—	—	31.8	—	—	—	—	48.9	—	—	
Conductivity (mS m ⁻¹)	95.0	—	98.9	—	102.6	—	71.2	—	—	66.9	—	—	—	—	69.8	—	36.1	
(total ions)	7.5	—	7.4	—	7.4	—	7.5	—	—	7.0	—	—	—	—	7.1	—	7.0	
pH	25-27	—	25-26	—	25-27	—	23-27	—	—	22-24	—	—	—	—	22-26	—	21-24	
Temperature (°C)	10-50	—	20-40	—	10-40	—	30-60	—	—	30-60	—	—	—	—	30-100	—	30-100	
Water velocity (cm sec ⁻¹)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

Table 2

Means and standard deviations for shell dimension ratios of 60 specimens of four *Septaria* species collected from two streams.

Species	Width/length		Height/length	
	\bar{x}	SD	\bar{x}	SD
<i>S. sanguisuga</i>				
Naivika Ck.	0.70	0.03	0.32	0.02
Naisogo Ck.	0.68	0.09	0.32	0.02
<i>S. bougainvillei</i>				
Naivika Ck.	0.73	0.04	0.32	0.03
Naisogo Ck.				
boulder substrate	0.75	0.04	0.32	0.03
bedrock substrate	0.74	0.04	0.33	0.03
<i>S. suffreni</i>				
Naivika Ck.	0.73	0.04	0.35	0.03
Naisogo Ck.	0.75	0.05	0.34	0.02
<i>S. lineata</i>				
Nasekawa R.	0.83	0.04	0.39	0.02
Lami R.	0.81	0.04	0.37	0.04

varied with substrate and region, and consequently, *S. macrocephala* and *S. sanguisuga*, living on bedrock slopes, had to withstand faster current flow to remain in this preferred region.

Recent research into the measurement of microhabitat flow around macroinvertebrates has used methods such as laser doppler anemometry (Statzner & Holm, 1989) in the laboratory and thermistor-based current meter in the field (Way et al., 1993). Way et al. (1993) used the last mentioned technique to measure the effect of current flow on the different shaped shells—conic, intermediate, and winged—of the Hawaiian limpet, *Neritina granosa*. They found that conic and intermediate morphs experienced less drag and lift when oriented parallel to the flow. The marine limpet, *Lottia pelta*, also experienced a sudden reduction in drag when the anterior was oriented upstream (Denny, 1989). However, as limpets graze randomly to flow, Way et al. (1993) doubted whether lift or drag were important selective forces for the evolution of shell morphology of *N. granosa*. They hypothesized that a strong, muscular foot minimized any drag or lift forces on different morphs, and that flow had little importance in determining shell morphology. A similar conclusion was reached by Statzner & Holm (1989) when discussing the shell shape of the freshwater limpet, *Ancylus*.

All Fijian *Septaria* species have a flat, streamlined shape and a strong, muscular foot—*S. sanguisuga* and *S. suffreni* were particularly difficult to dislodge—and the shape of the shell of each species was the same in all regions of the streams.

The four species, *S. bougainvillei*, *S. suffreni*, *S. macrocephala*, and *S. sanguisuga*, lived in swiftly flowing current in both the middle and upper regions, while the distri-

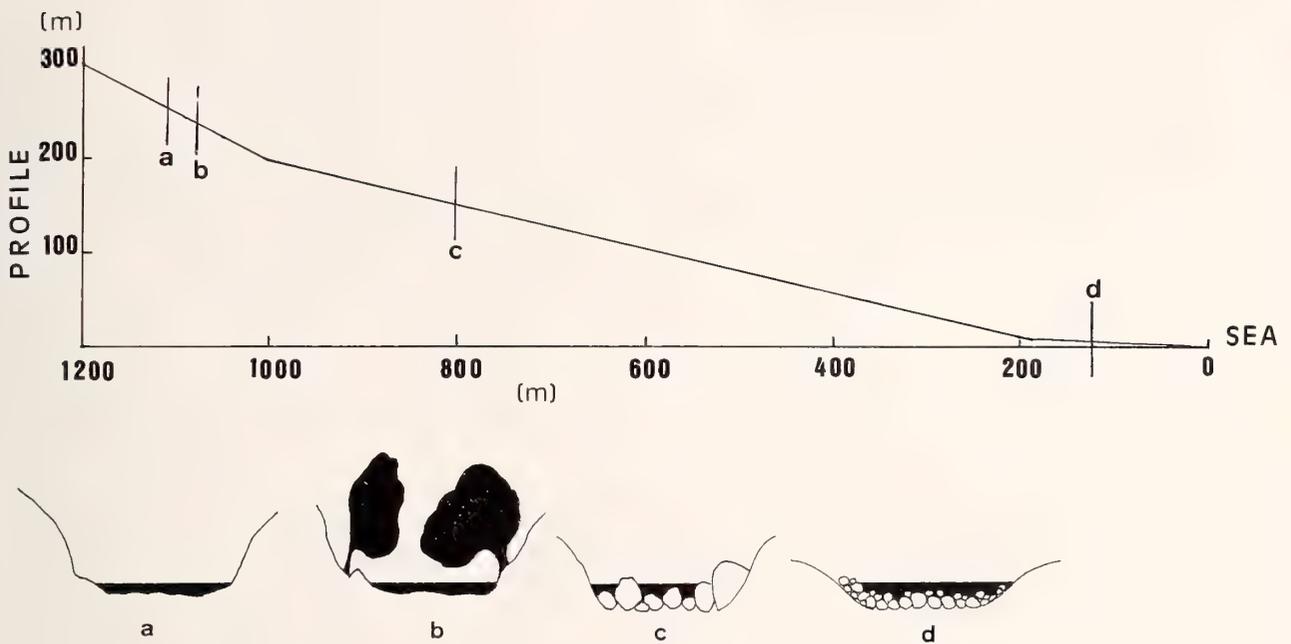


Figure 3

Diagram showing a generalized profile of the Naisogo and Naivika Creeks with cross sections of the sampling sites a-d. a. sunny bedrock slope b. shaded bedrock slope c. boulders and rocks region d. region influenced by the tide with pebbles and cobbles substrate.

bution of *S. lineata* was restricted to the tidal region where it encountered lower current speed. It probably has limited distribution because it is unable to tolerate water with low ion content. *S. lineata* may have developed a wider and higher shell because of the greater availability of ions for shell building in its habitat. Other brackish water and tidal neritids, such as the Hawaiian *Neritina vespitina* Sowerby, and the Indo-Pacific species *Neritina auriculata* Lamarck and *Neritina dilatata* (Broderip), have wide, thin shells also (Haynes, 1988b; Maciolek, 1978; Pontier & Marquet, 1990).

S. bougainvillei was the most abundant species in the middle region with rock and boulder substrate, where it encountered swift current and water temperatures similar to those of the bedrock slopes. However, during floods, it could find shelter by moving to the downstream side or underneath boulders. Possibly, *S. bougainvillei* and *S. suffreni* were found less often on the bedrock slopes because their slightly wider shell was less suited to fit into narrow cracks in the rocks during flooding.

S. macrocephala and *S. sanguisuga*, with the narrowest shells, were most abundant on bedrock slopes where they encountered the strongest currents. They could more easily fit into narrow rock crevices when the stream flooded. *S. sanguisuga* had a horizontal flat septum (Figure 1D) that helped it to hold fast to the rock, while most *S. macrocephala* shells were eroded (Figure 1E) because they could hold less securely to the substrate and were often washed downstream and battered against the rocks. Chemical action is

unlikely to have caused the shell erosion, because *S. sanguisuga* live in the same non-acid water (pH 7-7.5) and they were rarely eroded.

There was evidence to suggest that interspecific competition was occurring on the bedrock slopes. In the Nais-

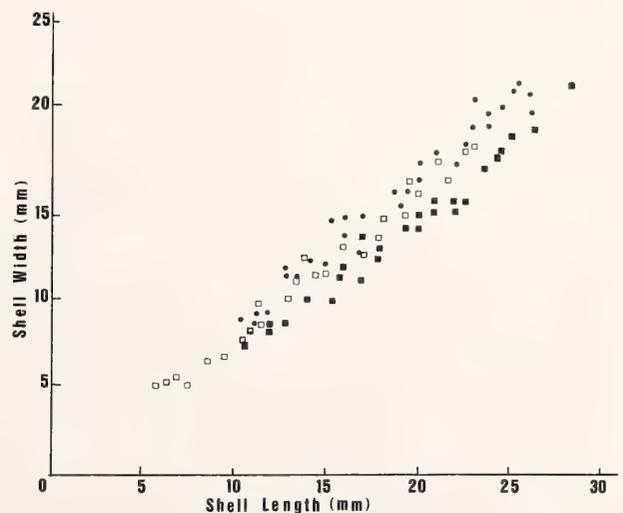


Figure 4

Relationship between the dimensions of shell length and shell width of *S. lineata* ● *S. bougainvillei* □, *S. sanguisuga* ■. (For the sake of clarity, all limpets measured are not plotted).

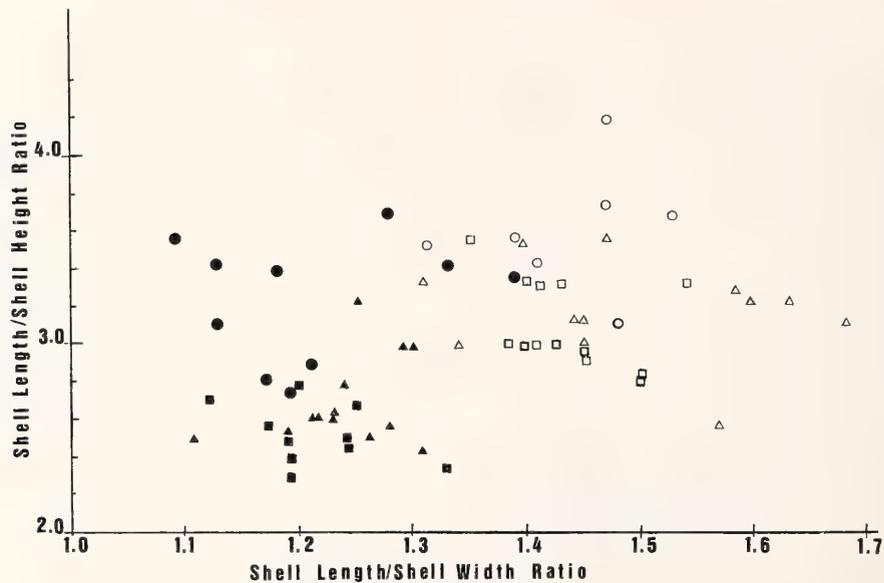


Figure 5

Relationship of shell length/shell width ratio and shell length/shell height ratio of *S. lineata* ● < 15 mm, ▲ 15–20mm, ■ > 20 mm. *S. sanguisuga* ○ < 15 mm, △ 15–20 mm, □ > 20 mm (for the sake of clarity, all limpets measured are not plotted).

ogo Creek where *S. macrocephala* density was high (29.6 m^{-2}), *S. sanguisuga* density was low (5.0 m^{-2}), while in the Naivika Creek, *S. sanguisuga* had a high density (27.6 m^{-2}), and *S. macrocephala* had a relatively low density (15.4 m^{-2}) (Table 1). The similarity of the total densities of all four *Septaria* species on the bedrock slopes in the Naisogo Creek (48.9 m^{-2}) and the Naivika Creek (48.4 m^{-2}) further strengthens the probability of interspecific competition occurring between the *Septaria* populations. However, at present no further work has been done to confirm competitive interactions.

ACKNOWLEDGMENTS

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Development of the Keyhole and Growth Rate in *Diodora aspera* (Gastropoda: Fissurellidae)

by

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Abstract. Scanning electron micrographs of shells of the fissurellid *Diodora aspera* (Rathke, 1833) show that the apical opening, or keyhole, begins development as a shallow notch in the anterior edge of the aperture. This notch deepens as the adjacent shell grows until finally it is closed off, forming a complete subapical keyhole. As the animal grows, enlargement of the keyhole by shell dissolution eventually results in its placement at the shell apex. Observations of the growth of marked individuals in an intertidal population, and of laboratory-raised juveniles, suggest that *D. aspera* grow from settling to 55 mm aperture length in about 9-13 yr. The ages of large (60 mm or greater) snails may be in excess of 20 yr.

INTRODUCTION

Holes, slits, and notches occur as elaborations of the shell in diverse mollusks. In the archaeogastropod (*sensu* Hickman, 1988) superfamilies Fissurelloidea and Pleurotomarioidea, where such elaborations are particularly common, they modify flow patterns through the mantle cavity. In the fissurellid *Diodora aspera* (Rathke, 1833), for example, respiratory currents enter the mantle cavity ventrally, behind the head, and exit dorsally through the apical opening or "keyhole" (Yonge, 1947). Members of the family Haliotidae have numerous holes in the shell, and flow patterns are correspondingly more complex. In *Haliotis kamschatkana* Jonas, 1845, respiratory currents enter the mantle cavity either ventrally or through one or two of the anterior holes, and exit through posterior holes (Voltzow, 1983). In both of these species, shell holes are positioned such that external flow can passively induce flow through the mantle cavity (Murdock & Vogel, 1978; Voltzow, 1983). Many other fissurelloideans (e.g., *Emarginula*) and pleurotomarioideans (e.g., *Pleurotomaria*) have marginal slits or notches in the shell instead of complete holes; the roles of these structures in modifying mantle cavity flow patterns, in particular with respect to induced flow, are less well known. The functions of holes, slits, and notches in these archaeogastropods may include improving sanitation in the mantle cavity by allowing wastes to exit without passing the gills and head (Yonge, 1947); enhancing respiratory flow by allowing water to travel unidirectionally through the mantle cavity; and, more specifically, en-

hancing respiratory flow by means of passively induced flow (Murdock & Vogel, 1978; Voltzow & Collin 1995).

Surprisingly, the timing and patterns of development of these distinctive shell features are poorly known. In fissurellids, patterns of keyhole development have for the most part been inferred from observations of one or a few specimens (e.g., Bandel, 1982), and rarely from observations of a series of developmental stages (e.g., Boggs, 1978). Such data are useful for developing and testing hypotheses on the evolution of shell holes, slits, and notches. Boutan (1885), for example, used observations on the development of the keyhole in *Diodora apertura* (Montagu) (as *Fissurella reticulata*: see McLean 1984) to support his argument that fissurellids with apical keyholes are evolutionarily more "advanced" than those with subapical keyholes or marginal slits. Data on patterns of keyhole development are also important in understanding the functional morphology of fissurellids. Changes in keyhole size and position during ontogeny, for example, should influence the ability of the animal to generate induced flow through the mantle cavity (Vogel, 1977). The size of the whole organism also affects such functional relationships. Among the fissurellids, growth rates have been studied in only five species: *Fissurella barbadensis* (Gmelin, 1791), *Diodora aspera* (Rathke, 1833), *F. latemarginata* (Sowerby 1834), *F. crassa* (Lamarck, 1822), and *Montfortula rugosa* (Quoy & Gaimard) (Ward, 1967; Palmer, 1968; Acuña, 1977; Bretos, 1978, 1980; Creese, 1981).

In this paper I describe both of these aspects of growth in the fissurellid *Diodora aspera*, which is often abundant

Table 1

Schedule of marking and recovery of *Diodora aspera*. Some snails were recovered repeatedly; for example, among the 21 snails recovered on 5 December 1994 were some that had previously been recovered and released again on 5 October 1994.

Date	Marked	Recovered
8 July 1994	50	—
5 October 1994	0	19
5 December 1994	33	21
28 January 1995	12	23
18 April 1995	13	27
12 July 1995	0	38
Total marked	108	

on intertidal and subtidal hard substrates along the west coast of North America. First, I describe the formation of the keyhole in laboratory-raised *D. aspera*. Second, I present data on the growth rates of a number of individually marked snails from an intertidal population. These growth rate data complement the unpublished data of Palmer (1968).

MATERIALS AND METHODS

Development of the Keyhole

Adult *Diodora aspera* were collected in February 1995 from the intertidal zone on the west side of San Juan Island, Washington, USA. (48°29'N, 123°4'W), and were transferred to a sea table at the Friday Harbor Laboratories. Within 24 hr of collection, a single female and several males spawned. Fertilized eggs were collected from the sea table and cultured in about 150 ml of seawater in a small bowl at 10–13°C. Crawling juveniles hatched out of the egg envelopes approximately 3 weeks after fertilization (W.B. Jaeckle, personal communication). A small stone encrusted with coralline red algae was placed in the dish with the juveniles; they remained on this stone for the next 7 months, grazing on the coralline algae and epiflora. Seawater in the dish was changed every 1–3 weeks, and no supplementary food was added. Living snails were photographed with a Wild M400 dissecting microscope equipped with a camera. I prepared shells for scanning electron microscopy by soaking juvenile snails in distilled water for several hours, dissolving tissue and periostracum with dilute sodium hypochlorite, and rinsing in 100% acetone. After air-drying, shells were mounted on stubs with double-sided tape and sputter-coated with gold and palladium. Specimens were photographed with a Jeol JSM-35 scanning electron microscope.

Growth Rates of *Diodora aspera*

The growth rate study was carried out in the intertidal zone south of False Bay on the west side of San Juan

Island. As a study site I chose a roughly rectangular outcrop of rocks about 23 m² in area and ranging in tidal height from approximately mean lower low water (MLLW) to 1 meter below MLLW. Several hundred *Diodora aspera* inhabited the outcrop, mainly in crevices and in overhangs where sponges and encrusting bryozoans were present. In July 1994 I collected 50 snails from this site, recorded their original locations, and transported them to the laboratory where I marked and measured each one. Measurements of aperture length, aperture width, height of the apex above the substrate, and length from the posterior edge of the keyhole to the posterior edge of the shell (Palmer, 1968) were made with vernier calipers. Because shells were often heavily eroded or overgrown with bryozoans, spirorbid polychaetes, or coralline red algae, measurement accuracy was only ±0.5 mm. Snails were marked by smoothing a small region of the posterior surface of the shell with a file, drying this region with a cloth, and applying a numbered bee tag with cyanoacrylate glue. Marked snails were returned to within a few centimeters of their original locations at low tide on the next day. On subsequent trips (Table 1) I recovered as many marked snails as possible, remeasured them, and replaced them on the next day. On these subsequent trips I also collected, marked, and measured new snails, replacing them on the next day (Table 1). Many tags were still attached after 1 year. Encrusting bryozoans and coralline red algae often grew over tags, probably reducing tag losses; this protective coating was easily scraped off in the field to reveal the tag underneath.

I used the graphic method of Kaufmann (1981) to select an appropriate growth model. Gompertz, logistic, and Bertalanffy curves all fit the data well. I fitted growth data to the the Bertalanffy growth model:

$$S_t = S_\infty (1 - be^{-Kt})$$

where S_t = size at age t (yr), S_∞ = asymptotic size (mm), K = Bertalanffy growth coefficient (yr⁻¹), and:

$$b = (S_\infty - S_0)/S_\infty$$

where S_0 = size at age t_0 (mm) (Medeiros-Bergen & Ebert 1995). Because all shell dimensions measured were highly correlated with aperture length (Figure 1), I chose to use length as a single index of size. Original and final lengths over the longest time period applicable for each snail were used to estimate the growth parameters S_∞ and K by nonlinear regression using the equation:

$$S_{t+\Delta t} = S_\infty - (S_\infty - S_t)e^{-K\Delta t}$$

Other techniques of fitting Bertalanffy curves to the data (e.g., Van Devender, 1978) generated similar estimates of the growth parameters.

Because few snails smaller than 20 mm in length were included in the intertidal samples, I only used the Bertalanffy model to predict size changes over time for snails greater than 20 mm in length. I estimated the ages of 20 mm snails by extrapolating from the growth of juveniles

raised in the laboratory, including those described above and several individuals that had been raised in a laboratory sea table for about 18 months.

RESULTS

Development of the Keyhole

Scanning electron micrographs of stages in the development of the keyhole are shown in Figure 2. At an aperture length of about 400 μm , a slight indentation appeared in the shell of *Diodora aspera* above the head, just to the right of the shell midline (Figure 2a). The rest of the shell continued to grow around this deepening notch (Figure 2b) until at a length of 500–600 μm , the two anterior edges of the notch began to turn in (Figure 2c). When these edges met (Figure 2d, e), the keyhole was essentially complete. An external view of the shell of an 125 d old animal showed a suture anterior to the keyhole where the two edges of the notch had fused (Figure 2e), but in older animals, sutures were not visible anterior to the keyhole in external (Figure 2f) or internal (Figure 3) views. Continued shell growth at the aperture eventually positioned the keyhole relatively nearer to the shell apex than to the growing shell edge (Figure 2f). As the snails continued to grow, the keyhole was enlarged by dissolution at its edges. Dissolution eventually destroyed the apical larval shell, leaving the keyhole at the apex of the shell. Most of the larval shell had been lost in an 18 month old, 4.5 mm long animal (Figure 4a), and all of it had been lost in an 18 month old, 7 mm long animal (Figure 4b).

Growth Rates of *Diodora aspera*

A total of 108 *Diodora aspera* (Table 1) were marked during the growth rate study. Marked snails were 45.5 mm in mean length (SD = 13.4, range = 12.5–70.5), and only seven snails less than 20 mm in length were marked. Of these marked snails, 68 different individuals (63%) were recovered at least once after 54–368 d in the field (mean = 204 d, SD = 109). Recovered snails were 48.9 mm in mean length (SD = 10.0, range 16–63.5), and only two snails less than 20 mm in length were recovered.

To standardize the growth data to a common time interval, I calculated growth rate ($\text{mm}\cdot\text{day}^{-1}$) and predicted size after 1 yr of growth (as growth rate multiplied by 365 d, plus initial size) for each of the 68 snails. These data are shown in the form of a Walford diagram in Figure 5a. The estimated parameters of the Bertalanffy growth model were $S_{\infty} = 59.84$ mm (SE = 1.20), and $K = 0.278$ yr^{-1} (SE = 0.024). Predicted length as a function of time for snails 20 mm or greater in initial shell length is shown in Figure 5b.

Growth rates of laboratory-raised juveniles were quite variable. In February 1996, 377 d after fertilization, juveniles had reached a mean length of 2.5 mm (SD = 0.64, $n = 26$). Two laboratory-raised juveniles fertilized in April 1994 (M. Strathmann, personal communication) were 4.5

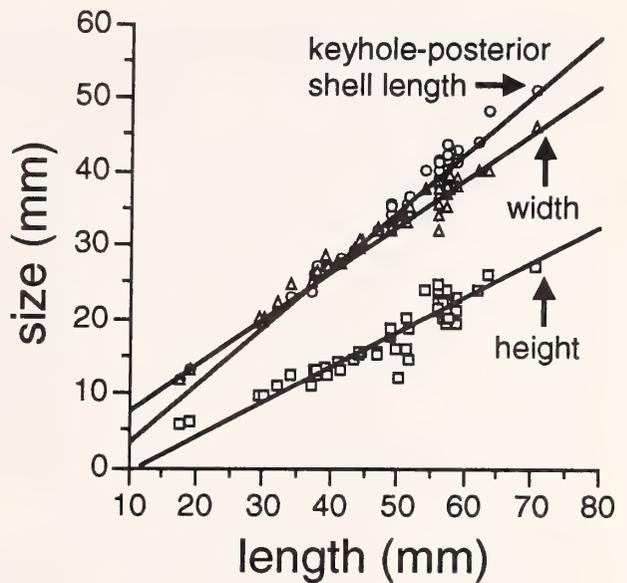


Figure 1

Aperture length of *Diodora aspera* (abscissa) plotted against length from the keyhole to posterior shell edge (circles: $y = 0.781x - 4.186$), aperture width (triangles: $y = 0.628x + 1.552$), and height of the apex above the substrate (squares: $y = 0.471x - 5.561$) (ordinate). Lines are reduced major axis regressions (Sokal & Rohlf, 1981, p. 550). The measurements are from the 54 snails recovered and marked at the 5 December 1994 sampling date.

and 7.0 mm in length 540 d after fertilization. Estimated growth rates for these two groups of juveniles are $2.4 \text{ mm}\cdot\text{yr}^{-1}$ and $3.9 \text{ mm}\cdot\text{yr}^{-1}$, respectively.

DISCUSSION

Development of the Keyhole

This study represents the most complete description available of the development of the keyhole in a fissurellid. Scanning electron micrographs of juvenile stages of *Diodora aspera* show that the keyhole first appears as a notch in the anterior of the shell (Figure 2). This notch soon closes, leaving a subapical keyhole on the anterior slope of the shell. As the keyhole is enlarged by dissolution, the earlier formed larval and juvenile shell are lost, and the keyhole comes to occupy its final apical position (Figure 4). A keyhole in an adult *D. aspera* is often 5–6 mm long; thus all of the shell represented in Figure 2f is eventually lost to keyhole enlargement. The outer and anterior portions of the larval shell are the first to be lost to keyhole enlargement, suggesting that dissolution is effected from the outside of the shell by mantle tissue protruding from the keyhole.

This basic pattern of keyhole development has been inferred to occur in some other fissurellids (e.g., *Fissurella* spp.: Bandel, 1982). However, in some species a selenizone

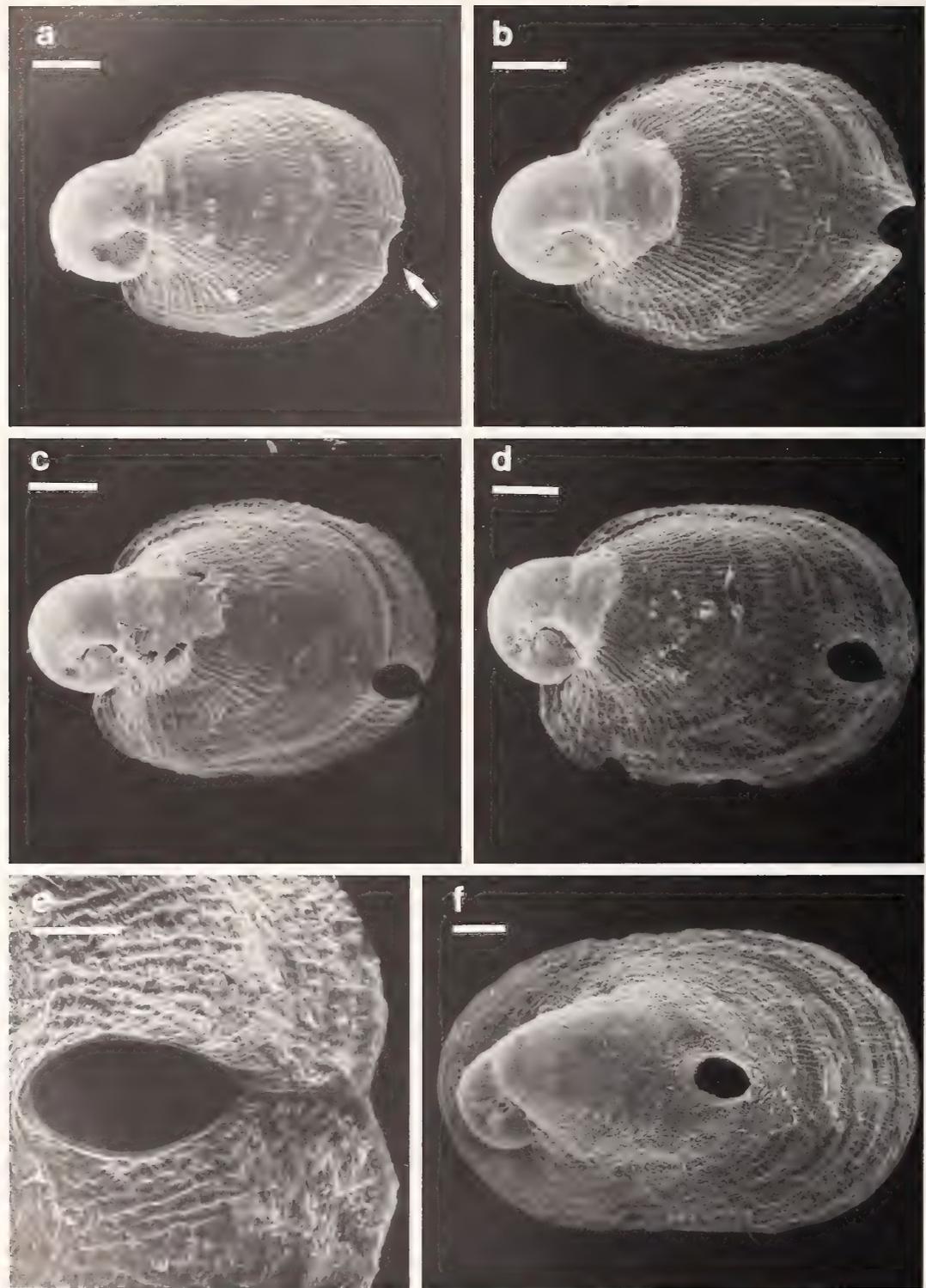


Figure 2

Scanning electron micrographs of the shells of juvenile *Diodora aspera*. All shells are oriented with their anterior ends to the right. a: 111 d post-fertilization. The arrow marks the shallow notch where the keyhole will develop. b: 111 d post-fertilization. c: 118 d post-fertilization. d: 125 d post-fertilization. e: Detail of the closed-off keyhole

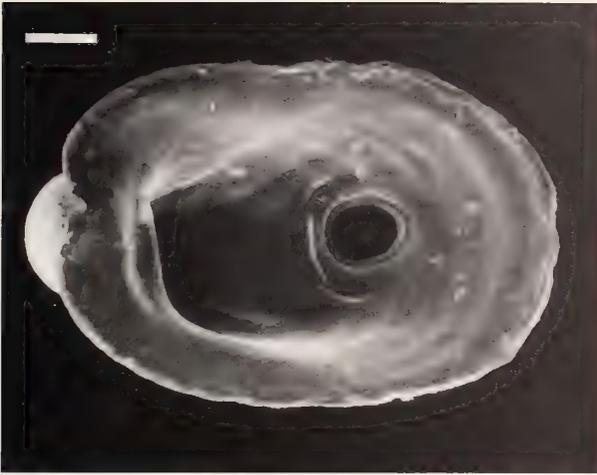


Figure 3

Scanning electron micrograph of the interior of the shell of a 146 d old *Diodora aspera*. The shell is oriented with its anterior end to the right. Note the absence of a visible suture in the shell anterior to the keyhole. Scale bar = 100 μm .

(a secondarily filled-in region of the keyhole or marginal slit) is present during development. In *Diodora granifera* (Pease, 1861), for example, the keyhole begins development as a shallow notch in the anterior of the shell, as in *D. aspera*. After the notch closes, the keyhole migrates anteriorly through combined effects of posterior shell deposition and anterior shell dissolution. The posterior filled portion (the selenizone) of the keyhole eventually erodes away, leaving a long narrow keyhole (Boggs, 1978). My data clearly indicate that in *D. aspera* no selenizone is formed. The absence of a selenizone in all developmental stages has previously been thought to be a unique characteristic of members of the genus *Fissurella* (McLean, 1984).

In *Diodora aspera* and other fissurellids, the structure of the underlying secretory mantle presumably mirrors that of the developing hole, slit, or notch. In *D. aspera*, then, when the notch in the shell closes off (Figure 2d), the notch in the underlying mantle closes as well. As in other species of *Diodora*, the mantle anterior to the keyhole in adult *D. aspera* is not split (Bandel, 1982). External views of the shells of an 125 d old *D. aspera* showed a clear suture between the fused edges of the notch (Figure 2e). This observation suggests that the two flaps of mantle anterior to the keyhole do not fuse immediately. Until they are completely fused, a suture in the shell is produced anterior to the keyhole. Neither external nor internal views revealed

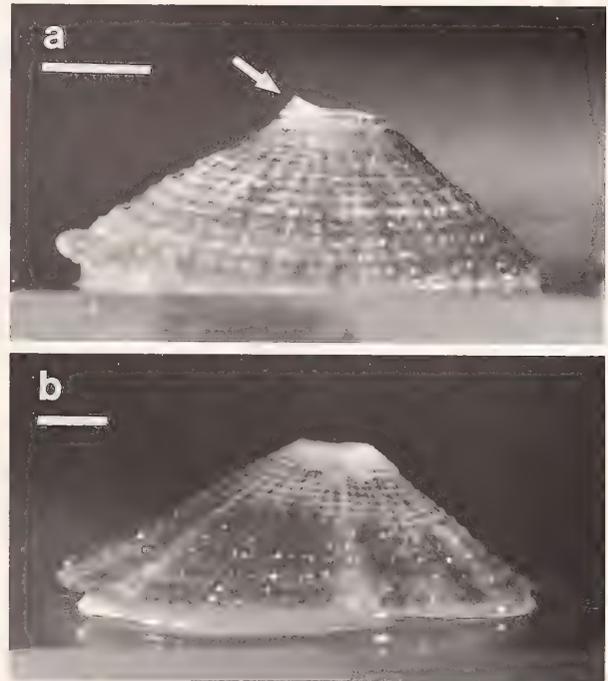


Figure 4

Light micrographs of two 18 month old *Diodora aspera*. Both snails are oriented with their anterior ends to the right. a: The larval shell has been partially dissolved due to enlargement of the keyhole. The arrow marks its remains. b: The larval shell has been completely dissolved and the keyhole is apical. a, b: scale bar = 1 mm.

sutures in the shells of older animals (Figures 2f, 3), suggesting that the suture is formed only briefly, and that once formed, it quickly disappears due to keyhole enlargement via shell dissolution. Interestingly, in haliotid pleurotomarioideans the mantle remains deeply slit even after a row of complete holes in the shell is formed (Crofts, 1929). In *Haliotis kamschatkana* (and presumably other haliotids), sutures between successive holes are visible in the shell throughout development as an external marker of the divided underlying mantle (Pernet, personal observation).

Boutan (1885) argued that the ontogeny of the keyhole seen in *Diodora apertura* reflects the phylogeny of the fissurellids. In his scenario, fissurellids with apically placed keyholes (e.g., *Diodora*) are derived from snails with sub-apical keyholes on the anterior slope of the shell (e.g., *Rimula*), which are in turn derived from snails which have only marginal notches or slits (e.g., *Emarginula*) (but see

of the specimen in d. f: 163 d post-fertilization. In the shells figured in b, c, and d, part of the outer layer of the early postlarval shell has eroded away, probably as a result of preparations for microscopy. a, b, c, d, f: scale bar = 100 μm . e: scale bar = 50 μm .

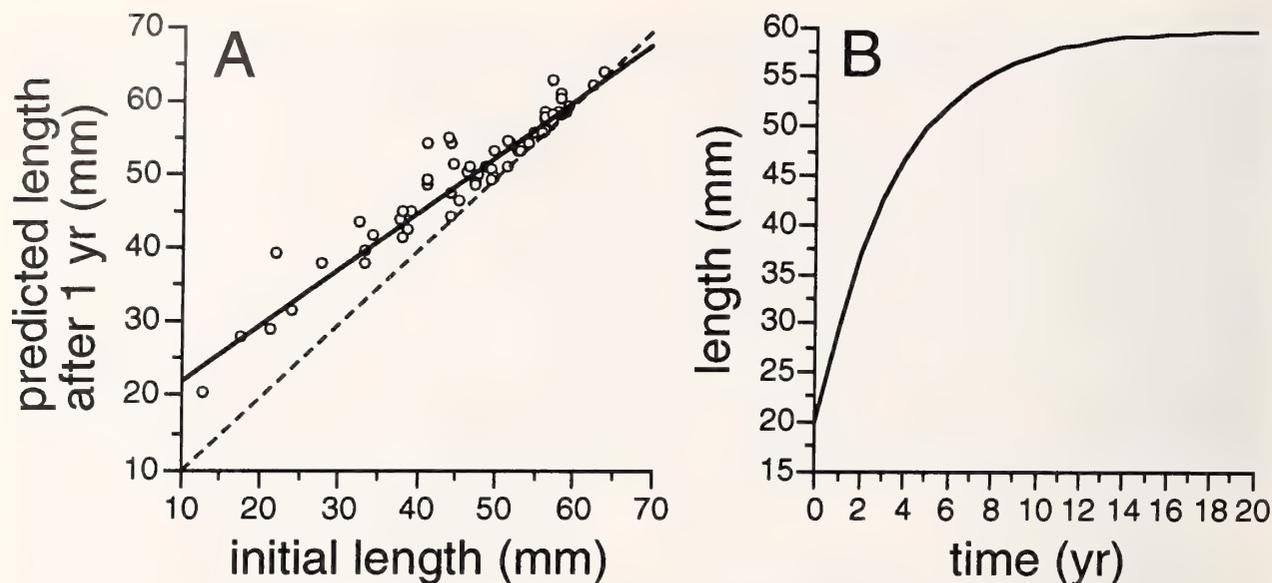


Figure 5

Growth in an intertidal population of *Diodora aspera*. a: Walford diagram of initial aperture length (abscissa) plotted against predicted length after 1 yr of growth (ordinate). The continuous line is a reduced major axis regression ($n = 68$, $y = 0.764x + 14.51$); the dashed line is the line of zero growth. b: Predicted age (abscissa) vs. length (ordinate) of *Diodora aspera* growing according to a Bertalanffy growth equation, with $S_{\infty} = 59.837$ (mm) and $K = 0.278$ (yr^{-1}). Growth is estimated from an initial length of 20 mm.

Garstang, 1928). Well-resolved phylogenies of the Fissurelloidea are needed to test this hypothesis. If Boutan's (1885) ideas are correct, then it is necessary to examine patterns of flow through the mantle cavities of these "ancestral" forms, and to assess the effects of induced flow on their respiratory currents, to evaluate the numerous hypotheses that have been proposed to explain the evolution of shell holes, slits, and notches in the fissurellids (Yonge, 1947; Voltzow & Collin, 1995).

Structures used to generate induced flow in organisms are more effective when the exit holes are large and are well elevated above the substratum (Vogel, 1977). In *Diodora aspera*, where both the diameter of the keyhole and its height above the substratum are positively correlated with size and age (Figure 1), larger snails should be better able than smaller snails to generate induced flow through the mantle cavity. Murdock & Vogel (1978) have shown that in large snails (about 50 mm aperture length), even slight ambient currents can dramatically increase flow rates through the mantle cavity. Because of scaling constraints, small snails may be largely unable to take advantage of such induced flow. Unfortunately, no empirical data relating patterns and rates of mantle cavity flow to size are available. Such constraints on flow in fissurellids are of interest both within species, as size increases over the course of development, and among species, where the maximum sizes of adults are quite variable (e.g., *D. granifera* reaches a maximum aperture length of 12 mm, and *D. aspera* 70.5 mm; Boggs, 1978; this study).

Growth Rates of *Diodora aspera*

The growth model developed here indicates that growth from an aperture length of 20 mm to a length of 55 mm should take about 7–8 yr (Figure 5b). This estimate of the growth rate of *Diodora aspera* corroborates that of Palmer (1968), who used similar mark-recapture techniques to examine the growth of *D. aspera* in Oregon subtidal and intertidal populations. He used the length from the posterior edge of the keyhole to the posterior edge of the shell as a measure of size. Since this dimension is strongly correlated with aperture length (Figure 1), his measurements can be converted to aperture length for comparison with the data presented here. His data suggest that it would take 6 yr for a snail to grow from 30 to 55 mm in aperture length. Adding 1–2 yr to allow for growth from 20 to 30 mm (Figure 5b), his estimate becomes 7–8 yr for growth from 20 to 55 mm, which is identical to my estimate.

Because of sampling biases, the model does not adequately describe the growth of small (< 20 mm length) individuals. To fill this gap, I estimated the growth rates of small snails raised in the laboratory. The estimated mean growth rates of small laboratory-raised snails increased almost twofold as the time intervals over which growth rates were measured increased, from $2.4 \text{ mm} \cdot \text{yr}^{-1}$ (for an interval of 377 d) to $3.9 \text{ mm} \cdot \text{yr}^{-1}$ (for an interval of 540 d). This increase in growth rate suggests that *Diodora aspera* actually follows a sigmoid growth curve; growth rate increases with size until an inflection point, after

which growth rate declines with increasing size. Taking $3.9 \text{ mm} \cdot \text{yr}^{-1}$ as a minimum estimate of growth rate (assuming that growth rate will continue to increase until it reaches an inflection point) suggests that a maximum age for a 20 mm snail is about 5 yr. Because this is a minimum estimate of growth rate, the actual ages of 20 mm snails may be considerably less than this. Using a range of 2–5 yr as an estimate of age for a 20 mm snail suggests that 55 mm snails might be 9–13 yr in age.

The data presented here indicate that snails 60 mm or greater in length may exceed 20 yr in age (Figure 5b). The largest *Diodora aspera* I have collected at this site was 70.5 mm long, and Abbott & Haderlie (1980) report that the maximum length of *D. aspera* is 70 mm. The discrepancy between the estimated value of S_{∞} (59.84 mm) and the maximum size of *D. aspera* in this population (70.5 mm) is due to the extremely slow growth rates of snails larger than 55 mm in length. Over the short time intervals over which growth was measured in this study, slow positive growth in these large snails could not be distinguished from zero growth. Thus, the annual growth increments for large snails estimated from these data (Figure 5a) are likely underestimates.

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NOTES, INFORMATION & NEWS

Passive Dispersal on Mountain Slopes: Shell Shape-Related Differences in Downhill Rolling in the Land Snails *Arianta arbustorum* and *Arianta chamaeleon* (Helicidae)

by

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Dispersal of land snails involves active movements and mechanisms like wind and stream drift, floating or rafting on floating vegetation, and attachment to insects, mammals, and to the plumage or nest material of birds (Rees, 1965; Dundee et al., 1967). In the Swiss Alps, the land snail *Arianta arbustorum* (Linnaeus, 1758) has frequently been observed to fall from vegetation and, due to its nearly globose shell, to roll down steep mountain slopes (Baur, 1984, 1986). In this way, individuals can disperse distances of more than 30 m on slopes partly covered by snow (Baur, 1984). One may assume that the probability of dispersing large distances by downhill rolling may depend on a variety of factors such as the inclination and fine structure of the slope, the vegetation height, the frequency and size of hindrances (e.g., rocks), as well as the shell shape of the snails. If shell shape matters, then species with globose shells would be expected to roll downhill more readily than species with slender or discoidal shells.

In this note we present the results of a field experiment that examined the downhill rolling of two co-existing land snail species (*Arianta arbustorum* and *Arianta chamaeleon* [L. Pfeiffer, 1842]) that differ in shell shape.

Materials and Methods

Arianta arbustorum is common in moist habitats in north-western and central Europe (Kerney et al., 1983), occurring at altitudes of up to 2700 m a.s.l. in the Alps (Baur & Raboud, 1988). *Arianta chamaeleon* lives in the south-eastern Alps (Kerney et al., 1983). Snails of both species have determinate growth, but differ in shell shape (ratio shell height/shell breadth): *A. arbustorum* has a more globose shell (shell shape 0.70–0.90), whereas *A. chamaeleon* has a flattened, nearly discoidal shell (shell shape 0.50–0.65) (Bisenberger, 1993).

Adult *Arianta arbustorum* and *Arianta chamaeleon* were collected on an alpine meadow partly covered with rock debris and rocks near Lake Wolay at an elevation of 1970 m in southwestern Carinthia, Austria (46°37'N, 12°52'E).

Sixteen snails from each species were individually marked on their shells with a permanent felt pen. Shell breadth and height of each snail was measured to the nearest 0.1 mm using vernier callipers. The shell breadth of *A. arbustorum* averaged 19.7 mm (SD = 0.7 mm), that of *A. chamaeleon* 19.0 mm (0.7 mm). The two species differed significantly in shell shape (ratio shell height/shell breadth; *A. arbustorum*: 0.80 ± 0.04 , range 0.74–0.86; *A. chamaeleon*: 0.57 ± 0.03 , range 0.53 – 0.62; $t = 18.68$, d.f. = 30, $P < 0.0001$).

The downhill rolling of the snails was examined on a NW-exposed snowfield (mean inclination: 32°, range: 27–35°), located 900 m from the site where the snails were collected at an elevation of 2000 m at the foot of Mount Seewarte on 28 July 1995. The snowfield, measuring 15 × 20 m, was partly covered with sand and scree material. The weather was favorable for snail activity during the experiment (12°C and rain). To simulate falling down from the vegetation or rocks, each test snail was placed on a flat piece of stone (measuring 30 × 10 × 10 cm) at the upper margin of the snowfield. The snails were gently pushed so that they fell 10 cm down onto the inclined snowfield. There, the snails either stopped after having glided a few cm, or they began to roll downhill on the snowfield. The distance traveled between the starting point and the place where a snail stopped was measured to the nearest cm. A maximum distance of 1350 cm was recorded for individuals that rolled beyond the lower margin of the snowfield. These snails would have dispersed much farther on larger snowfields. Each snail was tested twice at each of two different starting points near the upper margin of the snowfield. This resulted in a total of 128 trials. At the end of the experiment, the snails were released at the site where they were collected.

Results and Discussion

The two species differed significantly in the distributions of the distances dispersed on the snowfield (Figure 1; $\chi^2 = 44.91$, d.f. = 6, $P < 0.001$). In *Arianta chamaeleon*, 62.5% of the trials ended within a distance of less than 2 m compared to only 12.5% in *Arianta arbustorum*. On the other hand, in only 4.7% of the trials, *A. chamaeleon* rolled downhill 12 m or more compared to 45.3% in *A. arbustorum*. Thus, individuals of the two species differed in the probability of beginning to roll once they landed on the inclined snowfield. *Arianta arbustorum* with a globose shell had a significantly higher probability of rolling downhill than *A. chamaeleon* with a more flattened shell.

Within-species variation in the total distance rolled (= sum of displacements in four trials) was not correlated with within-species variation in shell shape (Spearman

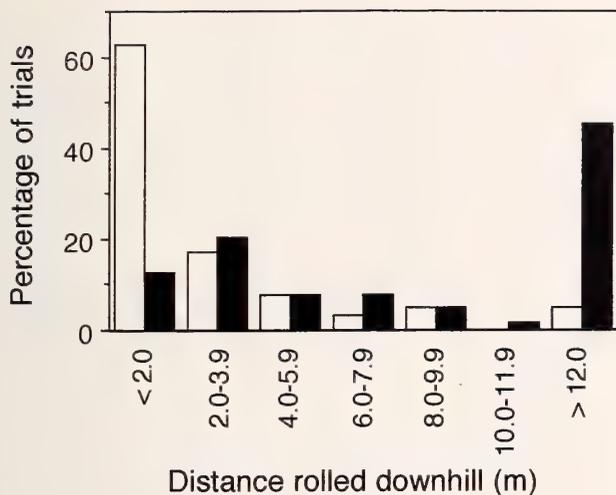


Figure 1

Distribution of distances rolled downhill on an inclined snowfield by *Arianta arbustorum* (solid bars) and *Arianta chamaeleon* (open bars).

rank correlation; *Arianta arbustorum*: $r_s = 0.10$, $n = 16$, $P = 0.70$; *Arianta chamaeleon*: $r_s = -0.46$, $n = 16$, $P = 0.07$). This suggests that the relatively small within-species variation in shell shape did not affect the probability of rolling downhill in any species.

Under natural conditions, crawling snails with extended soft body, and resting snails retracted in the shell have been observed to fall from the vegetation. In the experiment, we used active snails with extended soft bodies. Some individuals retracted into the shell when rolling downhill; other individuals had their soft body extended. However, the probability of rolling downhill did not appear to be affected by the state of the soft body (retracted or extended) in any of the species.

In both species, the repeatability of this means of dispersal (comparing the distances dispersed in four repeated trials; cf. Falconer, 1981) was low (*Arianta arbustorum*: $r = 0.10$, $F_{15,48} = 1.37$, n.s.; *Arianta chamaeleon*: $r = 0.13$, $F_{15,48} = 1.54$, n.s.). This suggests that the heterogeneity of the snowfield (uneven surface, pieces of stones) had a major effect on the distance rolled by a single snail.

The passive downhill dispersal examined in this study can partly be compensated for by active uphill movements of the snails. When placed on an inclined surface, *Arianta arbustorum* tends to move upward due to its negative geotactic orientation behavior (Baur & Gosteli, 1986). In fact, uphill movements of tagged *A. arbustorum* have been recorded on mountain slopes in the Swiss Alps (Baur, 1984, 1986). Active uphill movements and passive downhill displacements result in high genotypic similarities among populations that live in the natural downward course on mountain slopes (Vismara, 1983).

Downhill rolling may frequently occur in snails living

on steep mountain slopes. However, in most cases, rolling snails are stopped either by the vegetation, or their descent ends in a depression of the uneven surface of the mountain slope. Nonetheless, downhill rolling can result in large distances dispersed. This means of dispersal is risky, but need not end fatally. In the Swiss Alps, 11 *Arianta arbustorum* were found at the completely snow-covered foot of a 30 m high rock wall; six individuals were alive (Baur, 1986). These snails came from the snow-free area above the rock wall.

Snails rolling downhill also run the risk of leaving suitable habitat. Individuals with a low probability of rolling downhill (species with nearly discoidal shells such as *Arianta chamaeleon*) might therefore leave their habitat patch less frequently than individuals with globose shells. This could be an advantage in a heterogeneous landscape, in which favorable habitat patches are surrounded by unsuitable environments.

Acknowledgments

We thank the "Amt der Kärnter Landesregierung" for permission (Ro- 511/2/1995) to work in the nature reserve "Wolayersee und Umgebung (Karnische Alpen)," the students of the field course "Ecology of Alpine Gastropods" for assistance, and H. Sattmann (Natural History Museum, Vienna) for organizing the field course. A. Baur, R. H. Cowie, M. Haase, H. Sattmann, and an anonymous reviewer commented on the manuscript. Financial support was received from the Swiss National Science Foundation.

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Hallaxa apefae Marcus, 1957
(Nudibranchia: Actinocyclusidae) from Ghana
(West Africa), Newly Recognized
as an Amphiatlantic Species

by

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The genus *Hallaxa* Eliot, 1909, introduced to replace the name *Halla* Bergh, 1878 (non *Halla* O. G. Costa, 1844, Polychaeta), has been recently revised worldwide by Gos-

liner & Johnson (1994), with the description of several new species. With this publication, 14 species of this genus are known throughout the world. Twelve of these species come from the tropical, subtropical, or temperate areas of the Indo-Pacific; one was described from the temperate Pacific coast of North America (*H. chani* Gosliner & Williams, 1975); and another, *H. apefae* Marcus, 1957, was based on two specimens collected in the subtropical coast of Brazil, West Atlantic.

During a collecting trip to the tropical coast of Ghana, West Africa (March 1993), we found a specimen that fit well with the original figure of Marcus (1957) and with the redescription made by Gosliner & Johnson (1994) of *H. apefae*. This finding constitutes the first record of this species after the original description, and the first one in the eastern Atlantic Ocean. Therefore, *H. apefae* must be added to the list of amphiatlantic gastropods.

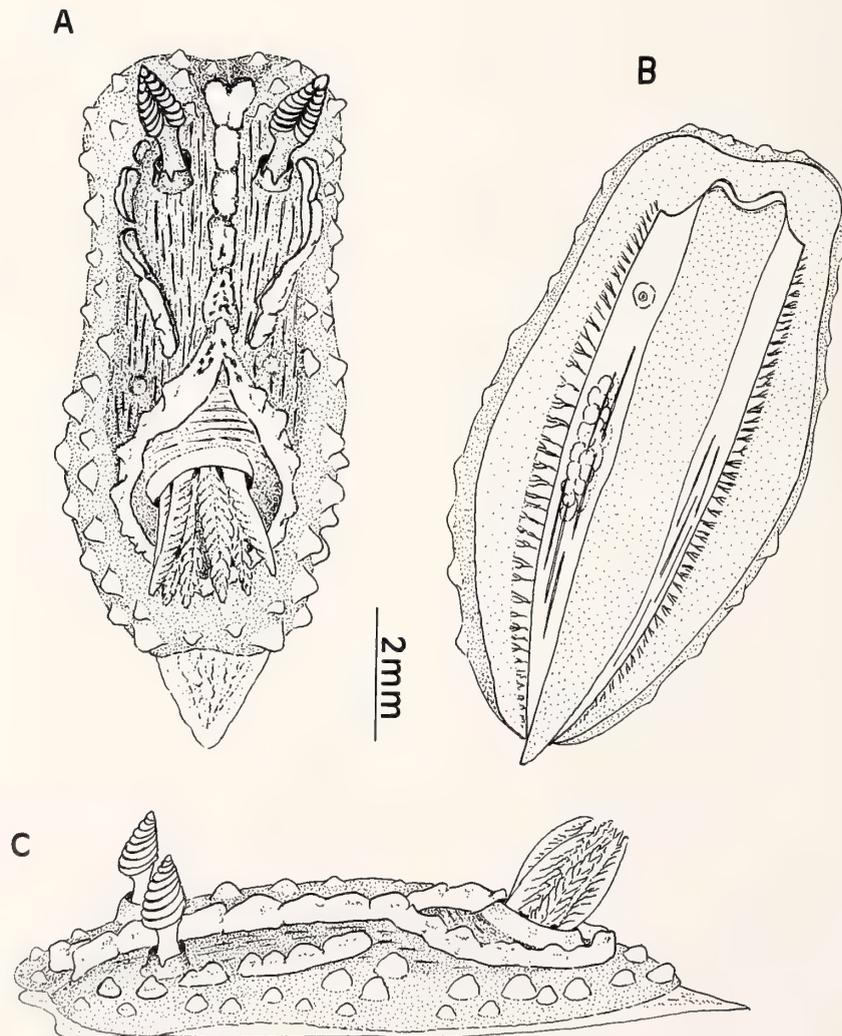


Figure 1

Hallaxa apefae: views of the living animal (MNCN 15.05/23760), A. dorsal view, B. ventral view, C. lateral view.

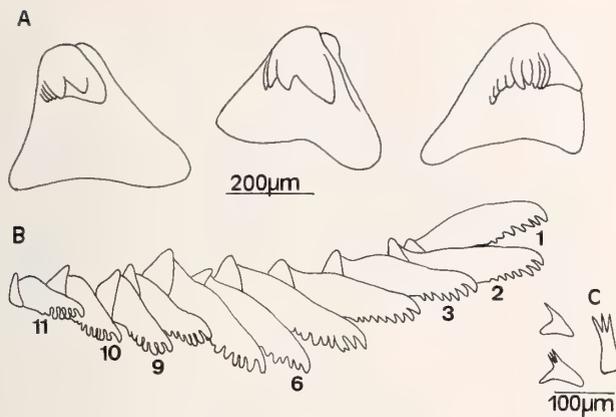


Figure 2

Hallaxa apefae (MNCN 15.05/23760), A. inner lateral radular teeth, B. outer lateral radular teeth, C. rodlets of the labial cuticle.

Description

Genus *Hallaxa* Eliot, 1909

Hallaxa apefae Marcus, 1957

Hallaxa apefae Marcus, 1957: 421–422, figs. 73–80; Gosliner & Williams, 1975: 309–405, figs. 9 (part), 10; Gosliner & Johnson, 1994: 157–158, figs. 2, 3.

Material: Takoradi (4°53'N, 1°46'W), Ghana, West Africa (6 March 1993): one specimen, 14 mm in length when extended, on the under surface of an intertidal rock covered by sponges. Museo Nacional de Ciencias Naturales de Madrid, Spain (MNCN): 15.05/23760.

External morphology: The body is very fleshy and round-ovoid in shape. The color is translucent light yellowish, with gray-brown spots over the notum. There is a large mid-dorsal crest, which extends from the rhinophores to the anterior part of the branchial plume (Figure 1A, C) where it divides, encircling the gills. Also, the animal has numerous, irregular raised tubercles over the notum, which are translucent. The body and the crests became smaller and broader when the animal was resting. The sides of the foot (Figure 1B) lack tubercles. Oral tentacles have not been observed.

The branchial plume has eight unipinnate gills, yellow, high, retractile, and disposed close together. The rhinophoral pocket is high, with an irregular edge. The bulbous rhinophores have eight broad lamellae, and they are narrow at their base.

Internal morphology: The labial cuticle consists of a ring of numerous rodlets (Figure 2C) with one to three denticles along their free margin. The radular formula is $30 \times (10-14.1.0.1.10-14)$. The inner lateral teeth (Figure 2A) have a very large base with a large central cusp. On their innermost side is one denticle, while on the outer side there are several. The outer lateral teeth (Figure 2B) are elon-

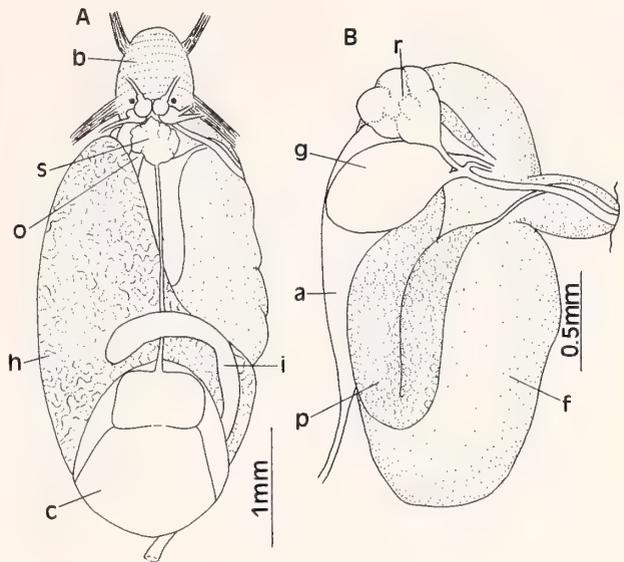


Figure 3

Hallaxa apefae (MNCN 15.05/23760), A. view of the internal organs: b, buccal bulb; c, heart; h, digestive gland + hermaphrodite gland; i, intestine; o, esophagus; s, blood gland; B. reproductive system: a, ampulla; f, female gland; g, bursa copulatrix; p, prostatic portion of vas deferens; r, receptaculum seminis.

gate with several denticles along the innermost edge. Their number is variable, from 10 in the distal part of the radula, to 14 in the proximal part. The esophagus is short and thin (Figure 3A). Salivary glands have not been found. The heart is large, and connects with a broad blood gland, placed just behind the central nervous system.

The deferent duct (Figure 3B) is thin and short, and it expands into a folded prostatic portion. The ampulla is very large. The bursa copulatrix connects with a large vagina, and with an irregular receptaculum seminis.

Discussion

Only two specimens of *Hallaxa apefae* were previously known, both from the type locality (Ubatuba, Brazil), the holotype and the one studied by Gosliner & Johnson (1994). The specimen studied here is identical to the external and internal morphology previously described by Marcus (1957) and Gosliner & Johnson (1994). Only a minor anatomical detail of the vagina (the presence of a vaginal diverticulum) depicted by Marcus (1975) is absent in our material. Following Gosliner & Johnson (1994), it is doubtful that Marcus actually observed this structure, also absent in the specimen studied by Gosliner & Johnson and in other species of this genus. Our record, from the coast of Ghana, constitutes the first citation of this species in the eastern Atlantic. Therefore, *Hallaxa apefae* is an amphiatlantic species and the only one of this genus known in the Atlantic Ocean.

The amphiatlantic mollusks have been the focus of at-

tention in recent years of several authors (García-Talavera, 1982; Ortea et al., 1988; Templado et al., 1990; Vermeij & Rosenberg, 1993; Fernandes & Rolán, 1994). Edmunds (1977) pointed out a high percentage of amphiatlantic species with regard to the opisthobranch fauna of Ghana.

More data are needed about the range of distribution of *H. apefae* and its larval development. The rarity of this species may be due to the difficulty in finding it (it is a very cryptic species on the sponges where it lives) and because the areas over which it probably extends are poorly known from the point of view of marine fauna.

Acknowledgments

We are grateful to Peter Ryall for his hospitality and assistance during our work in Ghana. Emilio Rolán and Xico Fernandes (recently deceased) assisted in the collection of opisthobranchs. We are also grateful to Terrence M. Gosliner and Barry Roth (Editor) for their helpful advice on the manuscript.

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International Commission on Zoological Nomenclature

The following Applications were published on 30 September 1996 in Volume 53, Part 3 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2935—*Lirobarleeia* Ponder, 1983 (Mollusca, Gastropoda): designation of *Alvania nigrescens* Bartsch & Rehder, 1939 as the type species.

Case 2977—*Arca pectunculoides* Scacchi, 1834 and *A. philippiana* Nyst, 1848 (currently *Bathyarca pectunculoides* and *B. philippiana*; Mollusca, Bivalvia): proposed conservation of the specific names.

The following Opinions concerning mollusks were published on 30 September 1996 in Volume 53, Part 3 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1844. *Aplysia juliana* Quoy & Gaimard, 1832 (Mollusca, Gastropoda): specific name conserved.

Opinion 1845. *Tropidoptera* Ancey, 1889 (Mollusca, Gastropoda): *Endodonta wesleyi* Sykes, 1896 designated as the type species.

BOOKS, PERIODICALS & PAMPHLETS

Systematics and Evolution of *Littorina*

by DAVID G. REID. 1996. Ray Society Publication, No. 164. x + 463 pp. ISBN 0 903874 26 1. Price £89.00.

Species of *Littorina* are studied by many researchers, among them, anatomists, cladists, ecologists, malacologists, and physiologists. The Fourth International Symposium on *Littorina* Research, held in Ireland this autumn (September 1996), is testament to the amount of research activity generated by this genus of marine gastropods. *Littorina* also is revered for the beauty and astonishing variation exhibited among the shells of its member species, an esthetic appeal that has enriched the lives of many shell admirers. The publication of *Systematics and Evolution of Littorina*, a monograph by David G. Reid, will enamor all of these audiences.

In the preface to this work, Reid states his four aims: (1) to review the taxonomic history of the genus and produce the first comprehensive systematic monograph in over a century, (2) to describe and illustrate the magnificent shell variation and summarize the numerous studies that have examined its causes, (3) to reconstruct the phylogeny of living species to provide a historical perspective from which to examine their comparative biology, and (4) to address their macroevolution, the speciation processes that have produced their diversity, the biogeographic history that has resulted in their current distribution, and the adaptations that have shaped their morphologies. Each of these aims he accomplishes with results that will interest different audiences to different extents: this monograph will serve as an important tool for researchers, and it also provides interesting reading material on its own.

The monograph consists of six chapters. In the introductory chapter (Chapter 1), Reid explains the tripartite division of the bulk of the monograph: a description of morphological characters (Chapter 3), a systematic description of all 19 extant species (Chapter 4), and an hypothesis of the macroevolutionary history of the genus (Chapters 5 and 6). The section describing the materials and methods (Chapter 2) consists of a very technical description of specimens, synonymies, and types, a list of the museums from which materials were borrowed, and a list of information used in the subsequent cladistic analysis (anatomical and shell characters and distribution patterns).

The description of morphological characters (shell and body; Chapter 3) includes a very interesting account of shell variation related to mode of development. Species of *Littorina* that develop planktotrophically (members of subgenera *Liralittorina*, *Planilittorina*, and *Littorina*) are pelagic spawners and exhibit less intraspecific variation than do non-planktotrophic developing, benthic spawners (members of the subgenus *Neritrema*). As a result, the planktotrophic, pelagic species are separated more readily based on shell characters than are their non-planktotrophic, benthic cogenitors. This section also includes an interesting and lucid account of the concept of ecotypes and ecotypic effects on shell variation.

The systematic descriptions (Chapter 4) comprise the majority of the work (337 pages). For each taxon, the description consists of a list of synonymous nomenclatures and type specimens, a review of taxonomic history, detailed descriptions of anatomy, shell, main features of identification, habitat, diet, and biogeographical distribution, and consideration of biochemical genetic data and (for the first time) fossil history. Also included with the species descriptions are maps of geographical distribution, detailed illustrations of the anatomical information, photographs of shells, and scanning electron micrographs of radulae.

The phylogeny (Chapter 5) proposed for *Littorina* is an amalgamation of separate cladistic analyses and consideration of morphological, fossil, allozyme, and DNA data. The hypothesis preferred by Reid is a combinable-components consensus of two cladograms, one based on morphological data and one based on DNA data. The cladogram based on morphological data, itself, is a strict consensus cladogram of 21 equally parsimonious cladograms, while the cladogram based on DNA data is a cladogram for 16 species (based on a maximum parsimony analysis of 12S and 16S ribosomal RNA genes and cytochrome-b mitochondrial genes) with the three species absent added to the cladogram "as indicated by the results of the separate analyses of each gene." These bold techniques will generate some lively discussions, adding to the flurry of activity surrounding the genus. However, Reid is cautious and emphasizes that "this [phylogeny] remains an hypothesis, to be tested and modified as further data become available." He also provides his morphological data matrix (his results, obtained using the computer program PAUP 3.1.1, are reproducible using Hennig86) and references, so inter-

ested readers can analyze the data themselves. Reid's analysis of morphological data differs from the analysis he performed in 1990 by the inclusion of three additional species (*L. kasatka*, *L. horikawai*, and *L. natica*) and the exclusion of four species (two species of *Mainwaringia*, *L. kurila*, and *L. neglecta*).

Equally controversial may be his interpretation of the cladogram. Reid (p. 361) considers the unresolved polytomy in the middle of the tree as representing a genuine episode of rapid speciation during the evolution of the genus, not simply the result of insufficient data. Later (p. 379), he states that this episode of rapid speciation may be viewed as an "adaptive radiation following the invasion of a new adaptive zone, including adaptation to cooler climatic conditions." Again Reid is cautious and qualifies his interpretation, acknowledging that "[s]ome analyses of allozyme frequencies have clustered *L. brevicula* and *L. mandshurica* more closely with *Neritrema* species than with *L. squalida* and *L. littorea*," a result that would separate the polychotomy.

The final section (Chapter 6) is a description of the macroevolutionary history of *Littorina* and consists of historical biogeographical, ecological, and morphological hypotheses of evolution, as determined by optimization onto the phylogeny. Perhaps the most elegant example of the use of optimization is the hypothesis of shell mineralogy evolution, wherein the origination of an outer calcite layer on shells corresponded with a shift in habitat from warm-temperate to cold-temperate and subarctic in an ancestral species. Since calcite is less soluble than aragonite, these events make plausible the hypothesis of an adaptive function for the calcite layer: the reduction of shell dissolution in cold water. This section also contains an informative description of species ranges, distribution patterns, and spawn types, and interesting discussions of several aspects of evolutionary theory, such as species concepts, modes of speciation, means of studying historical biogeography, and methods for studying adaptations.

The (300 mm × 210 mm hardcover) book is written very clearly and contains in excess of 1300 references on *Littorina*, some of which still are in press, and, so, should remain a popular source of information concerning *Littorina* for many years to come. There are very few typographical errors or inconsistencies (I noticed only two: the name of the post office for the Delaware Museum of Natural History is now Wilmington, not Greenville (p. 10), and node 16 on the cladogram is best characterized by the egg groove of the pallial duct, not the shape of outer marginal teeth, as claimed (p. 361)). The illustrations, micrographs, photographs, and figures are of excellent quality (this had the unfortunate effect that maps seemed sparse and lacking in detail, in comparison); however, the lack of numerals

on nodes in the optimization figures made reading the interpretation of the optimizations inconvenient, as readers are required to turn pages constantly.

Though the monograph is replete with technical information, it still reads as a book about natural history, especially the final two chapters. Ultimately, it is the origination of the outer calcitic layer, large pelagic egg capsules, and enlarged salivary glands that Reid contends are responsible for the success of *Littorina*. If this hypothesis is accepted by gastropod researchers, it will be Reid's style of combining an informative, scholarly systematic description within an historical narrative that will be responsible for the success of *Systematics and Evolution of Littorina*.

This book can be ordered from Intercept Limited, P.O. Box 716, Andover, Hants. SP10 1YG, U.K. Tel: + 44 (264) 334748. Fax: + 44 (264) 334058.

J. R. Stone

Molluscan Types of the Albatross Expeditions to the Eastern Pacific Described by W. H. Dall (1908)

by ALAN R. KABAT. 1996. Bulletin of the Museum of Comparative Zoology 155(1): 1-31 (12 September). US ISSN 0027-4100.

This paper documents the type material of 215 species of mollusks described by William Healey Dall in his 1908 monograph of the shelled mollusks and brachiopods collected by Alexander Agassiz during the three cruises of the *Albatross* in the tropical Pacific. The species are predominantly deep-water marine taxa. The historical context is clearly and succinctly described. The division of type specimens between the Museum of Comparative Zoology at Harvard University and the Smithsonian Institution, as well as other curatorial problems, has resulted in some errors and omissions in the literature, which this paper rectifies.

Coral Reef Animals of the Indo-Pacific

by TERENCE M. GOSLINER, DAVID W. BEHRENS & GARY C. WILLIAMS. 1996. Sea Challengers, 4 Somerset Rise, Monterey, California 93940. vi + 314 pp. ISBN 0-9300118-21-9. \$45.00.

Advertised as a field guide, this eight-by-ten-inch (20.5 × 25.5 cm), glossy, softbound book continues in the format familiar to users of the Sea Challengers series: four color photos down each page, accompanied

by informal identification and natural history notes. The "animals" of the title are all invertebrates, because, as the foreword notes, numerous other books exist on the fishes and other vertebrates of the Indo-Pacific. The photographs (1100 species pictured in life against predominantly natural backgrounds), by 50 skilled nature photographers, are the great strength of this work. There is scarcely a "bad" (i.e., inartistic or uninformative) picture here, although it is questionable whether all of the photos, even with text, are adequate for identification of the animals. For example, the identification notes for "*Octopus* sp. 3" (one of eight pictured species of *Octopus* considered to be undescribed) merely state "here seen hiding in a bubble shell (*Bulla vernicosa* . . .)." I also found the posing of a scaphopod (p. 178) on a colorfully encrusted rock somewhat jarring to my expectations.

The lack of any indication of scale in the photos or text is potentially confusing. For these malacologically oriented eyes, the problem was most severe in the Arthropoda, where tiny shrimp and superficially similar but much larger crustaceans are shown at about the same size.

The introduction makes some interesting—and, for a popularly oriented work, unexpected—points about the desirability of recognizing only monophyletic groups in a classification and the fallacy of formal ranks. The tone of these sections is cheerful ("Determining evolutionary relationships: Are you out of your tree?" and "Unequal classification: How rank can you get?"), laying out some of the systematist's concerns for the lay reader. The portrait of the authors inside the back cover shows that they are cheerful too.

Coral Reef Animals of the Indo-Pacific is certain to enrich the experience of the diver, the aquarist, and the student of coral reefs. As an identification guide, it can probably get the user close. Like other such "show-and-tell" guides, this book does not present the universe of possibilities within a clade, as would a monograph with keys. With the above limitations kept in mind, it should make a fine field companion for work or pleasure on the reefs of the Indo-Pacific.

B. Roth

The Non-Marine Molluscs of the Maltese Islands

by FOLCO GIUSTI, GIUSEPPE MANGANELLI, & PATRICK J. SCHEMBRI. 1995. Monografie XV, Museo Regionale di Scienze Naturali, Torino. 607 pp. ISBN 88-86041-24-1. L. 130.000.

This is a beautifully realized monograph of the fossil and Recent land and freshwater Mollusca of the aforesaid islands of the central Mediterranean. It begins with

an introduction to the physical geography of the Maltese Islands (Gozo, Malta, and outlying islets), their position and size, geology, soils, climate, and human influence on the landscape. A shorter chapter on vegetation is contributed by Edwin Lanfranco, followed by a phylum by phylum consideration of the islands' fauna. The general biogeography of the islands (including fossil evidence) is considered briefly on pp. 45–49, and the subject is revisited with respect to mollusks on pp. 516–524. The biogeography mainly proceeds from a cataloguing of species with various types of distributions (perhaps the phylogenetic relationships of Mediterranean-area nonmarine mollusks are not well enough understood for a consideration of sister-group relations), and, in common with island biogeography elsewhere, tends to focus on dispersal and potential sources of colonization. All of the above sections are fully referenced.

The chapter, "The Mollusca: General Organization and Morphology" (pp. 55–86), contains helpful introductory matter for readers who do not deal with molluscan anatomy on a day-to-day basis. "A Brief History of Malacological Research in the Maltese Islands" places the present work in a historical context, and an "Analytical Key for the Identification of Species" helps the reader get to the right place in the text.

The heart of the monograph, the catalogue of species, includes 78 species. Synonymies are given for all species. Taxonomic material at higher levels is generally limited to a statement of type species or type genus, with annotations as necessary. (I was pleased to see that type genus synonymic notes take the following form: "*Agriolimax* Mörch, 1865, is a junior synonym of *Deroceras* Rafinesque, 1820" [p. 284]. The shorter form with the equals sign, so often encountered—e.g., "*Agriolimax* = *Deroceras*"—is equivocal as to which is the right name to use.)

Material examined is listed, including locality name, UTM reference, collector, date, and number of specimens. Characters for identification or differential diagnosis are listed, separately from the more complete description that follows. The latter includes shell, body, genitalia, and radula. Information on habitat and general distribution (i.e., outside of the Maltese Islands), paleontology, and conservation status on the islands follow. Where necessary, comments on taxonomy, identification, or other points of interest are given under "Remarks."

Typically, a full-page photograph is devoted to the shells of one species, showing a range of variation. Only in a few cases was it necessary to illustrate specimens from other than a Maltese Islands locality. The photographs of slugs (never a very promising subject for portraiture) are particularly good. Smaller shells are shown in SEM. The anatomical drawings are in a style

that will be familiar to readers of the many fine systematic papers published out of the Dipartimento di Biologia Evolutiva of the University of Siena. Reproductive organs are shown in three dimensions as if seen in the dissecting dish, rather than compressed into a plane by slide mounting.

The results are summarized in a section of conclusions, including biogeography as mentioned above and a careful consideration of threat status to the Maltese malacofauna. The sum total is a book that will be of lasting value to a wide spectrum of readers. It may be ordered from Museo Regionale di Scienze Naturali, Via Giolitti 36, 10123 Torino, Italy.

B. Roth

Manuscripts

Manuscripts must be typed, one side only, on A4 or equivalent (e.g., 8½" × 11") white paper, and double-spaced throughout, including references, figure legends, footnotes, and tables. All margins should be at least 25 mm wide. Text should be ragged right (i.e., not full justified). Avoid hyphenating words at the right margin. Manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics; no other manipulation of type faces is necessary on the manuscript. Metric and Celsius units are to be used. For aspects of style not addressed here, please see a recent issue of the journal.

The Veliger publishes in English only. Authors whose first language is not English should seek the assistance of a colleague who is fluent in English before submitting a manuscript.

In most cases, the parts of a manuscript should be as follows: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, footnotes, tables, and figures. The title page should be a separate sheet and should include the title, authors' names, and addresses. The abstract should be less than 200 words long and should describe concisely the scope, main results, and conclusions of the paper. It should not include references.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

The "literature cited" section should include all (and only) references cited in the text, listed in alphabetical order by author. Each citation must be complete, with all journal titles *unabbreviated*, and in the following forms:

a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. *The Veliger* 35:245–272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend. Avoid vertical rules.

Figures and plates

Figures must be carefully prepared and submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited. Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures. Photographs for halftone reproduction must be of good quality,

trimmed squarely, grouped as appropriate, and mounted on suitably heavy board. Where appropriate, a scale bar may be used in the photograph; otherwise, the specimen size should be given in the figure legend. Photographs should be submitted in the desired final size.

Clear xerographic copies of figures are suitable for reviewers' copies of submitted manuscripts. It is the author's responsibility to ensure that lettering will be legible after any necessary reduction and that lettering size is appropriate to the figure.

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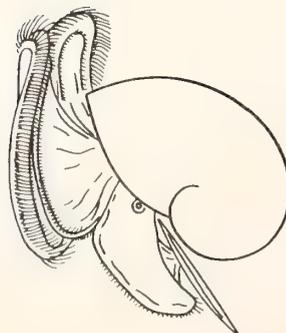
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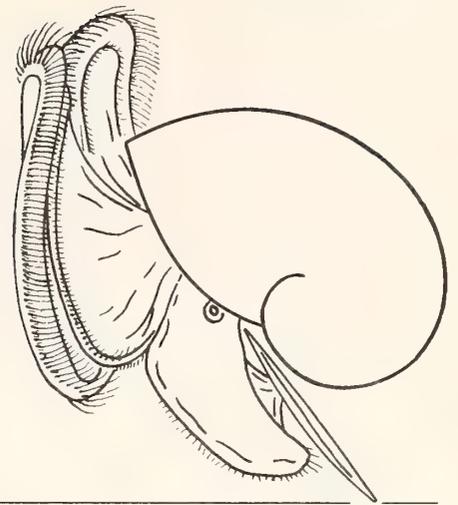
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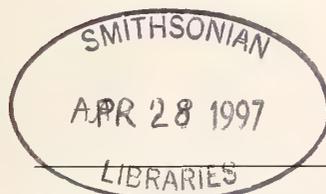
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THE VELIGER

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Spawn and Development of *Fusinus closter* Philippi, 1850 (Gastropoda: Prosobranchia) from the Venezuelan Caribbean

by

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Abstract. The spawn mass and embryonic development of *Fusinus closter* are described. Communal spawning was observed both in the field and in the laboratory. The spawn mass of each female consists of 100-150 egg capsules. The egg capsule measures about 10 mm in height, 7 mm in maximal width, and 3 mm in minimal width (at the stalk area). The exit-plug is located on one of the sides and measures $1.5 \pm \text{SD } 0.15$ mm. Each capsule contains between 200-400 eggs (mean $291 \pm \text{SD } 73$), measuring between 230 and 270 μm in diameter. Only 6% of the eggs complete their development; the rest are nurse eggs that disintegrate prior to their ingestion by the embryos. Fluorescence studies on the nurse eggs indicate that these disintegrate after the migration of the follicular cells to the animal pole, suggesting that they are fertilized. An intracapsular veliger stage is reached 25 days after deposition. This stage is characterized by a large velum and a shell measuring between 898 and 1443 μm (mean $1075.9 \pm \text{SD } 110.8$ μm). Hatching takes place 6 to 7 weeks after oviposition as crawling juveniles measuring $1.6 \pm \text{SD } 0.13$ mm in shell length.

INTRODUCTION

Fasciolarids are common in the southern Caribbean and include species of *Fusinus* Rafinesque, 1815, *Fasciolaria* Lamarck, 1799, *Leucozonia* Gray, 1847, *Pleuroploca* Fischer, 1884, and *Latirus* Montfort, 1810. The reproductive biology of the genus *Fasciolaria* has received considerable attention (Glaser, 1905; Hyman, 1923, 1935; Lamy, 1928; Bacci, 1947; D'Asaro, 1970a, 1986; Penchaszadeh & Paredes, in press). Most of the studied *Fasciolaria* species (*F. tulipa* Linné, 1758, *F. tulipa* var. *distans*, *F. salmo* Wood, 1828, *F. lilium hunteria* Perry, 1811) complete their development within an egg capsule; the embryos ingest nurse eggs and hatch as crawling juveniles. *Fasciolaria trapezium* Linnaeus, 1758, cited as *Fasciolaria audouini* Jonas from the Red Sea (Gohar & Eisawy, 1967) is the only reported *Fasciolaria* species that hatches as a veliger larva.

The nominal genera *Fusinus* Rafinesque, 1815, and *Fusus* Bruguière, 1798 (which according to Petit & Wilson, 1991 should be considered as the same genus), have been less studied than *Fasciolaria*. Lamy (1928), Fioroni &

Schmekel (1976), Amio (1963), Fioroni & Portmann (1968), and Portmann (1955) have described the egg capsules, embryogenesis, and metamorphosis of *Fusus* species, and Flores (1978) presented data on the reproduction of *Fusinus closter* Philippi, 1850. As in most *Fasciolaria* species, many *Fusinus* and *Fusus* species show a complete intracapsular development with no planktonic stage. Two different sources of extraembryonic nutrition have been reported, nurse eggs in *Fusus perplexus* A. Adams (Amio, 1963) and the perivitelline fluid in *Fusus syracusanus* Linnaeus, 1758 (Fioroni & Portman, 1968).

In this paper, information on the spawn mass and developmental biology of *Fusinus closter* is presented.

MATERIALS AND METHODS

Specimens

Voucher adult material has been deposited in the American Museum of Natural History, New York, catalog number 226437.

Adult specimens and egg capsules were collected in Feb-

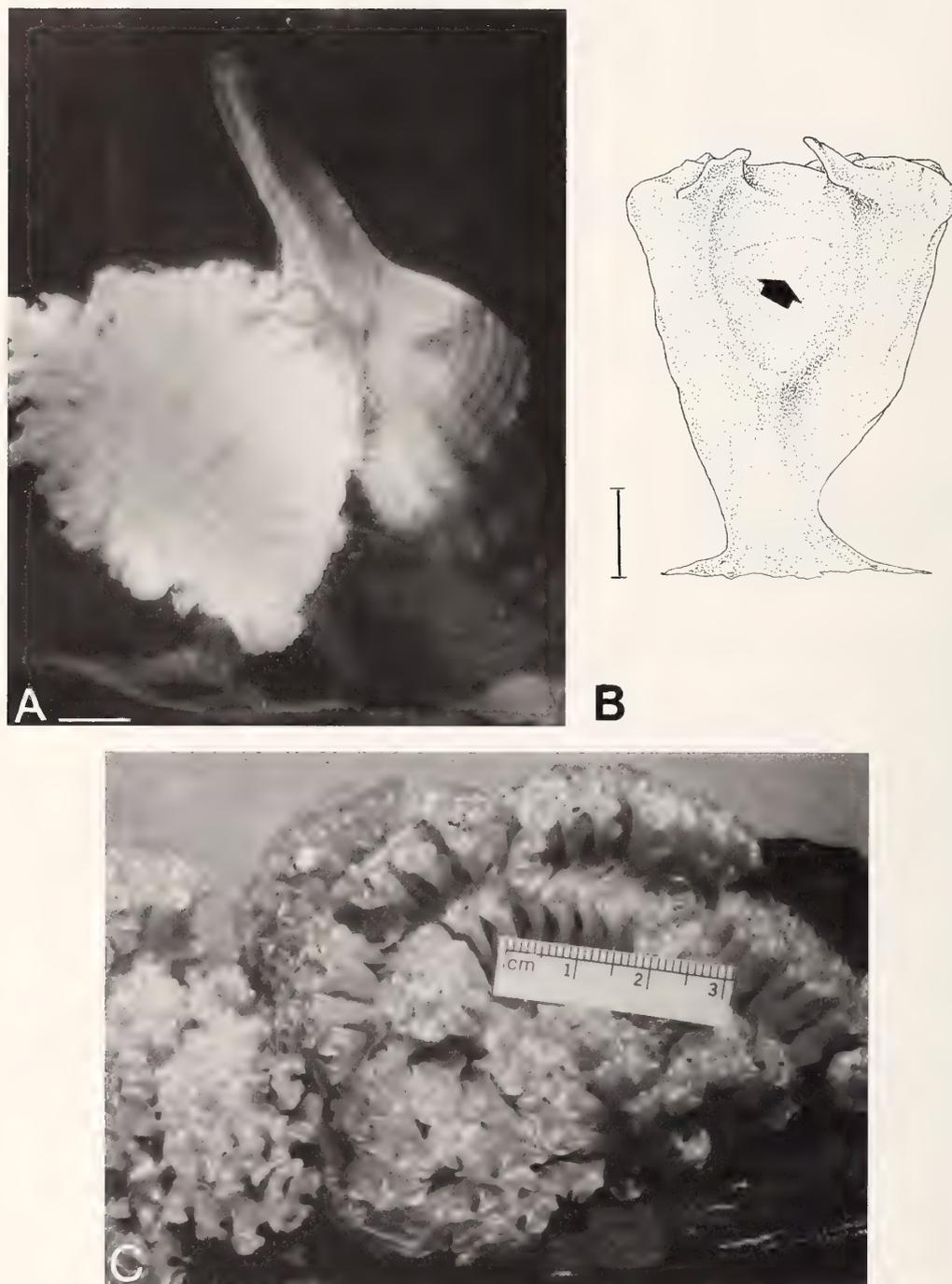


Figure 1

Fusinus closter: A. Spawning female, scale bar 1 cm. B. Egg capsule, arrow indicates escape aperture for hatchlings, scale bar: 2 mm. C. Communal spawn mass.

ruary 1992 at Isla Caribe, Chacopata, northern Araya Peninsula, Estado Sucre, Venezuela ($10^{\circ}42'11''\text{N}$, $63^{\circ}52'57''\text{W}$) between 0.6 and 4 m depth. The adults were found on *Thalassia testudinum* beds, and the spawn at-

tached to hard substrates such as empty *Pinna* and other bivalve shells. Animals and egg capsules were maintained in aquaria at a temperature of 25–27°C and salinity of 35 ppt in aerated, non-circulating seawater.

Development

A total of three spawn masses collected from the field, as well as spawn from two females obtained under laboratory conditions, were examined. The following aspects of the spawn were studied: (1) number and size of egg capsules deposited per female; (2) number and size of eggs and developing embryos within the capsule; (3) observations of the different stages of development, and (4) time of embryonic development from egg to hatching. The capsules were carefully opened at the exit-plug, and the eggs or embryos were released into a dish containing seawater. Observations were made with live material with the exception of the fluorescent stained material. All measurements were performed with an ocular micrometer.

Fluorescence Labeling

In order to observe the process of egg maturation and cleavage, the eggs and first division stages were stained with the fluorochrome Hoechst 33258, a specific stain for DNA. The egg material was fixed in a glutamine-acetate (GA) buffer containing 4–6% formalin for 12 hours. This buffer was prepared with 250 mM N-methyl glucamine, 250 mM K-gluconate, 50 mM HEPES, and 10 mM EGTA. The pH was adjusted to 7.4 with acetic acid. After fixation, the material was rinsed twice with GA buffer and a third time with GA buffer containing 0.5 $\mu\text{g}/\text{ml}$ of the fluorochrome Hoechst 33258. After 30–60 minutes, the samples were rinsed twice with GA buffer. Observations were carried out with a Leitz MPV 3 epifluorescence microscope equipped with filters for Hoechst fluorescent probes.

RESULTS

Spawn masses (Figure 1) were found in the field between February and May. Communal spawning behavior was observed both in the field and under laboratory conditions. Within the resulting clusters (Figure 1C), the spawn masses of each female could be easily detached one from the other since all the egg capsules from a single female were attached to a common basal membrane by a stalk. Each such individual spawn mass was formed of about 100 to 150 capsules (Figure 1A). Individual egg capsules (Figure 1B) were slightly flattened, and measured $9.9 \pm \text{SD } 1.3$ mm in height ($n = 48$), $7.4 \pm \text{SD } 1.2$ mm in maximal width ($n = 44$), and $2.7 \pm \text{SD } 0.5$ mm in minimal width (at the stalk; $n = 48$). The exit-plug for the hatchlings was located on one side (Figure 1B). The plug covering this exit aperture was opaque with a truncated elliptical shape, measuring $1.5 \pm \text{SD } 0.15$ mm ($n = 48$) in maximal vertical length.

The number of eggs per capsule varied from 196 to 410 (mean $291 \pm \text{SD } 73$, $n = 9$). The eggs were pink and measured approximately $260 \mu\text{m}$ in diameter. Observations of the fixed and stained eggs with the fluorescence microscope showed that they were surrounded by attached

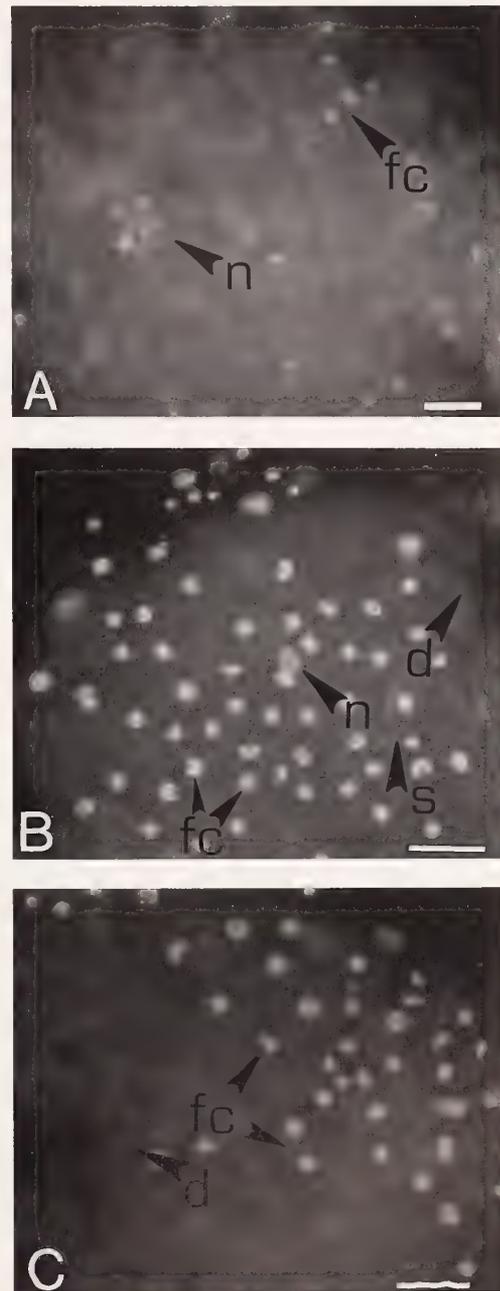


Figure 2

Uncleaved eggs of *Fusinus closter* observed under fluorescence. **A.** Recently spawned egg with nucleus in meiosis prometaphase. Follicular cells are attached to the egg (Day 1). **B.** Nurse egg with nucleus in mitosis prophase, prior to the first cleavage. Follicular cells migrating to the animal pole. A spermatozoa is observed inside the egg. A portion of the egg is starting to disintegrate (Day 2). **C.** Nurse egg with all follicular cells at the animal pole. A large portion of the egg has disintegrated, the nucleus was lost in the process (Day 3). Scale Bar: $25 \mu\text{m}$. Abbreviations: d, disintegrating portion; fc, follicular cells; n, nucleus; s, spermatozoa.

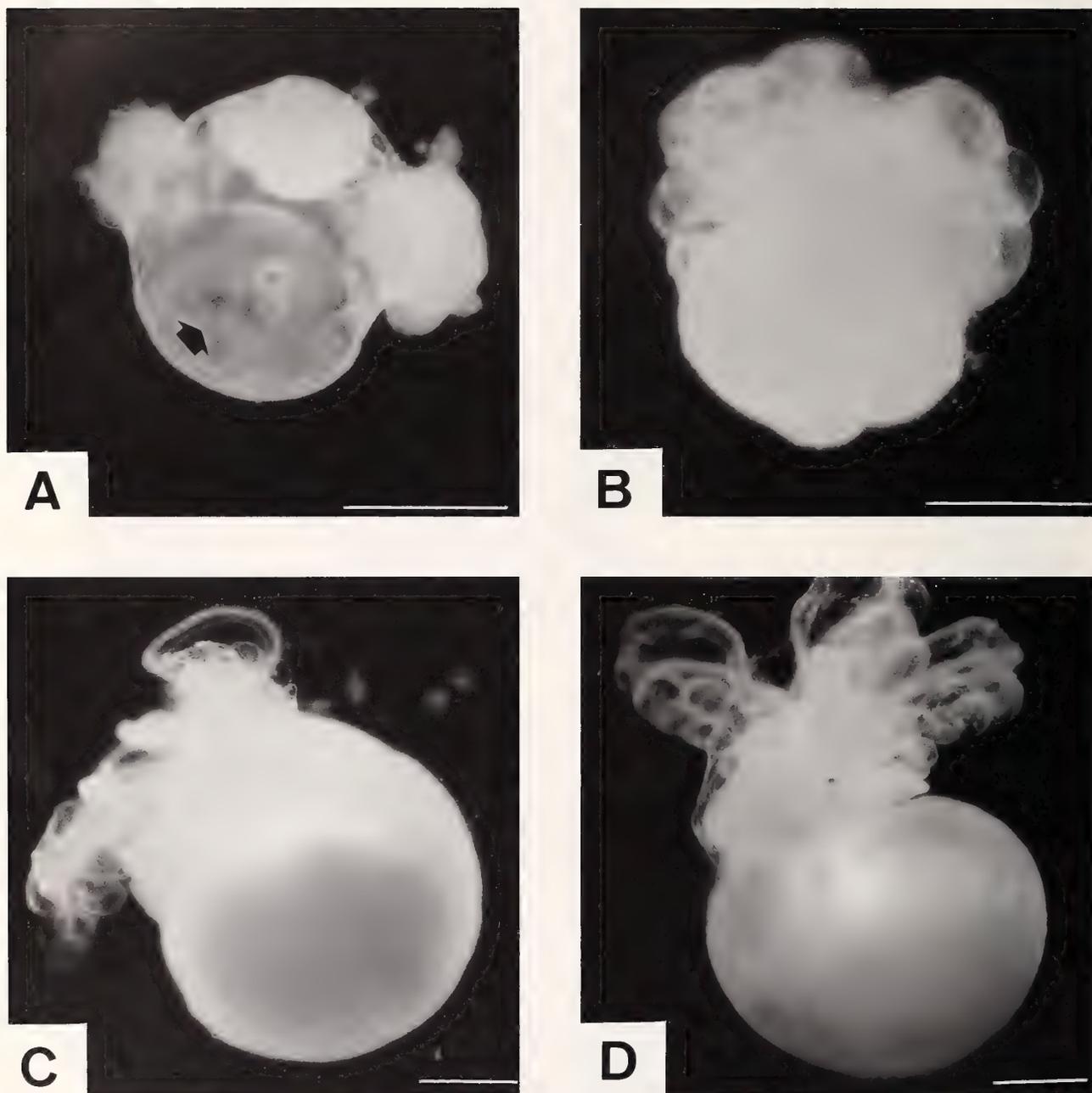


Figure 3

Development of *Fusinus closter*. **A.** Embryo with stomodaeum empty (indicated by arrow, 10–14 days). **B.** Embryo with stomodaeum full of yolk particles (21 days). **C.** Early intracapsular veliger (23 days). **D.** Intracapsular veliger (24 days). **E.** Intracapsular veliger (25 days). **F.** Intracapsular pediveliger stage (30 days). **G.** Prehatching stage (40 days). **H.** Hatching stage (45–50 days). Scale Bar: 250 μm .

follicular cells (Figure 2A), which, after fertilization, migrated toward the animal pole. The first four cleavages occurred within the first 4 days. The embryo at the 16 cell stage measured 275.9 μm in diameter.

On average, only 17 (± 8 ; $n = 39$ egg capsules) eggs per capsule underwent cleavage representing 6% of the total.

The remaining uncleaved eggs began to disintegrate by the third day (the nucleus showed no signs of division, Figure 2B). The disintegration starts after the migration of the follicular cells to the animal pole (Figure 2C). Besides the eggs and nurse eggs, free spermatozoa were observed inside the egg capsules. As the material used for

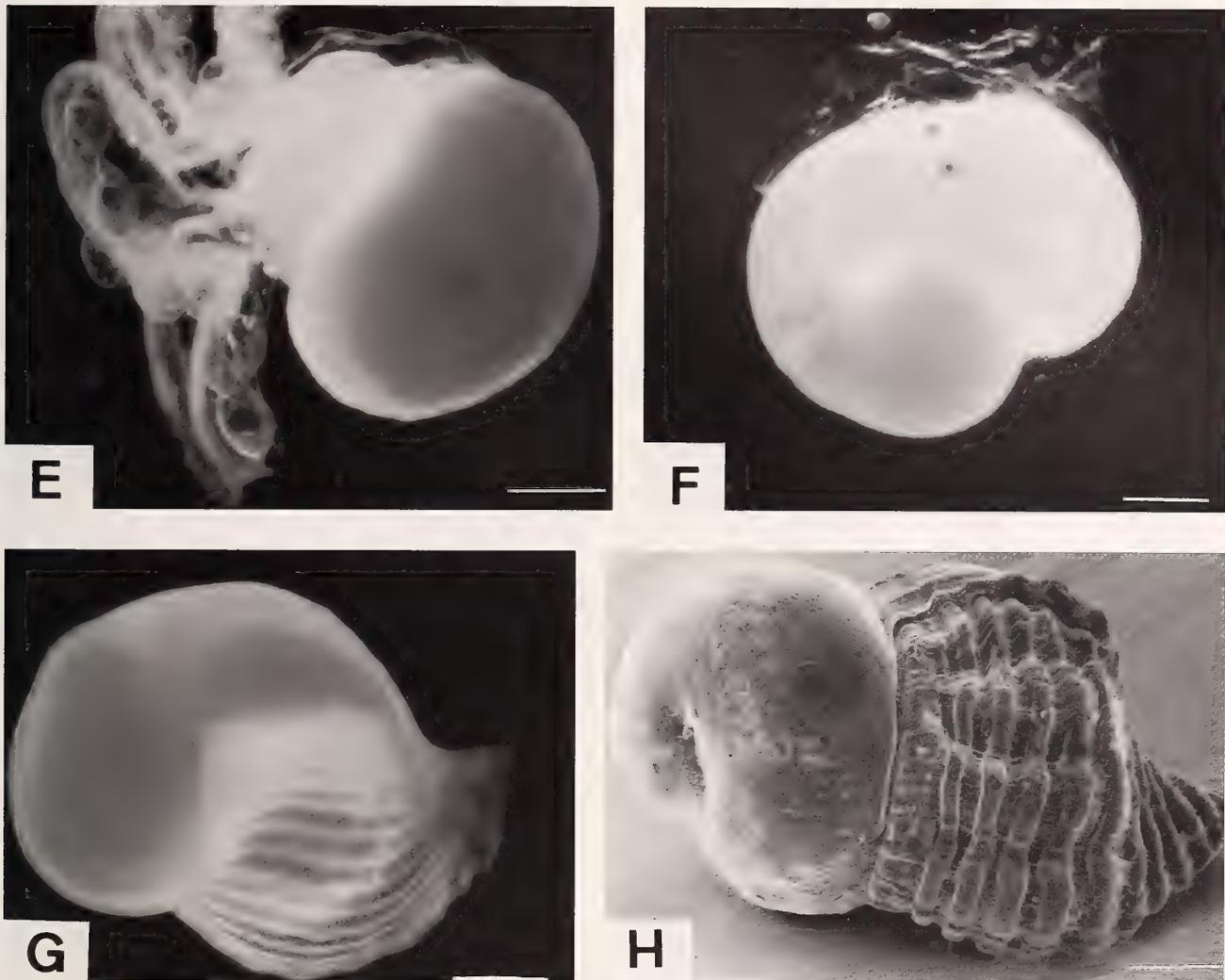


Figure 3

Continued.

fluorescent observations was preserved, we were unable to observe the motility of the spermatozoa.

By the second week, the embryos had acquired a saclike shape, the sac corresponding to the empty stomodaeum, and the whole embryo looked like a transparent balloon with a ciliated mouth (Figure 3A). The size of the embryos was highly variable (between 156 and 1092 μm in maximal length). At this stage, the embryos started to ingest the disintegrated nurse eggs, which entered the stomodaeum through the anterior buccal part propelled by the cilia. By the third week, the nurse egg material had been totally ingested; the stomodaeum was completely filled (Figure 3B), and a velum had started to develop (Figure 3C, D). By 3½ weeks, an intracapsular veliger stage was reached (Figure 3E), its shell measuring approximately 1.1 mm in length. The velum was well developed with two long, thin lobes, and this veliger could swim when excapsulated in seawater. At the fourth week, an intracapsular pedi-

veliger stage was reached, characterized by a crawling foot and a reduced velum (Figure 3F). The foot and the shell were light orange, the shell measuring 1.4 mm in length. Between the fifth and the sixth weeks, the velum of the pediveliger had resorbed almost completely; the shell was dark orange and measured around 1.4 mm in length (Figure 3G). Hatching as crawling juveniles occurred between the sixth and the seventh weeks (Figure 3H), the shell being dark orange with red ribs. In some hatchlings, velum remnants were observed. The size of the juvenile averaged 1.6 mm in shell length (Table 1).

DISCUSSION

Flores (1978) first observed the communal spawning behavior of *Fusinus closter* and described clusters deposited by up to nine females, each individual egg mass consisting of one layer.

Table 1
Developmental period of *Fusinus closter*.

Stage	Time (days)	Size of embryos (μm)	
		Mean \pm SD	Range (n)
Egg	0	259.6 \pm 18.9 234–273	(29)
4-8-16 cells	4	275.9 \pm 22.3 234–312	(40)
Embryo	10–14	531.8 \pm 216.5 156–1092	(22)
Intracapsular veliger	25	1075.9 \pm 110.8 898–1443	(58)
Intracapsular pediveliger	30	1369.4 \pm 141.9 780–1560	(79)
Prehatching	40	1432.7 \pm 113.0 1170–1560	(53)
Hatching	45–50	1607.1 \pm 128.1 1404–1872	(24)

As pointed out by Knudsen (1950), there are two different types of egg capsules in the family Fascioliidae: the plano-convex type and the vase-shaped type with expanded apical collars attached to each other by a common basal membrane. Examples of the plano-convex type are known for *Fusus syracusanus* (Fioroni & Portmann, 1968), *Fusus rostratus* Pelseneer 1911 (Lamy, 1928), "*Fusinus*" *rostratus* and "*Fusinus*" *syracusanus* (Von Manfred Diehl, 1970), and *Glaphyrina vulpicolor* Sowerby (Pilkington, 1974). Examples of the vase-shaped type are known for several *Fasciolaria* species (Lamy, 1928; Gohar & Eisawy, 1967; D'Asaro, 1970a, b; 1986; among others), for *Fusus gracillimus* Adams & Reeve (Knudsen, 1950), and for *Fusinus closter* (present work). An important difference between vase-shaped egg capsules is the location of the exit-plug for the hatchlings. In *Fasciolaria* species, the plug is always located on the apical plate (Gohar & Eisawy, 1967; D'Asaro, 1970a, b, 1986; Flores, 1978; Penchaszadeh & Paredes, in press). In *Fusinus* and *Fusus* species, this plug is located on the convex side (Lamy, 1928; Portmann, 1955; Amio, 1963; Fioroni, 1966; Fioroni & Portmann, 1968; Flores, 1978). With the exception of *Fusus gracillimus*, all studied *Fusus* species deposit plano-convex egg capsules. Even when the *Fusus* and *Fusinus* debate is nomenclatural, capsular morphology could perhaps be a biological contribution to the taxonomic status of the two genera. The importance of reproductive patterns as a contribution to classification has been noted by Penchaszadeh (1988) in several South American prosobranch species.

Only a small proportion of the eggs of *F. closter* complete their development to the hatching stage, the rest being nurse eggs. This is not an uncommon feature among species of *Fasciolaria* and *Fusus*. Previous studies conducted on *Fasciolaria tulipa*, *F. tulipa* var. *distans*, *F. salmo*, *F. liliun hunteria*, *F. audouini*, *F. tulipa hollisteri*, and *Fusus perplexus* indicate that approximately 90% of the eggs are nurse eggs (Glaser, 1905; Bacci, 1947; Hyman, 1923; Amio, 1963; D'Asaro, 1970a, b, 1986, and Penchaszadeh & Paredes, in press).

Two interesting observations result from fluorescence studies. The first was the presence of free spermatozoa inside the egg capsule, which suggests that fertilization could also take place inside the egg capsule. The second was the presence of follicular cells on both normal and nurse eggs of *Fusinus closter*. The gastropod oocyte is usually large (around 200 μm or more), within a chorion, and surrounded by follicular cells (Biggelaar & Guerrier, 1983). These cells are also said to be feeding cells as they transport and provide nourishment for the egg. Bivalve oocytes do not have follicular cells and are much smaller; see Biggelaar & Guerrier, 1983. Follicular cells surrounding the egg usually migrate to the animal pole after fertilization before the emission of the polar bodies and then detach from the egg. This was observed in both normal and nurse eggs, indicating that nurse eggs are probably also fertilized. The literature discussing the origin of the nurse eggs is based on hypotheses which are still to be proved. The first, proposed by Hyman (1935) for *Fasciolaria tulipa*, involved abnormal spermatozoa. The second, proposed by Staiger (1951) for *Buccinum undatum* Linnaeus, 1758, involved possible genetic factors in the egg. A third hypothesis, proposed by West (1979) for *Colus stimpsoni* Mörch, indicated that nurse eggs are not a result of fertilization by atypical sperm but rather the result of normally fertilized eggs which are defective or lack factors that trigger or control zygote cytokinesis. Hadfield (1989) suggested for the vermetid *Petalococonchus montereyensis* Dall, 1919, that the fate of individual eggs is determined in the egg capsule.

The mechanism by which the nurse eggs of *F. closter* are ingested is different from other species. Fioroni (1967) reported three different mechanisms of adelphophagy: (1) rotation of the nurse eggs by the embryos with the help of the velum, the foot, or the cephalic vesicle. Such rotation detaches peripheral yolk particles from the egg which enter the stomodaeum by ciliary action; (2) mechanical destruction of the nurse eggs by the embryo by means of the ciliated cells of the velum, and (3) direct swallowing of the whole nurse egg by the embryo (as in *Fasciolaria tulipa* and *F. tulipa hollisteri*). The disintegration of the nurse eggs of *Fusinus closter* prior to their ingestion by the embryos is not produced mechanically since the velum has not yet developed. This therefore represents a fourth mechanism of adelphophagy. Such a mechanism in which the nurse eggs disintegrate into small fragments that do not result from numerous abnormal cleavages (as proposed for the vermetid *Petalococonchus montereyensis* by Hadfield & Iaea, 1989) has been previously suggested by Penchasza-

deh (1976) in two species of the genus *Trophon* Montfort, 1810, and reported by Miloslavich & Penchaszadeh (1992) in the vermetid *Dendropoma corrodens* d'Orbigny, 1842. The present misunderstanding in the literature regarding the origin of the yolk particles found in the egg capsules could be clarified only if the initial uncleaved egg stage was observed, which is also very important as it gives trustworthy information on the actual egg diameter and if nurse eggs are used as extraembryonic food.

The velum of *Fusinus closter* develops after the nurse egg material has been totally ingested. The same sequence occurs in *Fasciolaria tulipa hollisteri* Weisbord, 1962, another fasciolarid that lives within the same geographic area and has an early, non-velar feeding stage (Penchaszadeh & Paredes, in press). In these two species, the velum does not have any role in the uptake of nurse eggs. However, in other species, the velum may have a significant function in feeding. Hadfield & Iaea (1989) examined in detail the velar lobes of the non-swimming intracapsular veliger of the vermetid *Petalocochnus montereyensis*, a species with direct development. These authors concluded that the velar lobes of *P. montereyensis* have been extensively modified and are used for feeding on the mass of nurse yolk derived from nurse eggs. Hunter & Vogel (1986) proposed that the velum in non-planktotrophic species could have a respiratory function.

In *Fusus syracusanus*, another source of extraembryonic nutrition has been reported by Fioroni (1966) and Fioroni & Portmann (1968). The embryos of this species, numbering seven to 12 per capsule, ingest the perivitelline fluid or intracapsular liquid in which they are embedded at a specialized ingesting preveliger stage. The intracapsular veliger is not only unable to swim but dies within 30 minutes when excapsulated in seawater (Fioroni, 1966). The evolution of prosobranchs seems to have started from forms that released the eggs directly into the sea to forms in which the eggs are contained in protective structures or egg capsules (Shuto, 1974). The fact that some species with direct development (intracapsular metamorphosis, as reviewed by Bouchet, 1989) still maintain in their embryology the intracapsular veliger stage leaves two possibilities. The first is the possibility of a facultative poecilogony, a phenomenon that, according to Bouchet, 1989, and Hoagland & Robertson, 1988, does not occur in gastropods. The second is the more likely possibility of facultative planktotrophy, given the feeding potential of some lecithotrophic larvae (Kempf & Todd, 1989).

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The Anatomy and Systematics of *Ceratoxancus*, a Genus of Deep-Water Ptychatractinae (Gastropoda: Turbinellidae) with Labral Spine

by

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Abstract. The anatomy of *Ceratoxancus* is characterized by a short or very short proboscis, the presence of an accessory salivary gland, the ventral odontophoral retractor passing through the nerve ring, and the position of the buccal mass at the proboscis base in contracted condition. These characters are shared by other representatives of the subfamily and confirm the classification of *Ceratoxancus* in the Ptychatractinae, until now based on shell and radula characters. *Ceratoxancus* Kuroda, 1952, comprises six species of which four are described as new from the New Caledonia region in deep water (530–830 m). *Ceratoxancus elongatus* Sakurai, 1958, is removed from the synonymy of *C. teramachii* Kuroda, 1952, and both species are recorded from the southwest Pacific. Species of *Ceratoxancus* with a long labral spine present numerous shell breakages, while toothless species have much fewer scars, and it is hypothesized that the tooth and outer lip are used in prey capture with accompanying shell breakage.

INTRODUCTION

The genus *Ceratoxancus* was introduced for the single species *C. teramachii* Kuroda, 1952, from deep water off Japan, and was tentatively assigned to the family Turbinellidae on the basis of its radula (Kuroda, 1952). A second species, *C. elongatus* Sakurai, 1958, was subsequently synonymized (Habe, 1964) with *C. teramachii*. Outside of Japan, *Ceratoxancus* has been reported in the literature only once, from Hawaii (Cernohorsky, 1977), and the genus is currently known from the shells of the two nominal species and the original description of the radula and operculum of *C. teramachii*.

In the present paper, we describe the anatomy of five species of *Ceratoxancus*, including the type species, and briefly discuss the taxonomic position of the genus. We review its species-level systematics, based on new material from the southwest Pacific, and describe four new species.

In forthcoming papers, we will describe the anatomy and revise the systematic contents of other genera of deep-water Turbinellidae, based on new, rich material from recent expeditions of the Muséum National d'Histoire Naturelle, Paris (MNHN). All material cited, unless otherwise stated, is stored in MNHN.

Abbreviations and text conventions: ag, anal gland; asg, accessory salivary gland; cme, cut mantle edge; ct, ctenidium; dd, dead collected specimen; dg, digestive gland; gL, gland of Leiblein; lv, live collected specimen; ml, mantle lobe; moe, glandular mid-esophagus; ne, nephridium; ng, nephridial gland; nr, nervous ring; od, odontophore; oe, esophagus; op, operculum; os, osphradium; p, penis; ped.n, pedal nerves; poe, posterior esophagus; pr, proboscis; prp, proboscis protractors; prs, rhynchodaeum (= proboscis sheath); s, siphon; sem.gr, open seminal groove; sem.p, seminal papilla; sg, salivary gland; st, stomach; t, head tentacle; tes, testiculus; vL, valve of Leiblein; vodr, ventral

odontophoral retractor; vpr, ventral proboscis retractor.

Repositories: AMNH, American Museum of Natural History, New York; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand, Wellington.

ANATOMY

The anatomy of the five species dissected is very similar. Therefore, it is described in full for the type-species *Ceratoxancus teramachii* and for *C. basileus* sp. nov., which is conchologically less similar to its congeners. Only major differences are mentioned for the other two species. Upon collection, material of *Ceratoxancus elongatus*, *C. niveus* sp. nov., and *C. basileus* sp. nov. had been dumped into alcohol, while material of *C. teramachii* and *C. melichrous* sp. nov. had been preserved in buffered formalin.

Ceratoxancus teramachii

The largest specimen (New Caledonia, MUSORSTOM 5, sta. DW337) was dissected. It has a shell length of 31.5 mm, last teleoconch whorl length 21.5 mm, aperture length 14.0 mm, siphonal canal length 3.6 mm, shell diameter 12.6 mm. A specimen sectioned (MUSORSTOM 5, sta. DW338) has a shell length of 14.9 mm, last teleoconch whorl length 10.9 mm, aperture length 6.6 mm, shell diameter 7.4 mm.

External anatomy (Figure 1A, B): The body consists of 3.75 whorls; the mantle spans one whorl, the nephridium 0.3 whorl, and the digestive gland 1.25 whorl. The body is pale yellowish. The operculum is medium-sized, occupying at least 0.4× aperture length (lower part of the operculum with nucleus damaged), elongate leaf-shaped and recurved, thin, transparent, and yellow (Figure 1C). The columellar muscle is attached in the upper third of the operculum. The foot is short ($L/W \approx 1.5$). The siphon is short, simple, pale greyish. The columellar muscle is very thick with three deep grooves corresponding to the columellar teeth. The mantle is thin, the mantle organs clearly visible through it. Near the siphon, the mantle has a rounded lobe with a longitudinal groove in the middle. This lobe forms the labral spine. The head is broad with short, stout tentacles and large eyes. The border between mantle cavity and the nephridium is represented by a deep cleft.

Mantle: The ctenidium is very long and occupies 0.75× mantle length, narrow ($L/W \approx 7.5$), with high hanging

leaflets. The osphradium is large, 0.75× as long and 1.5× as wide as the ctenidium, asymmetrical with the right side nearly twice as broad as the left. The hypobranchial gland is covered with a thick mucus layer and is not transversely pleated. The anal gland is seen through the mantle as a narrow dark strip.

Digestive system: The organs of the body haemocoel are compact (Figure 1D). The proboscis in the contracted state is very short (about 2 mm), smooth, and occupies only about half of the rhynchodeal cavity. The rhynchodaeum (= proboscis sheath) is thick-walled and lined with a tall epithelium. The very powerful paired muscles, probably functioning as ventral proboscis retractors, are attached latero-ventrally to the anteriormost part of the rhynchodaeum and to the bottom of the body haemocoel. This probably indicates that the whole rhynchodaeum takes part in proboscis evertion, and when the proboscis is completely everted, these retractors are attached to the inner wall of the proboscis. Apart from the major retractors, there are a few smaller retractors attached to the rhynchodaeum laterally, and posteriorly to the anterior ventral retractor.

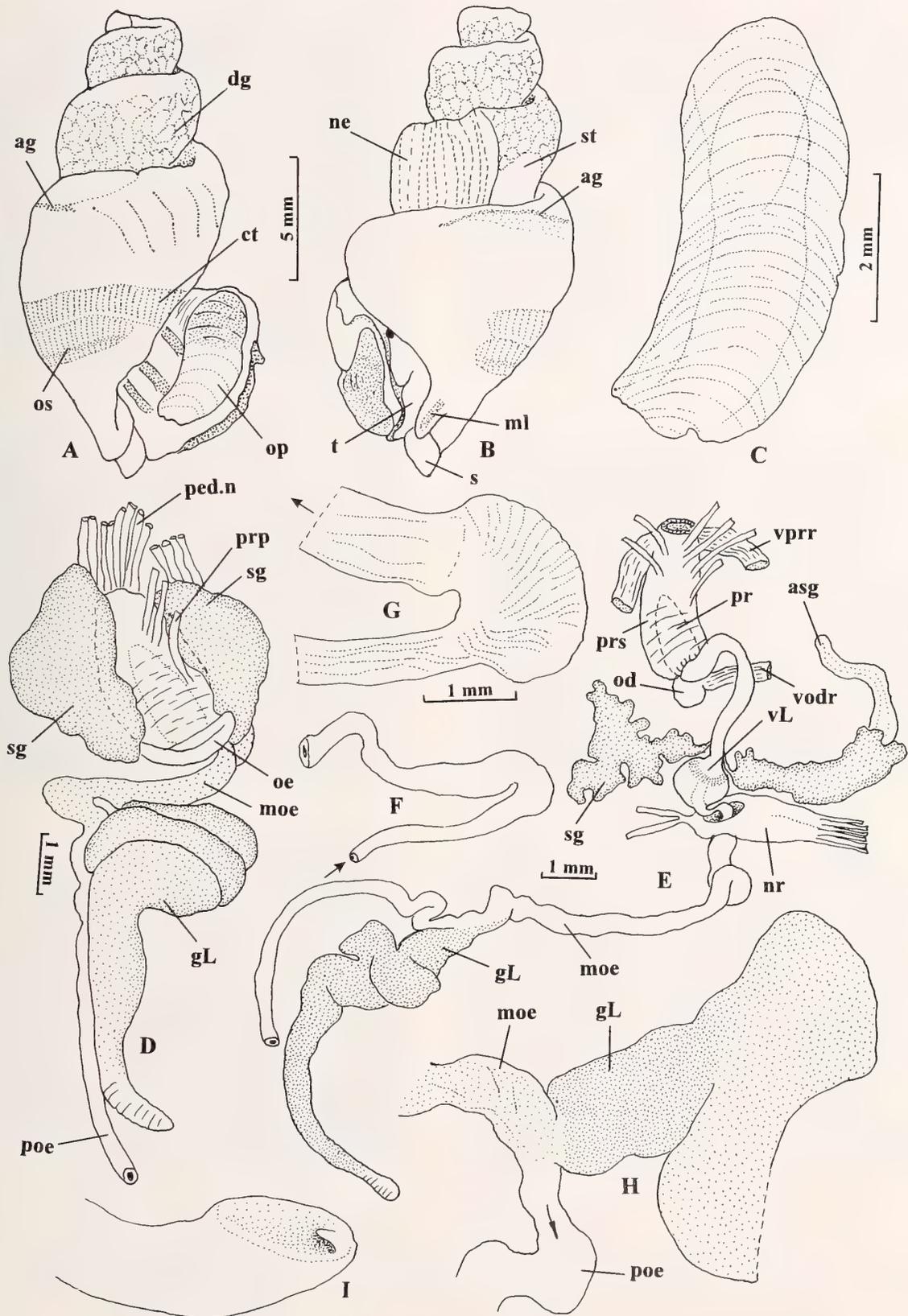
The buccal cavity is lined with a thick cuticular layer. The buccal mass is long and muscular, and projects beyond the rear of the retracted proboscis. In longitudinal sections the radular diverticulum is seen to open into the buccal cavity at the proboscis base in its contracted state. The odontophoral subradular cartilages are paired, not fused anteriorly. The large, paired ventral odontophoral retractors pass through the nerve ring, follow the bottom of the cephalic haemocoel, and join the columellar muscle.

The radula (Figure 2A–D) is about 3.8 mm long (12% of shell length and 27% of aperture length) and about 165 μm broad (0.52% of shell height and 1.17% of aperture length); it projects beyond the rear of the proboscis, and consists of about 180 transverse rows. The rachidian teeth are very closely spaced (Figure 2B), thus preventing the examination of the shape of the basal part. They bear three sharp cusps, emanating from the posterior edge of the basal part. The central cusp is nearly twice as long as the lateral ones. The lateral teeth are unicuspid, with a long, narrow base (Figure 2C). The length of the lateral tooth base equals 0.66× the rachidian width.

After leaving the proboscis, the esophagus forms a short loop before opening into the valve of Leiblein (Figure 1E). Between the valve and the opening of the gland of Leiblein, the esophagus is rather widened and apparently glandular. This part, representing the mid-esophagus, is long and

Figure 1

Anatomy of *Ceratoxancus teramachii*. A–H, female (MUSORSTOM 5, sta. DW337, shell height 31.5 mm). I, male (MUSORSTOM 5, sta. DW338, shell height 14.9 mm). A, B, body, removed from the shell; C, operculum; D, organs of the body haemocoel in natural position; E, organs of the body haemocoel, expanded; F, outer view of the stomach in the same scale as E; G, outer view of the stomach; H, opening of the gland of Leiblein into mid-esophagus, from the ventral side; I, tip of the penis.



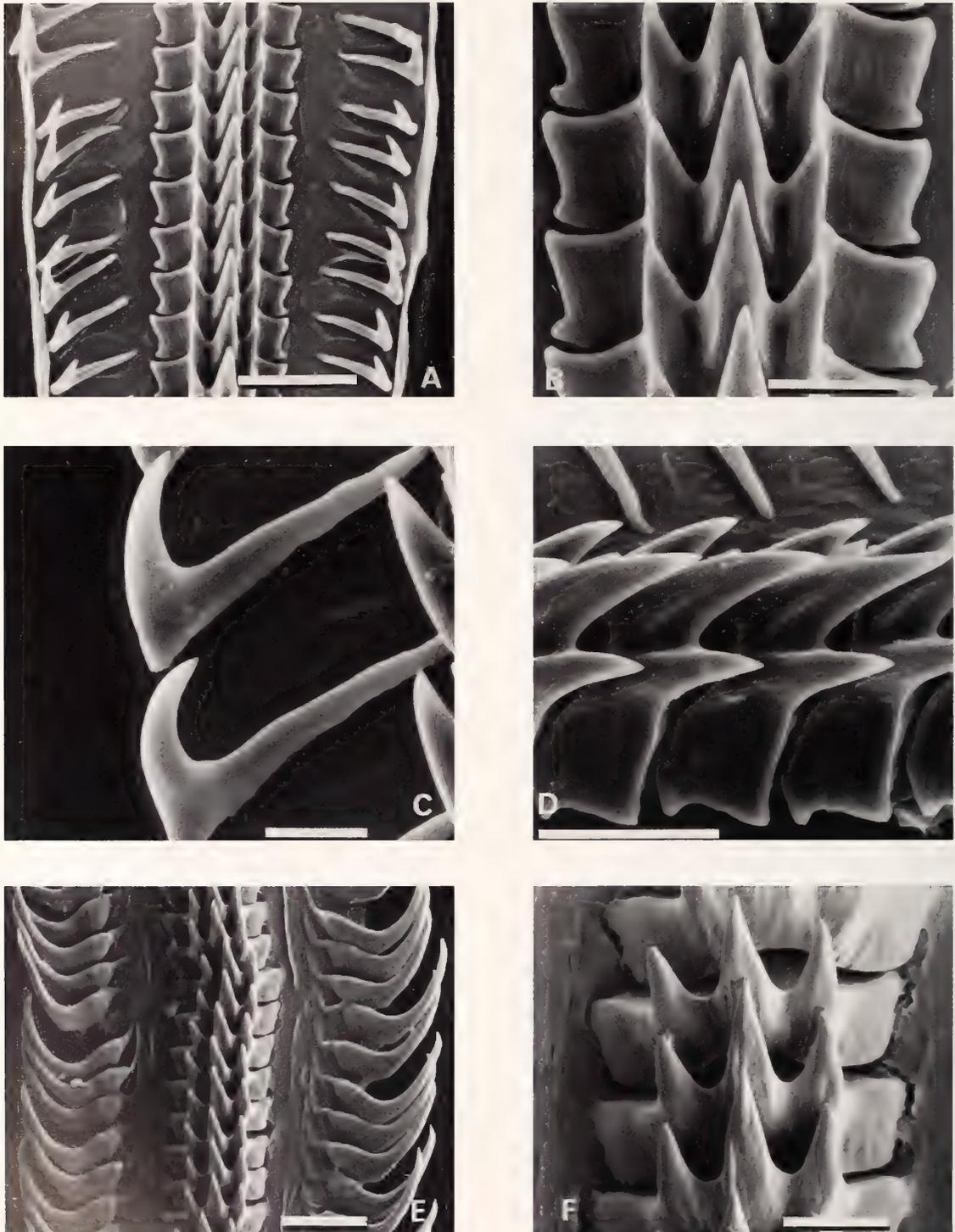


Figure 2

Radulae of *Ceratoxancus* spp. *Ceratoxancus teramachii* (A-D) (MUSORSTOM 5, sta. DW337): A, dorsal view of the radular ribbon; B, enlarged rachidian teeth; C, enlarged lateral teeth; D, lateral view of rachidian teeth. *Ceratoxancus melichrous* Kantor & Bouchet, sp. nov. (E, F) (BATHUS 3, sta. DW 776): E, dorsal view of the radular ribbon; F, enlarged rachidian teeth. Scale bars 50 μm (A, E); 20 μm (B, D, E); 10 μm (C).

convoluted. When the organs of the haemocoel are stretched by dissection, the glands lie on both sides of the valve of Leiblein, which is well defined, much broader than the esophagus, and pyriform, with a conical ciliary valve. The posterior esophagus runs along the left side of the gland of Leiblein and opens into the stomach.

The stomach is very small by comparison to the anterior foregut, and broadly U-shaped. The fixation of the specimen does not permit examination of the inner anatomy of the stomach. Judging from the outer view (Figure 1G), the stomach has a small caecum and seemingly a single duct of the digestive gland, situated near the esophagus opening. Typhlosoles of even size can be seen through the stomach wall. The gland of Leiblein is large, greenish-gray in fixed specimen, tubular, coiled anteriorly and simple posteriorly. In the posterior part, the transverse folds are seen through the gland wall. The gland opens into the esophagus through a duct without defined constriction (Figure 1H).

The salivary glands are paired, approximately equal-sized, rather large and loose, situated on both sides of rhynchodaeum, partially covering it dorsally and laterally. When the organs of the haemocoel are extended, the glands lie at both sides of the valve of Leiblein. Immediately after leaving the glands, the salivary ducts enter the walls of the esophagus in front of the valve of Leiblein. There is a single, long, tubular accessory salivary gland, partially embedded in the right primary salivary gland. Gland histology is typical for neogastropods, consisting of a thick outer epithelial layer and thin inner ones, delimited with a layer of circular muscle fibers.

The highly concentrated circumesophageal nerve ring is situated in the position typical for Muricoidea, just posterior to the valve of Leiblein.

Male reproductive system: The sectioned specimen was a mature male. The penis is long, occupying nearly the whole length of mantle cavity, narrow, with a deeply concave anterior surface and small conical papillae (Figure 1I). It is possible that the concavity is an artifact due to fixation. The seminal duct is open while running on the floor of mantle cavity toward the penis base, and deeply embedded and nearly closed in the penis body. A very narrow slit follows along the inner side of the penis and connects the duct with the exterior.

Ceratoxancus elongatus

The dissected specimen (New Caledonia, MUSOR-STOM 4, sta. CP199) has a shell length of 23.7 mm, last teleoconch whorl length 15.4 mm, aperture length 8.2 mm, siphonal canal length 2.5 mm, shell diameter 8.8 mm. The operculum is vestigial (checked in two specimens) (Figure 4C), oval, and about 1 mm in length (i.e., less than 12% of aperture length). The foot is attached on nearly the whole surface of the operculum. The mantle edge is slightly

scalloped but lacks a pronounced lobe corresponding to the labral spine.

The odontophore with radula lies completely outside the retracted proboscis. The radula (Figure 3C, D) is about 2.3 mm long (9.7% of shell length and 28% of aperture length) and about 130 μm broad (0.54% of shell height and 1.58% of aperture length), consisting of about 145 transverse rows. The rachidian basal parts have a shallowly arched anterior edge and a semi-rounded posterior edge, which is overlapped by the following tooth (Figure 3D), each bearing three nearly equal-sized short, blunt cusps, emanating from close to the anterior edge of the basal part. Lateral teeth are unicuspid, relatively much smaller than in *C. teramachii* and with a shorter base. The length of the lateral tooth base is $0.38\times$ the width of the rachidian.

The gland of Leiblein is a little smaller than in *C. teramachii*.

The dissected specimen was a mature male. The long penis lacks a defined papilla.

Ceratoxancus melichrous sp. nov.

The dissected specimen (Norfolk Ridge, BATHUS 3, sta. DW 776) has a shell length of 18.6 mm, last teleoconch whorl length 12.4 mm, aperture length 6.5 mm, shell diameter 6.8 mm.

External anatomy: The upper body was torn off during extraction from the shell. The remaining part is pale yellowish and consists of two whorls (Figure 4A, B), the mantle spanning one whorl, the nephridium 0.3 whorl. The operculum is rather large, thin, transparent and yellow, elongate leaf-shaped and slightly recurved, occupying $0.5\times$ aperture length. The columellar muscle is attached in the upper third of the operculum. The siphon is short, simple, and pale greyish. The columellar muscle is very thick with two deep grooves corresponding to the columellar teeth. The mantle edge is even, without lobe. The mantle is thin, and the ctenidium and osphradium are clearly visible through it. The head is broad with short stout tentacles and large eyes.

The salivary glands are completely fused, situated on the left side of the proboscis sac, and totally envelop the valve of Leiblein. The salivary ducts are paired. The mid-esophagus is at least twice as short as in *C. teramachii*. The gland of Leiblein has less pronounced tubular form than in *C. teramachii* and is not coiled in the anterior part. The accessory salivary gland was not found in the specimen dissected, although it may have been present and embedded in the primary salivary gland. The odontophore is contained within the retracted proboscis, but the radula sac is slightly protruding beyond its rear end.

The radula (Figure 2E, F) is about 2.4 mm in length (12.9% of shell length and 36.9% of aperture length) and

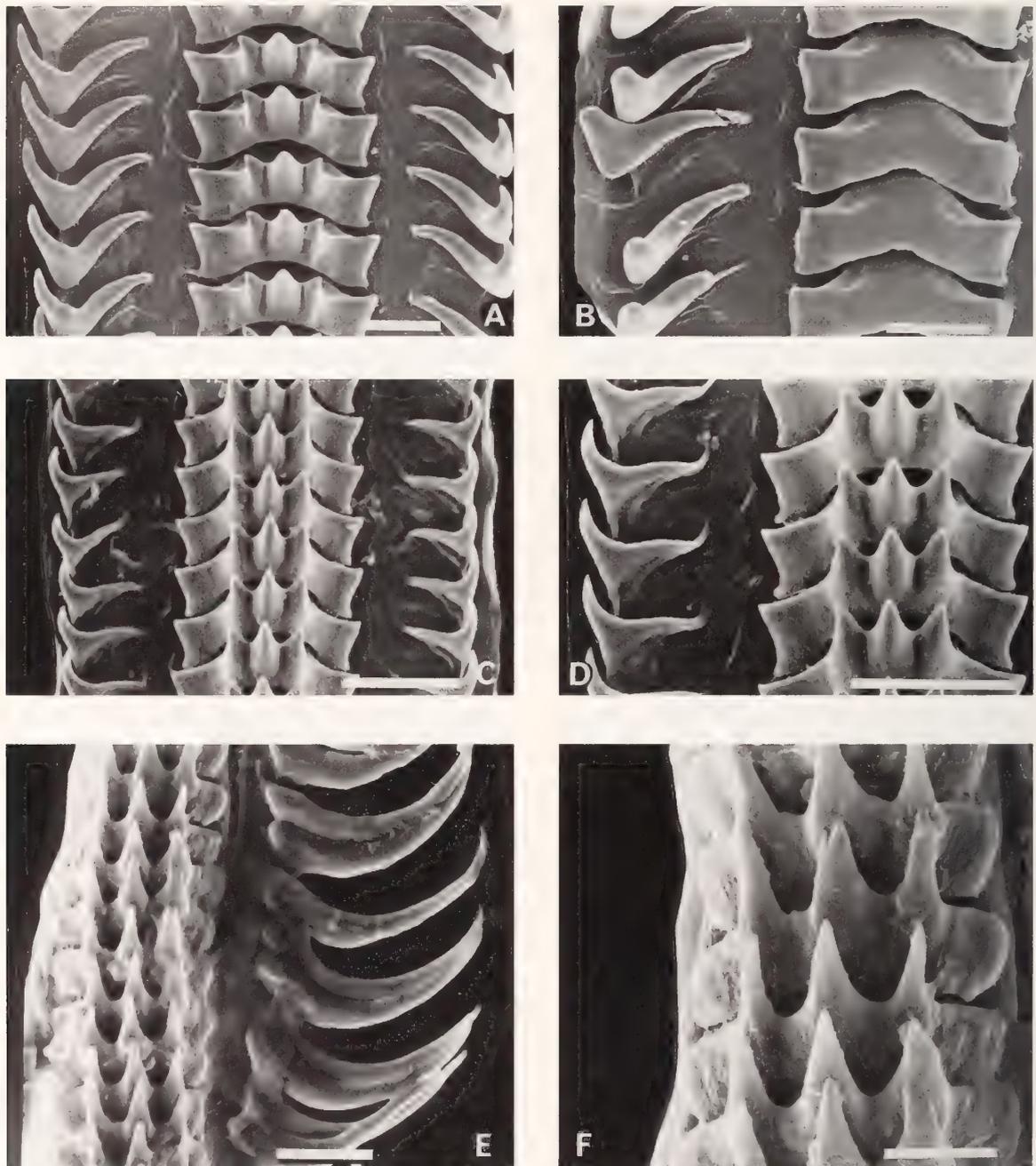


Figure 3

Radulae of *Ceratoxancus* spp. *Ceratoxancus basileus* Kantor & Bouchet, sp. nov. (A–B) (BIOCAL sta. DW33): A, dorsal view of the radular ribbon; B, enlarged posteriormost part of the ribbon, showing the worn rachidian and lateral teeth. *Ceratoxancus elongatus* (C–D) (MUSORSTOM 4, sta. CP199): C, dorsal view of the radular ribbon; D, enlarged rachidian and lateral teeth. *Ceratoxancus niveus* Kantor & Bouchet, sp. nov. (E, F) (BIOCAL, sta. DW 51): E, dorsal view of the half of radular ribbon; F, enlarged rachidian teeth. Scale bars 50 μm (A, B, C, D); 20 μm (E); 10 μm (F).

about 186 μm broad (1.0% of shell height and 2.86% of aperture length), consisting of about 130 transverse rows, and is relatively wider than in the other species. The rachidians (Figure 2F) have a shallowly arched anterior edge

of the basal part, three sharp, rather long cusps, emanating from the posterior edge, the central cusp the longest. Lateral teeth are unicuspid, long, with a short base. Length of the lateral tooth base is $0.47 \times$ the width of the rachidian.

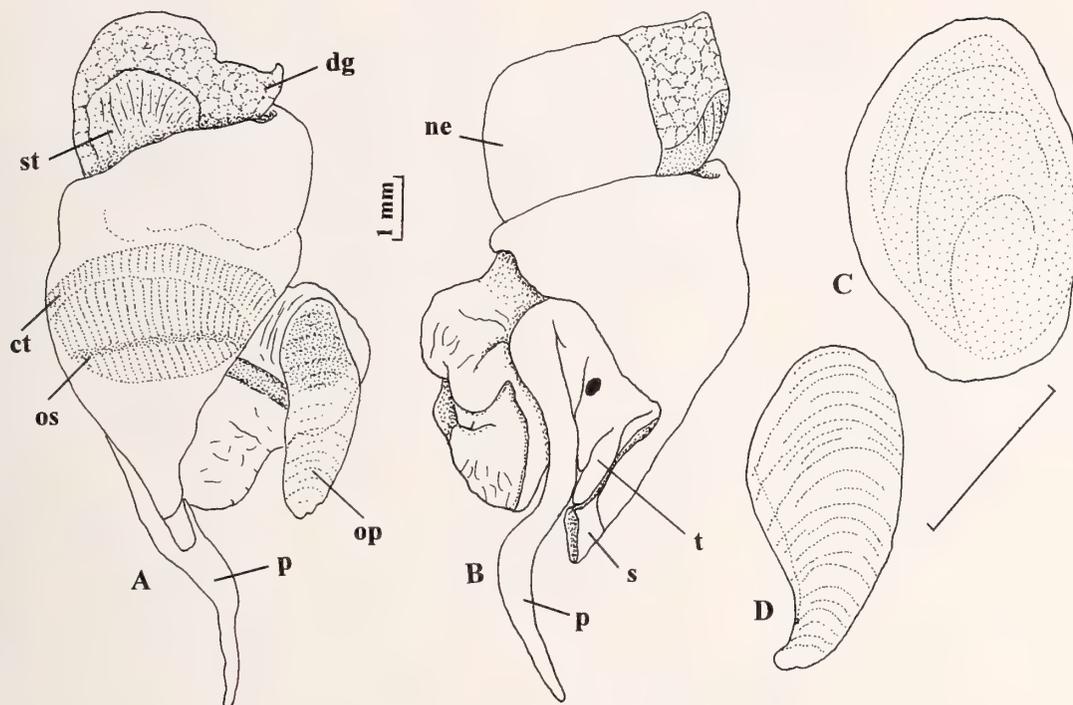


Figure 4

A–B, *Ceratoxancus melichrous* Kantor & Bouchet, sp. nov. (BATHUS 3, sta. DW 776, shell height 18.6 mm): body, removed from the shell; C, operculum of *C. elongatus* (MUSORSTOM 4, sta. CP199, shell length of 23.7 mm); D, operculum of *C. niveus* Kantor & Bouchet, sp. nov. (BIOCAL, sta. DW 51, shell height 9.35 mm). Scale bars 0.5 mm (C), 1 mm (D).

Male reproductive system: The penis is long, protruding anteriorly in the studied specimen, rather narrow, tapering anteriorly, and without a pronounced papilla.

Ceratoxancus niveus sp. nov.

The specimen with dried body (Norfolk Ridge, BIOCAL, sta. DW 51) has a shell length of 9.35 mm, last teleoconch whorl length 6.2 mm, aperture length 3.9 mm, shell diameter 3.5 mm. The body was softened in potassium bicarbonate and extracted from the shell.

The operculum is medium-sized, leaf-shaped, with the nucleus turned to the left (Figure 4D), and occupies $0.45 \times$ the aperture length. The large eyes are situated at the base of long and narrow cephalic tentacles. The specimen is an adult male, the penis is long and flattened, apparently with an open seminal groove, and lacking a pronounced seminal papilla. The proboscis (protruding through the mouth opening) is medium-long, thick at the tip, narrowing toward the mouth opening. The odontophore with radula is situated at the proboscis tip.

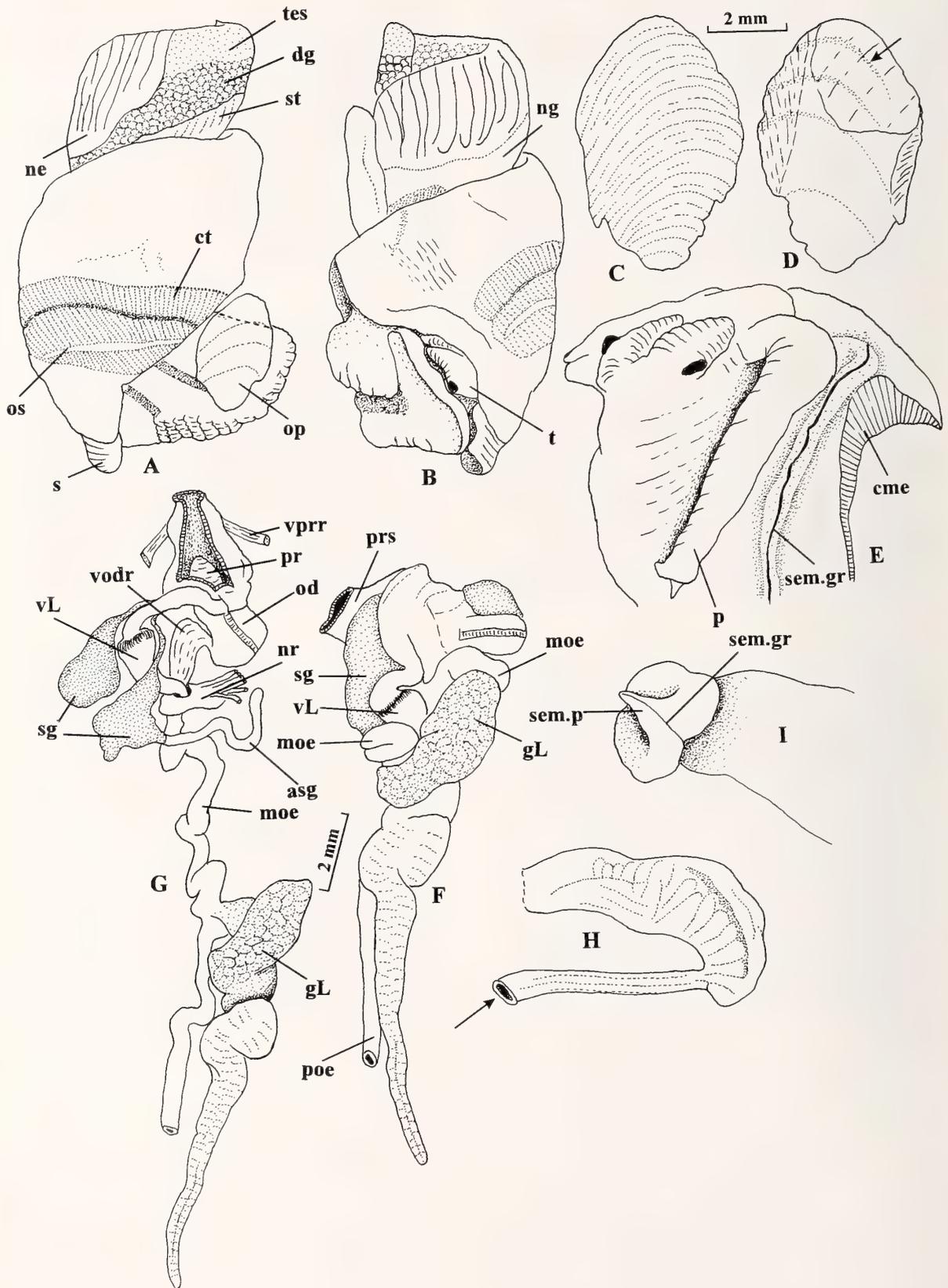
The radula (Figure 3E, F) is narrow, width about $69 \mu\text{m}$ (0.73% of shell height and 1.76% of aperture length). The rachidian (Figure 3F) basal part has a nearly straight anterior edge and three equal, widely spaced, sharp, and rather long cusps, emanating from the posterior edge. The

lateral teeth are unicuspid and long, with a very short base, length of the base $0.27 \times$ the width of the rachidian.

Ceratoxancus basileus sp. nov.

The dissected specimen (New Caledonia, BIOCAL, sta. DW33) is 48.1 mm high, diameter 17.5 mm, last whorl height 31.5 mm, aperture height 16.8 mm.

External anatomy (Figure 5A, B): The upper body whorls were torn off during extraction from the shell. The remaining part is pale yellowish and consists of 2.25 whorls, the mantle spanning 1.2 whorls, the nephridium 0.4 whorl. The operculum is medium-sized, occupying $0.37 \times$ aperture length (lower part of the operculum with nucleus damaged), oval, thin, semi-transparent, and yellow-brown (Figure 5C, D). The columellar muscle is attached to the upper third of the operculum. The foot is rather long ($L/W \approx 2.3$). The siphon is rather short and simple. The columellar muscle is thick with two deep grooves, corresponding to columellar plaits. The mantle has a thickened edge, but is thin posteriorly, and the mantle organs are clearly visible through it. Due to the high retraction of the animal inside the shell, the mantle partially covers the head. The head is narrow with short stout tentacles and large eyes. The border between the mantle cavity and the nephridium



is represented by a deep cleft. The nephridium consists of 13 vertical lamellae, which are visible through its wall.

Mantle: The ctenidium is very long and occupies $0.9 \times$ mantle length, narrow ($L/W \approx 9.5$), with high hanging leaflets. The osphradium is large, $0.5 \times$ as long and $2 \times$ as wide as the ctenidium, asymmetrical, with the right side $1.5 \times$ broader than the left. The hypobranchial gland is covered with a thick mucus layer and is transversely pleated. The anal gland is absent.

Digestive system: The organs of the body haemocoel are compact (Figure 5F). The proboscis in the contracted state is extremely short (less than 1 mm), smooth, and occupies only about $\frac{1}{4}$ of the rhynchodaeum cavity. The rhynchodaeum (= proboscis sheath) is thick-walled and lined with tall epithelium.

The paired, rather thin muscles, functioning as ventral proboscis retractors, are attached latero-ventrally to the anteriormost part of the rhynchodaeum and to the bottom of the body haemocoel. This probably indicates that all the rhynchodaeum takes part in the proboscis eversion, and in the completely everted position of the proboscis, these retractors are attached to the inner wall of proboscis.

The buccal mass is very large and muscular, situated beyond the base of the retracted proboscis. The radular diverticulum opens into the buccal cavity at the proboscis base in its contracted state. The odontophoral subradular cartilages are paired, not fused anteriorly, but connected with transverse muscle. They are $1.5 \times$ shorter than the radular sac. The large ventral odontophoral retractor passes through the nerve ring, follows the bottom of the cephalic haemocoel, and joins the columellar muscle.

The radula (Figure 3A, B) is about 5.5 mm in length (11% of shell length and 33% of aperture length) and about $430 \mu\text{m}$ broad (0.89% of shell height and 2.55% of aperture length), and consists of about 140 transverse rows. The rachidian teeth have a shallowly arched anterior edge on the basal part, and a semi-rounded posterior edge, slightly overlapped by the following tooth (this is more clearly seen on the most distal part of the radula where the cusps are worn off, Figure 3B), with a short, blunt, and thick median cusp and two much thinner lateral cusps emanating close to the anterior edge of the basal part. Lateral teeth are unicuspid, with a long narrow base, length of tooth base $0.65 \times$ the width of the rachidian base.

After leaving the proboscis, the esophagus soon opens into the valve of Leiblein (Figure 5G). Between the valve and the opening of the gland of Leiblein, the esophagus is significantly widened and glandular. This part, representing the mid-esophagus, is very long and convoluted. When the organs of the haemocoel are stretched by dissection, the glands lie on both sides of the valve of Leiblein, which is well defined, much broader than the esophagus, and pyriform, with a conical ciliary valve. The non-glandular posterior esophagus is rather thin, runs along the left side of the gland of Leiblein, and opens into the stomach.

The thin-walled, broadly U-shaped stomach is rather large by comparison to the anterior foregut. The fixation of the specimen does not permit an examination of its inner anatomy. Judging from the external view (Figure 5H), the stomach has a very small caecum and a single duct of the digestive gland, situated near the esophageal opening. The gland of Leiblein is large, pale greenish anteriorly, thin-walled, tubular, coiled anteriorly and simple posteriorly; it opens into the esophagus through a duct without distinct constriction. Acini are clearly seen through the gland.

The salivary glands are paired, approximately equal-sized, medium-sized, surrounding the rhynchodaeum and the buccal mass. When the organs of the haemocoel are extended, the glands lie on both sides of the valve of Leiblein. They narrow toward the short ducts, which enter the walls of the esophagus in front of the valve of Leiblein. There is a single long, tubular accessory salivary gland, partially embedded in the right primary salivary gland.

The highly concentrated circumesophageal nerve ring is situated in the position typical for Muricoidea, just posterior to the valve of Leiblein.

Male reproductive system: The penis is moderately short, occupying less than half the length of the mantle cavity, narrow, and very flattened, with a flattened anterior surface and distinct conical papilla. The seminal duct opens while running on the floor of the mantle cavity toward the penis base (Figure 5E), and is deeply embedded in the penis body. A very narrow slit follows for a short distance along the inner side of the penis and probably connects the duct with the exterior. For most of the penis length, the duct seems to be closed and becomes open again at the base of the papilla (Figure 5I).

Figure 5

Ceratoxancus basileus Kantor & Bouchet, sp. nov. (BIOCAL, sta. DW33, shell height 48.1 mm). A, B, body, removed from the shell; C, D, operculum (C, from outer side, D, from inner side, an arrow indicates the place of attachment of the columellar muscle); E, anterior part of the body, mantle removed to show the penis; F, organs of the body haemocoel in natural position; G, organs of the body haemocoel, expanded. Proboscis sac opened to show the proboscis; H, outer view of the stomach, same scale as F, G; I, tip of the penis.

SYSTEMATICS

Genus *Ceratoxancus* Kuroda, 1952

Type species: (by monotypy) *Ceratoxancus teramachii* Kuroda, 1952.

Ceratoxancus teramachii Kuroda, 1952

(Figures 1, 2A–D, 6A–J, 8C, D)

Ceratoxancus teramachii Kuroda, 1952:70–71 (30–31), figs. 1–4.

Ceratoxancus teramachii: Sakurai, 1958: figs. 3, 4; Cernohorsky, 1973:131, fig. 16; Cernohorsky, 1977:28, fig. 2; Higo & Goto, 1993:274.

NOT *Ceratoxancus teramachii*: Shikama & Horikoshi, 1963: 95, pl. 76, fig. 4; Habe, 1964:104, pl. 33, fig. 21.

Type material: Holotype in Toba Aquarium (not seen); 1 paratype AMNH 169039.

Type locality: Off Kii Peninsula, Japan.

Material examined: JAPAN. Off Tosa, 365 m, 1 lv, paratype (AMNH 169039). Off Tosa, 275 m, 1 lv (AMNH 169026).

CORAL SEA. MUSORSTOM 5: R/V *Coriolis*. CHESTERFIELD PLATEAU. Sta. DW337, 19°54'S, 158°38'E, 412–430 m, 1 lv adult (dissected). Sta. DW338, 19°52'S, 158°40'E, 540–580 m, 1 lv subadult (sectioned). Sta. DC378, 19°54'S, 158°38'E, 355 m, 1 lv. Sta. DC379, 19°53'S, 158°40'E, 370–400 m, 1 lv. Sta. CP389, 20°45'S, 160°54'E, 500 m, 1 lv subadult. ARGO BANK. Sta. DW300, 22°48'S, 159°24'E, 450 m, 1 lv subadult. Sta. DW306, 22°08'S, 159°21'E, 375–415 m, 1 dd.

NEW CALEDONIA. BIOCAL: R/V *Jean-Charcot*, sta. DW66, 24°55'S, 168°22'E, 505–515 m, 1 dd. BIOGEOCAL: R/V *Coriolis*, sta. DW253, 21°32'S, 166°29'E, 310–315 m, 1 dd. SMIB 3: R/V *Vauban*, sta. DW1, 24°56'S, 168°22'E, 520 m, 1 lv, 4 dd. Sta. DW2, 24°53'S, 168°22'E, 530–537 m, 1 dd. Sta. DW5, 24°55'S, 168°22'E, 502–512 m, 1 lv, 1 dd. Sta. DW6, 24°56'S, 168°21'E, 505 m, 1 lv. Sta. DW7, 24°55'S, 168°21'E, 505 m, 1 dd. BERYX 11: R/V *Alis*, sta. DW10, 24°53'S, 168°21'E, 565–600 m, 1 dd. Sta. DW40, 23°41'S, 168°01'E, 240–300 m, 1 dd. SMIB 8: R/V *Alis*, sta. DW146–147, 24°55'S, 168°22'E, 508–532 m, 1 lv, 2 dd. Sta. DW149, 24°55'S, 168°22'E, 508–510 m, 2 dd. Sta. DW150, 24°54'S, 168°22'E, 519–530 m, 1 lv, 1 dd. Sta. DW152, 24°54'S, 168°22'E, 514–530 m, 1 lv, 2 dd. Sta. DW169, 23°37'S, 167°42'E, 447–

450 m, 1 lv. BATHUS 3: R/V *Alis*, sta. DW817, 23°42'S, 168°16'E, 405–410 m, 1 dd. BATHUS 4: R/V *Alis*, sta. DW918, 18°49'S, 163°16'E, 613–647 m, 1 dd.

LOYALTY RIDGE. MUSORSTOM 6: R/V *Alis*, sta. DW471, 21°08'S, 167°54'E, 460 m, 1 dd. Sta. DW478, 21°09'S, 167°54'E, 400 m, 1 dd.

VANUATU. MUSORSTOM 8: R/V *Alis*, sta. DW977, 19°25'S, 169°29'E, 410–505 m, 1 dd.

Distribution: Off Kii and Tosa, Japan, in ca. 275–365 m, Hawaii, in 340–375 m; new records from the Coral Sea, New Caledonia, Loyalty Islands, and Vanuatu, alive in 355–540 m.

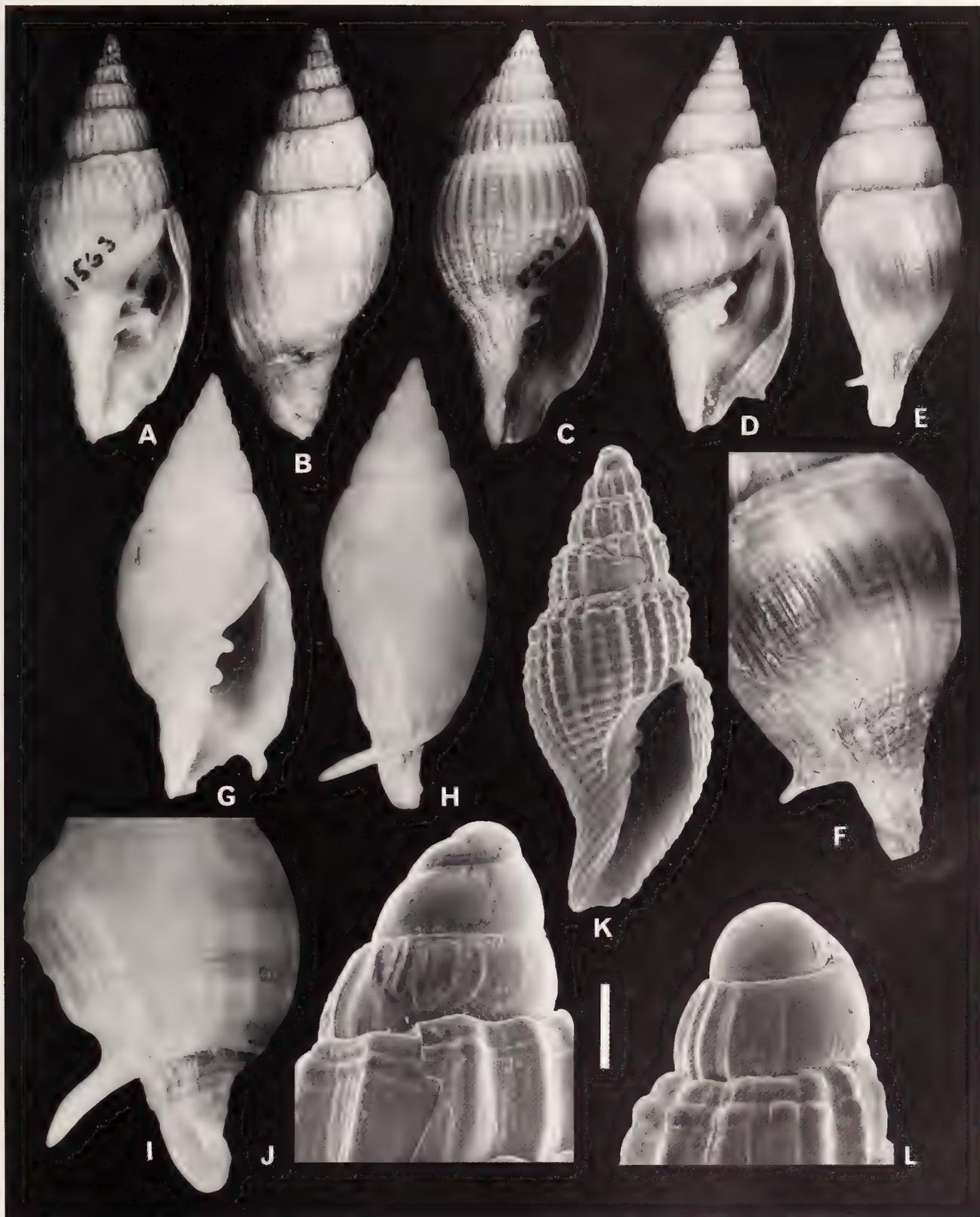
Description: (based on material from New Caledonia and the Chesterfield Plateau) Shell ovoid, fusiform, solid, consisting of 2.5 protoconch and up to 7.5 moderately convex teleoconch whorls. Protoconch I smooth, with large nucleus, diameter 375 μ m; protoconch II consisting of two whorls, first whorl smooth, second whorl with an adapical row of granules, a basal keel that is just covered by the successive whorl, and six strong opisthocyrt axial ribs before the protoconch/teleoconch boundary. Early teleoconch whorls flat-sided, later whorls moderately convex, with moderately to deeply channeled suture. Sculpture consisting of strong orthocone ribs crossed by weaker spiral grooves, and much finer incremental lines, 11–14 very distinct and strong ribs per whorl on first three whorls, more numerous but gradually fading on subsequent whorls. Last adult whorl with low, broad, and indistinct axial varices. Spiral sculpture not sharply defined, apart from one or two stronger grooves at shoulder, and ca. 12 well-defined cords on base of last adult whorl. Incremental scars of labral spine forming deep sulcus with raised edges on base of last whorl. Aperture ovoid, elongate, comprising ca. 46–51% of total shell height. Outer lip thin, straight, with strongly projecting labral spine. Siphonal canal broad, very short. Inner lip with very thin, glossy callus. Columella with three plaits, adapical one strongest.

Specimens from New Caledonia have a yellowish-tan background color and three brown spiral bands with indistinct margins: a narrow adapical one, a broader one at periphery, and one encircling the labral sulcus. Specimens from the Coral Sea are uniformly grayish beige without spiral bands. Protoconch pale yellowish. Periostracum thin, light yellowish gray.

Dimensions of largest adult: shell length 31.5 mm, last teleoconch whorl length 21.5 mm, aperture length 14.0

Figure 6

Ceratoxancus teramachii (A–J). A, B, paratype, 30 mm (AMNH 169039); C, Japan, off Tosa, 275 m (AMNH 169026), 30 mm; D–F, New Caledonia (SMIB3, sta. DW5), 30.0 mm, F, labral spine; G–I, Coral Sea (MUSORSTOM5, sta. 379), 28.7 mm, I, labral spine; J, protoconch (MUSORSTOM5 sta. 306). *Ceratoxancus niveus* (K, L), K, holotype, 8.8 mm; L, protoconch of paratype (BIOCAL, sta. DW51). Scale bar (protoconchs) 500 μ m.



mm, siphonal canal length 3.6 mm, shell diameter 12.6 mm.

Remarks: Our specimens from the southwest Pacific match the original description and material from Japan (illustrated by Sakurai, 1958: figs. 3, 4, and material in AMNH). In Japan, however, the axial sculpture may persist onto the last adult whorl; such sculptured specimens superficially resemble *C. elongatus* and have been confused with it (see below under that species).

In the majority of specimens, the outer lip is broken and thus the labral spine is absent. Nevertheless, in four specimens with intact outer lip, the degree of prominence of the labral spine varies greatly (Figure 6) from a discrete rounded or triangular projection to a very long, sharp spine with a length reaching 30% of aperture length.

Ceratoxancus elongatus Sakurai, 1958

(Figures 3C, D, 4C, 7A–D, 8A, B)

Ceratoxancus elongatus Sakurai, 1958: 161, figs. 1, 2.

Ceratoxancus elongatus: Habe, 1961:68, pl. 33, fig. 21; Cernohorsky, 1973:130; Hasegawa & Saito, 1995:29, pl. 5, fig. 4.

Ceratoxancus teramachii: Shikama & Horikoshi, 1963:95, pl. 76, fig. 4; Habe, 1964:104, pl. 33, fig. 21.

Type material: Holotype in National Science Museum, Tokyo, NSMT-Mo 70251 (illustrated by Hasegawa & Saito, 1995).

Type locality: Off Tosa, Japan, “from a somewhat deep bottom but the exact depth is not known.”

Material examined: NEW CALEDONIA. BIOCAL: R/V *Jean-Charcot*, sta. DW51, 23°05'S, 167°45'E, 680–700 m, 2 lv, 1 dd. Sta. DW66, 24°55'S, 168°22'E, 505–515 m, 2 lv, 3 dd. MUSORSTOM 4: R/V *Vauban*, sta. DW159, 18°46'S, 163°16'E, 585 m, 2 dd. Sta. DW196, 18°55'S, 163°24'E, 460 m, 1 dd. Sta. CP199, 18°50'S, 163°14'E, 595 m, 1 lv (dissected). CHALCAL 2: R/V *Coriolis*, sta. DW72, 24°55'S, 168°22'E, 527 m, 3 lv, 3 dd. Sta. DW74, 24°40'S, 168°38'E, 650 m, 3 dd. SMIB 3: R/V *Vauban*, sta. DW1, 24°56'S, 168°22'E, 520 m, 1 dd. Sta. DW2, 24°53'S, 168°22'E, 530–537 m, 1 dd. Sta. DW3, 24°55'S, 168°22'E, 513 m, 1 lv. Sta. DW5, 24°55'S, 168°22'E, 502–512 m, 1 dd. Sta. DW7, 24°55'S, 168°21'E,

505 m, 1 dd. BERYX 11: R/V *Alis*, sta. DW39, 23°37'S, 167°40'E, 490–500 m, 1 dd. SMIB 8: R/V *Alis*, sta. DW146–147, 24°55'S, 168°22'E, 508–532 m, 1 lv, 1 dd. Sta. DW148, 24°56'S, 168°21'E, 510 m, 1 dd. Sta. DW149, 24°55'S, 168°22'E, 508–510 m, 4 dd. Sta. DW152, 24°54'S, 168°22'E, 514–530 m, 1 lv, 2 dd. BATHUS 2: R/V *Alis*, sta. DW721, 22°54'S, 167°17'E, 525–547 m, 1 lv. BATHUS 3: R/V *Alis*, sta. DW809, 23°39'S, 167°59'E, 650–730 m, 5 dd. Sta. DW825, 23°22'S, 168°00'E, 597–605 m, 1 dd. BATHUS 4: R/V *Alis*, sta. DW918, 18°49.02'S, 163°15.80'E, 613–647 m, 1 dd. R/V *Alis*, sta. CP922, 18°48'S, 163°19'E, 600 m, 1 dd.

LOYALTY RIDGE. MUSORSTOM 6: R/V *Alis*, sta. DW468, 21°06'S, 167°33'E, 600 m, 1 dd. Sta. DW483, 21°20'S, 167°48'E, 600 m, 1 lv. BATHUS 3: R/V *Alis*, sta. DW776, 24°44'S, 170°08'E, 770–830 m, 2 dd. Sta. DW778, 24°43'S, 170°07'E, 750–760 m, 1 lv. Sta. DW781, 23°54'S, 169°46'E, 625–640 m, 2 dd. Sta. DW786, 23°54'S, 169°49'E, 699–715 m, 1 dd. Sta. DW787, 23°54'S, 169°48'E, 695–702 m, 1 dd. Sta. DW790, 23°49'S, 169°48'E, 685–715 m, 1 dd. Sta. DW794, 23°48'S, 169°49'E, 751–755 m, 1 dd.

VANUATU. MUSORSTOM 8: R/V *Alis*, sta. DW1128, 16°02'S, 166°38'E, 778–811 m, 1 dd.

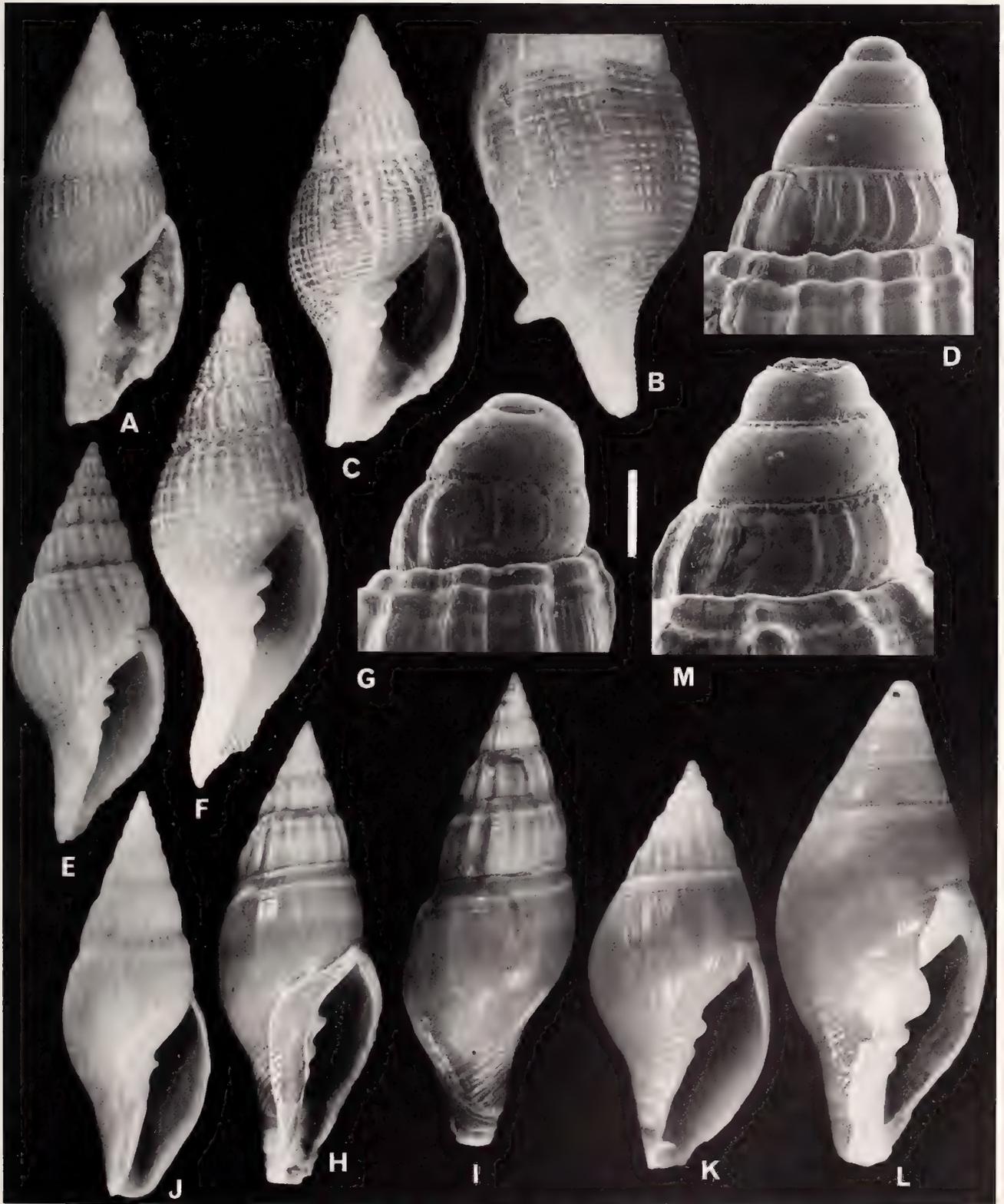
KERMADEC ISLANDS. R/V *Akademik Nesmeyanov*, 30°28.0'S, 178°37.2'W, 1000 m, 1 dd (NMNZ M249892).

Distribution: Off Tosa, Japan; new records from New Caledonia, Loyalty Ridge, Vanuatu, and Kermadec Islands, alive in 515–750 m, shells in 460–1000 m.

Description: (based on material from New Caledonia). Shell slender, fusiform, solid, consisting of 2.5 protoconch and up to 7+ moderately convex teleoconch whorls. Protoconch I smooth, with large nucleus, diameter 325 μ m; protoconch II consisting of two whorls, smooth with a narrow adapical band of irregular tubercles, a basal keel that is just covered by successive whorls, and six to nine strong opisthocyrt axial ribs before the protoconch/teleoconch boundary. Teleoconch whorls convex, with impressed suture. Sculpture consisting of strong orthocline ribs crossed by distinct spiral grooves, producing a muricated appearance. Number of axial ribs increasing from ca. 15 on the first teleoconch whorl to 32–40 on adult whorls, where they are broader and less sharply defined.

Figure 7

Ceratoxancus elongatus (A–D). A, New Caledonia (MUSORSTOM 4, sta. DW159), 20.4 mm; B, labral spine of the same specimen; C, New Caledonia (BIOCAL, sta. DW66), 18.5 mm; D, protoconch (BIOCAL, sta. DW51). *Ceratoxancus melichrous* Kantor & Bouchet, sp. nov. (E–G), E, holotype, 20.4 mm; F, New Caledonia (BATHUS 3, sta. DW776), 21.8 mm; G, protoconch of paratype (BATHUS 3, sta. DW 776). *Ceratoxancus basileus* Kantor & Bouchet, sp. nov. (H–J), H, I, holotype (dead collected shell without periostracum), 56.1 mm; J, New Caledonia (BIOCAL, sta. DW33, live collected shell with periostracum), 48.1 mm. *Ceratoxancus leios* Kantor & Bouchet, sp. nov. (K–M), K, holotype, 21.0 mm; L, New Caledonia (SMIB 8, sta. DW193–196), 38.0 mm; M, protoconch of holotype. Scale bar (protoconchs) 500 μ m.



Exposed part of early spire whorls with four or five incised grooves, of which one or two at shoulder are stronger. About 25 grooves on last adult whorl, plus 15, more closely set, on base and canal. Incremental scar of the labral spine similar to other grooves beside it. Aperture ovoid, elongate, comprising ca. 42–46% of total shell height. Outer lip thin, straight, with small projecting labral spine. Siphonal canal broad, short. Inner lip with thin, glossy callus. Columella with three plaits, the adapical one stronger.

Color uniform brown, periostracum very thin, transparent.

Dimensions of largest adult (protoconch, and part of first teleoconch whorl, missing): height 32.2 mm, last whorl height 22.5 mm, aperture height 12.0 mm, siphonal canal length 6.5 mm, diameter 12.6 mm.

Remarks: The New Caledonia specimens match the original description of *Ceratoxancus elongatus*. They differ from *C. teramachii* by the more narrow proportions, more convex outer lip, impressed suture, reticulated sculpture extending to the last adult whorl, and shorter labral spine. There is no doubt that two species are involved, and *Ceratoxancus elongatus* must be removed from the synonymy of *C. teramachii*. The two species co-occur in the same area of the Norfolk Ridge (ca. 24°55'–25°00'S, 168°20'E) and have even been taken together in the same haul (BIOCAL sta. DW66). Moreover, both species differ greatly in the operculum morphology. While in *C. teramachii* the operculum is medium-sized with terminal nucleus occupying at least 0.4× aperture length, in *C. elongatus* it is vestigial with subcentral nucleus, and occupies less than 0.13× aperture length.

Japanese authors have persistently confused the two species of *Ceratoxancus*. Habe (1961: pl. 33, fig. 21) illustrated a specimen (the holotype according to Hasegawa & Saito, 1995: 29) of *C. elongatus* under that name, but the same shell was subsequently identified as *C. teramachii*, with the comment that *C. elongatus* is “an elongate form” of it (Habe, 1964: 104). Shikama & Horikoshi's (1963: pl. 76, fig. 4) illustrated specimen of *C. teramachii* also belongs to *C. elongatus*. Habe's synonymization appears to have been followed to this day in the Japanese literature (Higo & Goto, 1993).

Ceratoxancus melichrous Kantor & Bouchet, sp. nov.

(Figures 2E, F, 4A, B, 7E–G)

Type material: Holotype and 1 paratype in MNHN.

Type locality: New Caledonia, Norfolk Ridge, SMIB 4: R/V *Alis*, sta. DW39, 24°56'S, 168°22'E, 525–560 m.

Material examined: CHALCAL 2: R/V *Coriolis*, sta. DW72, 24°54'S, 168°22'E, 527 m, 1 dd. SMIB 4: R/V *Alis*, sta. DW39, 24°56'S, 168°22'E, 525–560 m, 1 dd (holotype). SMIB 8: R/V *Alis*, sta. DW150, 24°54'S, 168°22'E, 519–530 m, 1 dd. Sta. DW152, 24°54'S, 168°22'E, 514–530 m, 2 dd. BATHUS 3: R/V *Alis*, sta.

DW776, 24°44'S, 170°08'E, 770–830 m, 3 lv (1 paratype, 1 dissected).

Distribution: New Caledonia: Norfolk Ridge, alive in 770–830 m, shells from 530 m.

Description: (holotype; description of protoconch based on paratype) Shell slender, fusiform, solid, consisting of 1.5 protoconch and seven moderately convex teleoconch whorls. Protoconch (present but corroded in holotype) paucispiral, diameter 650 μm, with small initial nucleus; smooth with a basal keel that is just covered by successive whorl, and one strong opisthocyrt varix marking the protoconch/teleoconch boundary. Teleoconch whorls convex, with impressed suture. Sculpture consisting of strong prosocline ribs crossed by distinct spiral grooves, producing a coarsely muricated appearance. Number of axial ribs increasing from 14 on the first teleoconch whorl to 25 on last adult whorl, where they are broader and less sharply defined in the last half-whorl before peristome. Exposed part of spire whorls with five incised grooves, which delimit a stronger spiral cord at shoulder. About 15 grooves on last adult whorl, plus 22, more closely set, on base and canal. No labral spine fasciole. Aperture ovoid, elongate, comprising ca. 34% of total shell height. Outer lip (damaged in holotype) thin, simple. Siphonal canal narrow, short, but distinctly set off. Inner lip with rather thick callus. Columella with three plaits, adapical one stronger.

Color uniform light yellowish brown, periostracum very thin, transparent.

Dimensions: height 20.4 mm, last whorl height 14.1 mm, aperture height 7.0 mm, siphonal canal length 4.4 mm, diameter 7.8 mm.

Remarks: *Ceratoxancus melichrous* is superficially very similar to *C. elongatus* but differs by: (a) its paucispiral protoconch, indicating non-planktotrophic development (vs. multispiral, indicating planktotrophic development in *C. elongatus*); (b) its coarser sculpture; (c) the lack of labral spine and/or labral spine fasciole; (d) its lighter color and smaller adult size. Even in the absence of a protoconch, the combination of coarse sculpture and light yellowish color permits identification of *C. melichrous*. Anatomically, *C. melichrous* differs from *C. elongatus* in having a shorter mid-esophagus and a gland of Leiblein that is not coiled in the anterior part.

C. niveus, which also has a paucispiral protoconch, differs by its finer sculpture, smaller adult size, and off-white color.

Etymology: *melichrous*, a Greek word meaning colored like honey.

Ceratoxancus niveus Kantor & Bouchet, sp. nov.

(Figures 3E, F, 4D, 6K, L)

Type material: Holotype (lv) and 5 paratypes (2 lv, 3 dd) in MNHN.

Type locality: New Caledonia, Norfolk Ridge, BIOCAL: R/V *Jean-Charcot*, sta. DW51, 23°05'S, 167°45'E, 680–700 m.

Material examined: Known only from the type material.

Description: (holotype) Shell slender, fusiform, solid, consisting of ca. one protoconch and 4.3 moderately convex teleoconch whorls. Protoconch paucispiral, diameter ca. 750 μm , with large nucleus, smooth; protoconch/teleoconch transition indistinct, six or seven strong axial ribs may belong to protoconch or teleoconch. Teleoconch whorls convex, with impressed suture. Sculpture consisting of strong prosocline ribs crossed by distinct spiral grooves, producing a coarsely muricated appearance. Number of axial ribs increasing from 15 on first teleoconch whorl to 27 on last adult whorl, where they remain sharply defined until behind the outer lip. Exposed part of spire whorls with four incised grooves, which delimit a stronger spiral cord at shoulder. About 20 grooves on last adult whorl, rather evenly spaced on shoulder, periphery and base, a little more crowded on canal. No labral spine fasciole. Aperture ovoid, elongate, comprising ca. 40% of total shell height. Outer lip sharp, thin, simple. Siphonal canal broad, short, indistinctly set off. Inner lip with narrow callus. Columella with three plaits, the abapical one almost indistinct.

Color uniform off-white, periostracum very thin, transparent.

Dimensions: height 8.8 mm, diameter 3.7 mm, last teleoconch whorl height 5.9 mm, aperture height 3.6 mm.

Remarks: *Ceratoxancus niveus* is separated from all other species of *Ceratoxancus* by the combination of small adult size, paucispiral protoconch, muricated sculpture, and white color. It most closely resembles *C. melichrous* but is distinguished by its large protoconch nucleus, finer sculpture, and color.

Etymology: *niveus*, Latin, snow white, in reference to the color of the shell.

Ceratoxancus leios Kantor & Bouchet, sp. nov.

(Figure 7K–M)

Type material: Holotype and 1 paratype in MNHN.

Type locality: New Caledonia, Norfolk Ridge. BATHUS 3: R/V *Alis*, sta. DW809, 23°39'S, 167°59'E, 650–730 m.

Material examined: NEW CALEDONIA. CHALCAL 2: R/V *Coriolis*, sta. DW74, 24°40'S, 168°38'E, 650 m, 1 dd. SMIB 8: R/V *Alis*, sta. DW193–196, 22°52'–23°00'S, 168°20'–168°22'E, 491–558 m, 1 dd (paratype). BATHUS 3: R/V *Alis*, sta. DW809, 23°39'S, 167°59'E, 650–730 m, 1 dd (holotype).

KERMADEC ISLANDS. R/V *Akademik Nesmeyanov*, 30°28.0'S, 178°37.2'W, 1000 m, 1 dd (NMNZ M249898).

Distribution: Norfolk Ridge and Kermadec Islands, shells only in 558–1000 m.

Description: (subadult holotype) Shell ovoid, fusiform, solid, consisting of 3+ (nucleus of protoconch I missing) protoconch and 5.5 moderately convex teleoconch whorls. Remaining part of protoconch I smooth, diameter 375 μm ; protoconch II consisting of 2.5 whorls, smooth, with an adapical row of granules, a basal keel that is covered by successive whorls, and six widely spaced, strong, opisthoclyt axial ribs before the protoconch/teleoconch boundary. Adapical teleoconch whorls weakly shouldered, later whorls more flat-sided, with shallowly impressed suture. Sculpture consisting of strong orthocline ribs crossed by weaker spiral cords/grooves, and much finer incremental lines. There are 11 very distinct and strong ribs per whorl on the first three adapical whorls, more numerous but gradually fading on subsequent whorls. Last adult whorl with low, broad, and indistinct axial varices. Spiral sculpture well defined on first 3.5 whorls, consisting of one strong cord at shoulder, forming a nodulous intersection with the axial ribs, and four weaker cords, one above and three below shoulder. Penultimate whorl with 17 low axial ribs that gradually become indistinct, crossed by four shallow spiral grooves above periphery. On last whorl, axial sculpture consists mainly of incremental scars, some of which are quite strong, and a few low and indistinct axial swellings; five shallow spiral grooves on the shoulder, periphery almost smooth, base with deeper grooves, six above labral notch, 12 below it, delimiting sharp spiral cords near siphonal canal. Incremental scars of labral spine shallow, distinct on part of the whorl, indistinct and merging with spiral grooves on part of the whorl. Aperture ovoid, elongate, comprising 43% of total shell height. Outer lip thin (not adult), without projecting labral spine. Siphonal canal broad, very short. Inner lip with thin glossy callus. Columella with three plaits, adapical one stronger.

Color: protoconch light yellowish tan; first three teleoconch whorls whitish, subsequent whorls gradually darkening to light chestnut brown on penultimate and last whorls, with the exception of a narrow whitish subsutural band.

Dimensions: height 21.0 mm, diameter 9.5 mm, body whorl length 14.7 mm, aperture height 9.0 mm.

Remarks: The specimen from SMIB 8 sta. DW193–196 is an old and worn adult with a broken outer lip, height 38.0 mm. Its last adult whorl has no trace of axial sculpture, but there are five spiral grooves above the shoulder and 15 at the base of the shell, below a broad, distinct, and continuous band corresponding to scars of a probably short labral spine.

C. leios differs from all other species of *Ceratoxancus* by the absence of axial sculpture on subadult and adult whorls. Juveniles consistently have 11 distinctly shouldered axial ribs instead of 11–14 broader ribs in juveniles of *C. teramachii*.

Placement of *C. leios* in *Ceratoxancus* is justified by the general shell morphology which resembles that of *C. teramachii*, and the presence of a labral spine fasciole below periphery of the last adult whorl.

Etymology: From the Greek *leios*, meaning smooth, with reference to the absence of shell sculpture on adult whorls.

Ceratoxancus basileus Kantor & Bouchet, sp. nov.

(Figures 3A, B, 5, 7H–J)

Type material: Holotype in MNHN.

Type locality: SMIB 2: R/V *Vauban*, sta. DW18b, 22°58'S, 167°20'E, 530–535 m.

Material examined: NEW CALEDONIA. BIOCAL, R/V *Jean-Charcot*, sta. DW33, 23°10'S, 167°10'E, 675–680 m, 1 lv. MUSORSTOM 4: R/V *Vauban*, sta. DW221, 22°59'S, 167°37'E, 535–560 m, 4 dd. Sta. DW223, 22°57'S, 167°30'E, 545–560 m, 1 dd. SMIB 2: R/V *Vauban*, sta. DW18b, 22°58'S, 167°20'E, 530–535 m, 1 dd (holotype). SMIB 3: R/V *Vauban*, sta. DW21, 22°59'S, 167°19'E, 525 m, 1 dd. BATHUS 2: R/V *Alis*, sta. DW720, 22°52'S, 167°16'E, 530–541 m, 1 dd.

Distribution: New Caledonia, alive in 675–680 m, shells from 525 m.

Description: Shell ovoid, fusiform, solid, glossy, consisting of 1.2+ protoconch and eight slightly convex, nearly flat teleoconch whorls, with shallow impressed suture. Nucleus and initial part of protoconch II chipped, remaining part smooth, corroded, with protoconch/teleoconch transition indistinct, diameter ca. 950 μ m. Sculpture consisting of strong orthocone ribs crossed by weaker spiral cords. There are 11–12 very distinct and strong ribs per whorl on first four whorls, more numerous on subsequent whorls, up to 19 on penultimate whorl. Last adult whorl almost smooth, with low, broad, and indistinct axial varices. Spiral sculpture poorly defined on all teleoconch whorls, except one strong cord at shoulder, forming a nodulous intersection with the axial ribs; four much weaker cords, one above and three below shoulder, distinct on early spiral whorls, obsolete on later whorls. In addition, there is a second-order sculpture consisting of fine incremental lines and fine spiral riblets. This sculpture is best seen in the depressions between main ribs and cords, and is especially distinct above the shoulder. On the last whorl, the only main sculpture present is the strong spiral cord at the shoulder, and the apparently smooth periphery is sculptured by fine spiral grooves and more indistinct incremental lines. There are 12 much stronger spiral cords toward the base of the whorl and on the siphonal canal. Aperture elongate, comprising 39% of total shell height. Siphonal canal rather broad, short. Inner lip with thin glossy callus (outer lip broken). Columella with three plaits, the adapical one stronger. Only two adapical plaits are seen in

apertural view, the third one is seen only when the shell is turned clockwise $\frac{1}{4}$ of a whorl.

Color: protoconch very light yellowish tan; first three teleoconch whorls whitish, subsequent whorls gradually darkening to light chestnut brown, with the exception of a light violet band centered on shoulder cord; transition from violet to brown very gradual.

Dimensions: height 56.1 mm, diameter 19.5 mm, last whorl height 38.3 mm, aperture height 21.6 mm.

Remarks: The live-collected specimen from BIOCAL sta. DW33 has a rather thick, smooth periostracum tightly adhering to the shell surface. It is worn on the axial ribs.

Ceratoxancus basileus is similar to *C. leios* and differs by its larger adult size, taller spire, and longer siphonal canal, as well as the absence of a labral spine or fasciole. In *C. basileus* the axial sculpture is present in subadults 50 mm high and becomes obsolete only on the last whorl of large adults; in *C. leios*, sculpture is restricted to juvenile whorls.

Etymology: From the Greek *basileus*: king, because this is the largest of the known species of *Ceratoxancus*.

DISCUSSION

Comparative Remarks

Six species of *Ceratoxancus* are recognized as a result of the present work, and they can be easily discriminated by a suite of conchological and anatomical characters (Table 1). Only *C. elongatus* and *C. melichrous* have a fairly similar general appearance, and accurate identification of single shells requires that protoconch characters are available.

In forthcoming papers, we will report on the anatomy of *Latiromitra* Locard, 1897, and *Benthovoluta* Kuroda & Habe, 1950, and discuss the phylogeny and classification of Ptychactractinae and Turbinellidae. The present discussion is therefore preliminary and aims only at placing *Ceratoxancus* in a broader context. In his review of the subfamily Ptychactractinae, Harasewych (1987) assigned to it seven genera: *Ptychactractus* Stimpson, 1865, *Surculina* Dall, 1908, *Benthovoluta*, *Metzgeria* Norman, 1879, *Cyomesus* Quinn, 1981, *Latiromitra*, and *Ceratoxancus*, and expressed doubts about the taxonomic position of the latter two. *Ceratoxancus* shares a number of anatomical characters with *Latiromitra* and *Benthovoluta* (based on our own unpublished results): (1) a short or very short proboscis, (2) paired proboscis retractors, (3) the position of the buccal mass and opening of the radular diverticulum into the buccal cavity at the proboscis base in its contracted position, (4) the ventral odontophore retractor passing through the nerve ring, (5) the presence of a single accessory salivary gland, (6) a large gland of Leiblein, (7) mid-esophagus with well-developed dorsal glandular folds, and (8) a small stomach. Therefore we may conclude that *Benthovoluta*, *Latiromitra*, and *Ceratoxancus* constitute a

Table 1

Conchological and anatomical characters discriminating the species of *Ceratoxancus*, n.a.: data not available.

	<i>teramachii</i>	<i>elongatus</i>	<i>melichrous</i>	<i>niveus</i>	<i>leios</i>	<i>basileus</i>
Maximum adult size (mm)	31.5	32.2	20.4	8.8	38.0	56.1
Number of protoconch whorls	2.5	2.5	1.5	1.0	3+	n.a.
Labral fasciole	Present	Present	Absent	Absent	Present	Absent
Sculpture on last adult whorl	Axial ribs variable spiral cords	Axial ribs + spiral cords	Axial ribs + spiral cords	Axial ribs + spiral cords	Smooth	Smooth
Operculum length/aperture length	>0.4	0.12	0.5	0.45	n.a.	0.37
Radula width/aperture length (%)	1.17	1.58	2.86	1.76	n.a.	2.55
Mid-esophagus/proboscis length	5	5	2.5	n.a.	n.a.	6.5
Salivary glands	Not fused	Not fused	Fused	n.a.	n.a.	Not fused
Accessory salivary gland	Present	Present	Absent?	n.a.	n.a.	Present
Penial papilla	Present	Absent	Absent	Absent	n.a.	Present
Anterior part of gland of Leiblein	Coiled	Coiled	Not coiled	n.a.	n.a.	Coiled

group which, judging from the radular morphology, should include the genus *Ptychatractus* and thus belong to the subfamily Ptychatractinae.

Anatomy is rather uniform among the species of *Ceratoxancus*. A character that varies significantly within the genus is the length of the mid-esophagus. It is long and coiled in *C. teramachii* and *C. elongatus* (thus in both species possessing a labral spine) and shorter in *C. melichrous*, which lacks a spine. Such differences may be connected with diet-specific feeding mechanisms. Reduction of operculum size has apparently occurred several times in the subfamily. Besides *C. elongatus*, where it is greatly reduced, a non-operculate species was found in *Latiromitra*, and in an unnamed species of *Benthovoluta*, the presence of the operculum seems to be intraspecifically variable (Bouchet & Kantor, unpublished observations).

There is also some variation in the radula of *Ceratoxancus* species. Two types of rachidian teeth can be recognized. In *C. teramachii* (Figure 2B), *C. melichrous* (Figure 2F), and to some extent also in *C. niveus* (Figure 3F), the rachidian teeth are rather long, with the cusps emanating closer to the posterior edge of the basal part. In *C. elongatus* (Figure 3D) and *C. basileus* (Figure 3B), the rachidian teeth are short with much shorter cusps, which emanate closer to the anterior edge of the basal part. There is no correlation between the form of the rachidian and lateral teeth. Thus, in *C. teramachii* the lateral teeth have a very long base (Figure 2C). Much shorter bases are found in *C. elongatus* and *C. basileus*. Conversely, in *C. melichrous* and *C. niveus*, the lateral teeth are very long, but their base is very short. This radular morphology is rather similar to that of other ptychatractines. The radula of *C. melichrous* resembles closely that of *Ptychatractus*

ligatus (Harasewych, 1987: fig. 19), while radulae of *C. elongatus* and *C. basileus* are very similar to that of *Latiromitra chaunax* (Bayer, 1971) (Harasewych, 1987: fig. 20). This is in contrast to radular morphology in Vasinae and Turbinellinae, the former having a bicuspid rachidian tooth, while in the latter it is very broad with long lateral flaps (Harasewych, 1987: figs. 21, 22). In Columbariinae, the rachidian teeth are similar in shape to those of Ptychatractinae, but differ in having a deeply arched base (Harasewych, 1983: figs. 9–12).

Mode of Development

The protoconchs of *C. melichrous* and *C. niveus* are both paucispiral and indicate non-planktotrophic development. However, the protoconch of *C. melichrous* has a small initial nucleus, it has 1.5 whorls with a distinct protoconch/teleoconch transition, and its color is light yellowish brown: this indicates most probably a lecithotrophic development, possibly with a short, free-swimming demersal phase. By contrast, the protoconch of *C. niveus* has a large initial nucleus and it has only one whorl with an indistinct transition to the teleoconch: this most probably indicates a development with intracapsular metamorphosis. The protoconchs of the other four species, *C. teramachii*, *C. elongatus*, *C. basileus*, and *C. leios*, are multispiral and indicate planktotrophic larval development.

The broad distribution of *C. teramachii* and *C. elongatus* is probably correlated with the good dispersal capacities of planktotrophic larvae and, based on their protoconch morphology, it is likely that *C. leios* and *C. basileus* will also be discovered in other parts of the Indo-West Pacific.

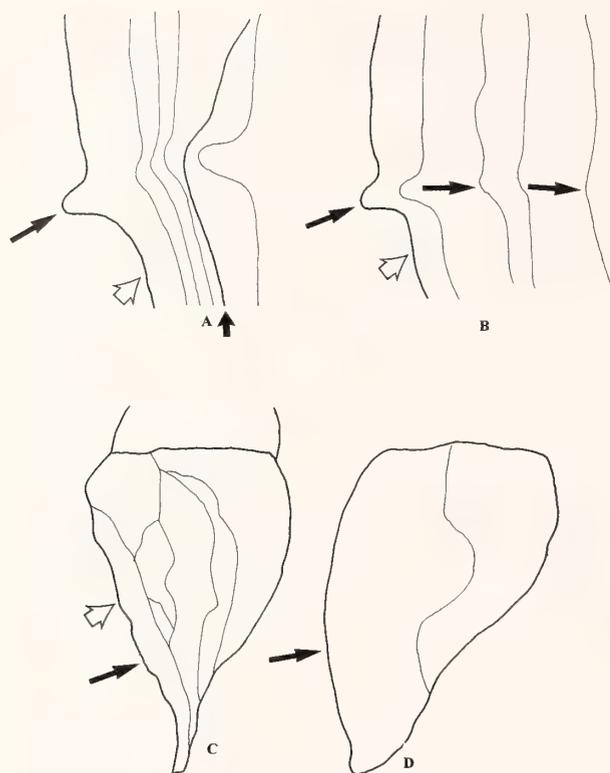


Figure 8

Ceratoxancus elongatus (A–B). A, shape of the incremental lines on the last teleoconch whorl, showing reappearance and progressive development of the labral spine after aperture lip breakage; B, shape of the incremental lines, showing variation of the labral spine length without aperture lip breakage. *Ceratoxancus teramachii* (C, D). C, last teleoconch whorl of the specimen with numerous scars of form A; D, last teleoconch whorl of the specimen with scar of form B. Large hollow arrows indicate aperture lip. Long filled arrows indicate the labral spine, or its position when the spine is not pronounced. Short filled arrow indicates the scar from shell breakage.

By contrast, *C. melichrous* and especially *C. niveus* may have a distribution restricted to the Norfolk Ridge, correlated with the poor dispersal capacities of their larvae.

What is the Function of the Labral Spine?

A remarkable feature of three species of *Ceratoxancus*, *C. teramachii*, *C. elongatus*, and probably *C. leios*, is the presence of a labral spine. The degree of spine development greatly varies from specimen to specimen, as well as during the lifetime of an individual. This is revealed by the shape of growth lines on the last teleoconch whorl. On the upper whorls, the spine fasciole is covered by successive whorls.

In *C. teramachii* and *C. elongatus*, there are numerous scars from breakages of the apertural lip (see below). As a rule, and as one would expect, immediately after the apertural breakage the spine is either absent or very short

(Figure 8A). In *C. teramachii*, over time it becomes longer until the next breakage. In *C. elongatus*, breakages are less frequent, and therefore, a longer part of the undamaged body whorl can be examined, revealing that the length of the spine may change even without visible signs of damage (Figure 8B). The limited material of *C. leios* does not allow an estimation of the variability of prominence of the spine. In the holotype, the growth lines on much of the last teleoconch whorl are only slightly bent at the position expected for the spine, suggesting that a spine was present, although short and blunt. Conversely, in the largest specimen (SMIB 8, sta. DW193–196), the spine was probably present on the whole length of the last teleoconch whorl.

All studied specimens of *C. teramachii* have scars from numerous breakages of the apertural lip (Table 2), starting on the very first teleoconch whorls. Their number ranges from 0.14 to 2.43 per teleoconch whorl, and specimens collected off New Caledonia have more numerous scars (mean = 1.81, σ = 0.45) than those from the Coral Sea (mean = 0.36, σ = 0.28). There are two forms of scars. The more numerous breakages are prosocline and affect the area of the labral spine (form A) (Figure 8C). Much fewer are shallow or moderately deep notches on the periphery of the whorl that do not affect the area of the labral spine (form B) (Figure 8D). In *C. elongatus*, there are also traces of numerous breakages of the apertural lip (Table 3), varying in number from 0.25 to 1.37 per teleoconch whorl (mean = 0.72, σ = 0.37), which is fewer than in *C. teramachii*. As in the case with the latter species, the scars were of both types, and type B scars were also less numerous. The number of shell breakages in *C. melichrous* and *C. basileus* was yet smaller (Tables 4, 5). One specimen of *C. basileus* presents a rather deep incision, about $\frac{1}{3}$ of a whorl, rather narrow and occurring in the lower part of the last whorl at the border of the canal. In all other specimens of *C. basileus*, the breakages were present only on the last whorls.

These numerous shell repairs may indicate unsuccessful attacks of predators such as crabs or may be connected with usage of the outer lip and labral spine for prey capture. In the latter case, the lip may be broken, e.g., during opening of valves of large bivalve mollusks. In shallow water, predatory crabs usually produce deep cuts in the shell to reach the body (Vermeij, 1993). Very similar scars were found in several specimens of *Benthovoluta claydoni* and *B. sp.*, collected off New Caledonia. The length of such incisions may reach half of a whorl without killing the mollusk. Type B scars in *C. teramachii* have some similarity to crab predation scars, although they are much shallower. Thus one can suppose that the scars of this type may represent unsuccessful attacks on the snails. In an attempt to evaluate the connection of shell damage to crab predation, we counted the number of breakages on the shells of two forms of *Cantharus*-like buccinids from New Caledonia with similar shell thickness, shape, and from the same localities and depth range (415–600 m). The

Table 2

Number of apertural damages in *Ceratoxancus teramachii* in relation to size and locality. (Only the major breaks were considered).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl	Source
30.0 (incomplete)	8	11	1.38	S New Caledonia
25.7 (incomplete)	7	17	2.43	S New Caledonia
22.4 (incomplete)	5	9	1.80	S New Caledonia
26.4 (incomplete)	5	9	1.80	New Caledonia
21.2	6.5	9	1.38	S New Caledonia
30.0	7.5	11	1.47	S New Caledonia
26.2 (incomplete)	5	12	2.40	S New Caledonia
			mean = 1.81	$\sigma = 0.45$
16.0	5.5	1	0.18	Coral Sea
18.3	6	5	0.83	Coral Sea
21.7	7	1	0.14	Coral Sea
15.0	5.5	2	0.36	Coral Sea
28.8	7.5	2	0.28	Coral Sea
			mean = 0.36	$\sigma = 0.28$

number of breakages per teleoconch whorl was significantly lower than in both species of *Ceratoxancus* with spine: mean values for these buccinids were 0.19 ($\sigma = 0.17$, $n = 13$) and 0.40 ($\sigma = 0.36$, $n = 11$). The number of breakages per whorl in the latter species of *Cantharus* is extremely close to that in *C. melichrous*. Moreover, type B scars are more numerous than those of type A.

As it is difficult to suppose that different species of *Ceratoxancus* have selectively different attractiveness to

predators, the numerous shell breakages may not be connected with predation by crabs. The labral spine in *C. elongatus* is much less developed than in *C. teramachii*, and totally absent in *C. melichrous* and *C. basileus*. Thus, the number of breakages in different *Ceratoxancus* spp. increases with the degree of development of the spine. Therefore, it seems likely that the apertural lip and particularly the spine are used for prey capture.

Nothing is known about feeding and diet of any species of the genus possessing a spine. The digestive tract in studied specimens did not contain any recognizable food particles. The only dissected specimen of *C. melichrous* had presumably sponge spicules and parts of minute crustaceans in the stomach and rectum. We can also suppose that *C. basileus* either drills, or rasps some prey with a very hard skeleton. This is indirectly suggested by the

Table 3

Number of apertural damages in *Ceratoxancus elongatus* in relation to size (all from New Caledonia).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl
20.4	6	6	1.00
18.0	5	1	0.25
18.7	5	4	1.25
17.5	5.2	2	0.38
15.5	5	3	0.75
16.4	5	5	1.00
19.2	5.4	2	0.37
19.5	5.5	3	0.55
22.1 (incomplete)	5.2	6	1.15
24.2	5.8	8	1.37
18.6	5	3	0.6
20.6	5.3	2	0.37
20.3	5.5	4	0.73
29.5 (incomplete)	6.2	6	0.98
20.1	5.5	2	0.36
		mean = 0.72	$\sigma = 0.37$

Table 4

Number of apertural damages in *Ceratoxancus melichrous* in relation to size (all from New Caledonia).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl
20.4	7	2	0.29
18.0	6.7	1	0.15
14.0 (incomplete)	4	4	1.00
15.2 (incomplete)	4	2	0.5
17.5	6	2	0.33
16.4	6.5	0	0.00
		mean = 0.38	$\sigma = 0.35$

Table 5

Number of apertural damages in *C. basileus* in relation to size (all from New Caledonia).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl
56.1	7.7	1	0.13
56.5 (incomplete)	8.0	3	0.38
54.2 (incomplete)	7.5	2	0.27
45.6 (incomplete)	7.5	3	0.4
43.5	7.5	2	0.27
49.7	8.5	1	0.12
50.0 (incomplete)	6.5	1	0.15
		mean = 0.25	$\sigma = 0.12$

extremely worn teeth on the bending plane of the radula (Figure 3B). This was not observed in spined species. Bivalves or barnacles may represent potential prey for the spined species of *Ceratoxancus*. Examination of the overall faunal composition at some stations that yielded *Ceratoxancus* revealed that no large bivalves with thick shell are present. Also, the barnacles present were easily opened with the fingernail, and it is hard to imagine how they could induce shell breakage on a potential predator. Thus the prey of *Ceratoxancus* remains unknown. The significant differences in the number of apertural breakages between populations of *C. teramachii* from New Caledonia and the Coral Sea may be connected with local differences in feeding regimes.

Note Added in Proof:

While the present paper was in press, new expedition material has been processed in MNHN. It contains new records of *Ceratoxancus* from Vanuatu and the Economic Zone of Wallis & Futuna (a French dependant territory NE of Fiji).

Ceratoxancus teramachii:

SW PACIFIC. MUSORSTOM 7: R/V *Alis*. WATERWITCH BANK. Sta. DW537, 12°30'S, 176°41'W, 325–400 m, 1 dd. Sta. DW573, 12°31'S, 176°52'W, 364 m, 1 lv.
COMBE BANK. Sta. DW542, 12°26'S, 177°28'W, 370 m, 1 lv.

Ceratoxancus elongatus:

SW PACIFIC. MUSORSTOM 7: R/V *Alis*. WATERWITCH BANK. Sta. DW575, 12°31'S, 176°52'W, 425 m, 1 dd. Sta. DW636, 13°39'S, 179°55'E, 650–700 m, 1 dd.

Ceratoxancus melichrous:

VANUATU. MUSORSTOM 8: R/V *Alis*, sta. DW978, 19°23'S, 169°27'E, 408–413 m, 1 lv.

Ceratoxancus leios:

SW PACIFIC. MUSORSTOM 7: R/V *Alis*. TUSCARORA BANK. Sta. CP562, 11°48'S, 178°22'W, 775–777 m, 1 dd. Sta. DW635, 13°49'S, 179°56'E, 700–715 m, 1 dd.

The new material confirms our supposition that *C. leios* has a broader SW Pacific distribution. It also confirms that *C. melichrous* probably has a short free-swimming demersal phase but, contrary to our supposition, it is not a Norfolk Ridge endemic.

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Reproductive Timing and Nutritional Storage Cycles of *Mytilus trossulus* Gould, 1850, in Port Valdez, Alaska, Site of a Marine Oil Terminal

by

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Abstract. *Mytilus trossulus* was investigated to determine the reproductive and nutritive cell storage cycles for this mussel in Port Valdez, a fjord within Prince William Sound, Alaska. Three intertidal sites within the boundaries of a marine terminal, and four sites remote from the terminal area were sampled. Mussels from Port Valdez exhibit a distinct annual cycle with gametogenic development throughout winter, during periods with freezing air and water temperatures, and demonstrate a summer-long spawning period. Nutritive cells generally decrease throughout late winter as gametogenesis proceeds to spawning, reaching minimal values during early summer. No differences between sites attributable to the proximity of mussels to the terminal area were apparent. The effects of stress, likely related to silt-laden waters derived from a nearby glacier, were observed at one site remote from the marine terminal. Regional differences in the reproductive cycles of *Mytilus* spp. are discussed.

INTRODUCTION

Most previous studies of mussels on the northern Pacific coast were presumed to investigate the life history of *Mytilus edulis* Linnaeus, 1758 (Seed & Suchanek, 1992). Recent literature indicates that *Mytilus trossulus* Gould, 1850, the species previously thought to be *M. edulis*, ranges along the Pacific coast from California to the Shumagin Islands, Alaska (McDonald et al., 1991; Geller et al., 1994). Thus, Emmett et al. (1987) documented the reproductive cycle for *M. trossulus*, rather than *M. edulis*, for the British Columbia coast, while Feder & Keiser (1980) investigated *M. trossulus*, rather than *M. edulis*, in Alaskan waters.

Stereological analysis of mantle tissue has been used extensively to document the reproductive and nutritive storage cycles for *Mytilus* spp. in laboratory and field studies (see review in Seed & Suchanek, 1992). Four stages of the reproductive cycle—developing, ripe, spawning, and spent—are identified as primary categories useful in describing reproductive timing and events (Seed & Suchanek, 1992). In mussels, nutrients are stored in the adipogranular cells (ADG) and vesicular connective tissue (VCT), which are the primary reserves of energy for reproduction (Gabbott & Peek, 1991). The main factors controlling reproduction and nutritional storage cycles are thought to be temperature and food availability. However, these cycles are apparently flexible, as mussels are able to adapt

to individual environments quickly (e.g., Lowe et al., 1994). No studies are available that integrate reproductive timing and nutrition storage cycles for Alaskan mussels.

Port Valdez is the terminus for a pipeline transporting crude oil from Prudhoe Bay, Alaska. Prior to receiving their oil cargo, tankers offload oil-contaminated ballast water at the marine terminal, which is processed onshore at a treatment plant and then discharged into the port (Colonell, 1980). A series of studies, initiated in the mid-1970s, indicated no or minor influence of Prudhoe Bay crude oil (Feder et al., 1990) and marine terminal operations on intertidal flora and fauna within Port Valdez (e.g., Shaw et al., 1986; Feder & Bryson-Schwafel, 1988; Anthony, 1995). An oil spill in outer Prince William Sound in March 1989 demonstrated that the potential for a major oil spill is always present wherever oil tankers operate. However, chronic exposure to hydrocarbons (e.g., small oil spills, naturally occurring seeps, and pollution from boat traffic) may be a greater concern for marine organisms (Kennish, 1992). Sublethal responses by mussels to stress (e.g., chronic exposure to hydrocarbons) include reductions of nutritive reserves and reproductive tissues; delayed, reduced, or suspended spawning; and increased gamete degeneration and resorption (Myint & Tyler, 1982; Arimoto & Feng, 1983; Lowe & Pipe, 1986; McCormick-Ray, 1987; Lowe, 1988). This paper examines the reproductive and nutritive cell cycles of Alaskan intertidal populations

of *M. trossulus* adjacent to and remote from the marine terminal in Port Valdez and compares these cycles to those reported for *Mytilus* spp. elsewhere.

THE STUDY AREA

Port Valdez (61°N, 146°30'W) is a fjord located within Prince William Sound, a subarctic embayment of the northeastern Gulf of Alaska. The shoreline consists of steep, rocky shores in the western end which merge into low-profile cobble beaches and extensive mud flats to the east. The mean annual air temperature is approximately 10°C, with sub-freezing temperatures in winter of -4° to -10°C, and a record low of -34°C (Hood et al., 1973). Surface-water temperature ranges from -2°C in winter to 16°C in summer (Jewett & Feder, 1977). The tidal range is approximately 6 m (Colonell, 1980). The port receives increased freshwater runoff and sediment loads from glacial rivers and streams from May to October resulting in low salinity (approaching 0‰) and a high sediment load in the upper water layer (10 m). No heavy sea ice forms in Port Valdez. Primary production in the port is typical of high latitude marine systems with a spring bloom in March–April and decreased production through the summer (Goering et al., 1973). A minor bloom occurs when the water turns over in fall. In winter, production ceases. Initiation of spawning by mussels is coincident with the occurrence of the spring bloom. Adult mussels are abundant intertidally and rare subtidally. Juveniles settle subtidally on algae or directly within mussel beds (Feder & Keiser, 1980; Feder & Bryson-Schwafel, 1988). The dominant invertebrate predators on mussels are the gastropod *Nucella* (abundant only on western shores where they prey on mussels throughout the year), and the seastars *Evasterias troschelli* (Stimpson, 1862) and *Pycnopodia helianthoides* (Brandt, 1835) (important predators on rocky shores and cobble beaches; Feder & Bryson-Schwafel, 1988). From spring to autumn, a freshwater lens prevents seastars from reaching intertidal mussels, but in winter, following a fall turnover, surface salinity increases, and these predators forage within the intertidal zone. The sea otter feeds on mussels throughout the port all year (Anthony, 1995). Seabirds occasionally prey on mussels (Hogan & Irons, 1988).

METHODS

Three intertidal sites—Berth 4 (B4), Mineral Creek (MC), and Sawmill Spit (SS)—were sampled from 1980 to 1982 (Figure 1) and four sites—Berth 5 (B5), Saw Island (SI), Gold Creek (GC), and Five Mile Beach (5M)—were sampled from 1989 to 1991. B4, adjacent to the marine terminal, is a moderately sloping beach with large rock outcrops in the lower intertidal; mussels occur in loosely defined clumps on the outcroppings. MC and SS are low-profile cobble beaches, and mussels are widely dispersed

throughout the shore. The B5 site (200–300 meters west of B4) and 5M are composed of steep rock faces, and mussels occur at both sites in a well-defined bed on the rock face. GC and SI consist of moderately sloping rock outcrops, and mussels occur in extensive, dense beds. B5 and SI are also within the terminal boundaries. Mussels were collected monthly from April, 1980 through September, 1982; some months were missed due to inclement weather. The 1989–1991 study assessed mussels from March to October, the months with highest biological activity. Sampling at SI was not initiated until April 1990. Surface-water temperature, salinity, and turbidity were collected in conjunction with mussel sampling. Environmental data from another site, Anderson Bay, is presented as a proxy for missing data values in 1989 and 1991. Environmental data for 1991 were obtained from the Solomon Gulch Fish Hatchery, Valdez.

Stereological techniques described for *M. edulis* elsewhere are used here. Mussels of various sizes (between 20 mm to the maximum size of 60 mm) were collected and fixed with 10% Baker's formal-calcium solution and stored in 70% ethyl alcohol. Histological preparation of mantle tissue followed procedures outlined by Lowe et al. (1982). Point counts of reproductive tissues in stereological analysis were summarized according to four categories—developing, ripe, spawning, and spent—derived from Seed (1976) and Kautsky (1982) (see also Seed & Suchanek, 1992). Nutritive cells were categorized following Lowe et al. (1982) into the adipogranular (ADG cells: containing proteins and lipids) and vesicular connective tissue (VCT: containing mostly glycogen) categories (Lowe et al., 1982). Point counts were made with a Weibel type-2 grid at each of 42 endpoints per field of view for 15 slides from separate mussels. Five fields of view were examined from one tissue section for each slide. Volume fractions were calculated according to Lowe et al. (1982) as the sum of point counts for a category divided by the total number of counts possible (210).

Statistical procedures were applied to assess differences between populations. Nonparametric two way rank ANOVA comparisons (the Friedman test), with time (date of collection) as the factor and population location as the treatment (Lowe et al., 1994), were used to compare mean point count data, and multiple comparisons were applied when significant differences ($\alpha < 0.05$) were observed. Comparisons included mean point counts for active reproductive tissue (the sum of developing, ripe, and spawning categories); the ADG and VCT categories; total nutritive tissue (the sum of ADG and VCT categories); and the ADG:VCT ratio (Lowe et al., 1982). Months in which not all sites were sampled and periods where data were not sampled monthly were excluded. For the 1989–1991 study, *a priori* Mann-Whitney rank sum tests were used to compare proportions of reproductive and nutritive cells between sites within the terminal area—B5 and SI—and those outside of the terminal area—5M and GC. Pearson correlation values (r and r^2) between reproductive and

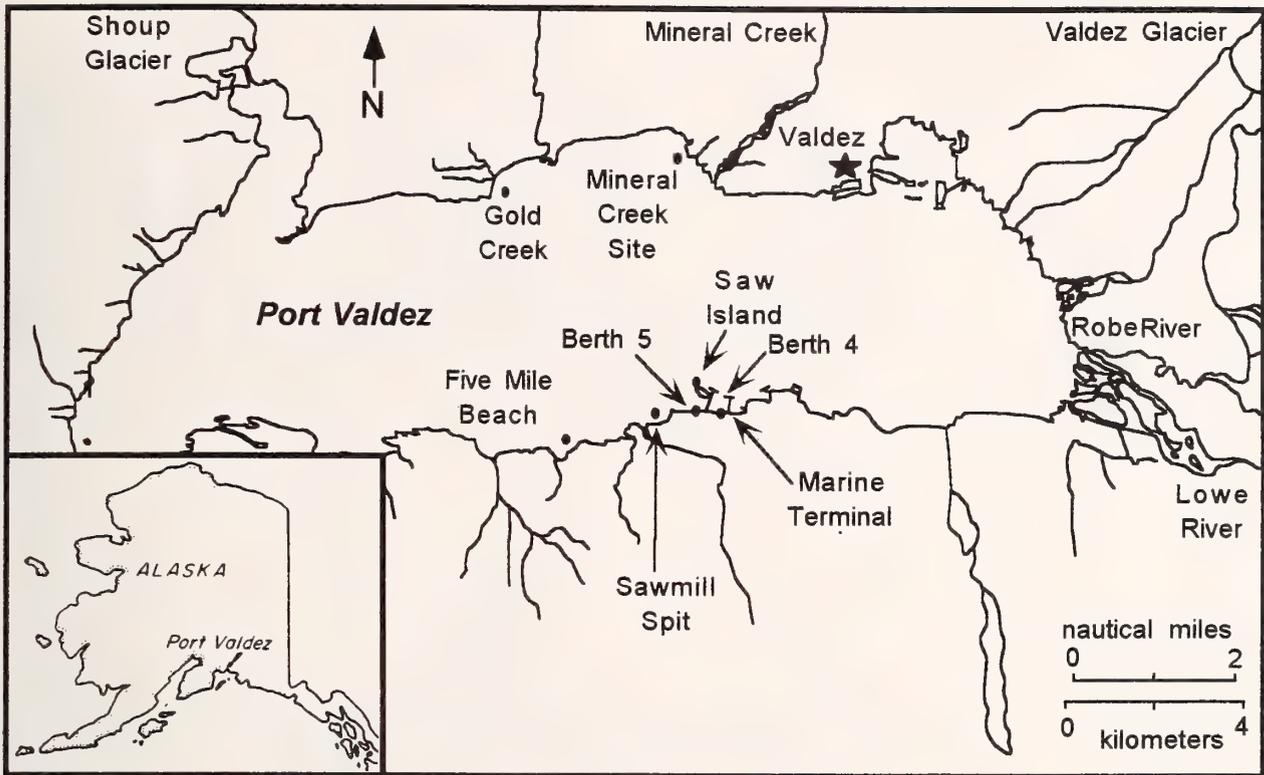


Figure 1

Map of intertidal sites sampled in 1980–1982 and 1989–1991. Sites sampled in 1980–1982 are Berth 4, Sawmill Spit, and Mineral Creek. Sites sampled in 1989–1991 are Berth 5, Five Mile Beach, Gold Creek, and Saw Island.

nutritive storage tissue volume fractions were determined for the time periods November 1980 to September 1981, November 1981 to September, March to October 1990, and March to July 1991. The coefficient of correlation (r) determines the direction (increasing or decreasing) and strength of the relationship between variables. The coefficient of determination (r^2) measures the amount of variation within each variable that is accounted for by any relationship between the variables. Both are useful statistics that measure the association of variables, in this case, the reproductive and nutritive storage cycles.

RESULTS

Observed surface-water temperature ranged from -2°C during winter to 14°C during summer (Figure 2). Surface-water salinity ranged from 0‰ in summer to 33‰ in winter. Surface-water turbidity ranged from 0.6 mg l^{-1} to 244.3 mg l^{-1} (the winter maximum) with a summer maximum of 209.6 mg l^{-1} . Mean surface-water turbidity tended to increase during summer, but winter values were often high as a result of storms and winter winds.

The reproductive and nutritive cycles for mussels in Port Valdez are shown in Figures 3 and 4. Volume fractions of developing follicles were typically first observed in No-

vember and increased throughout the winter. Ripe follicles were typically observed in March–April and occasionally occurred as early as February. In March of 1991, unusually high proportions of ripe follicles were observed at all sites. Spawning follicles were generally observed in low proportions by March–April and high proportions by May and June. The proportion of spawning follicles generally decreased after July and were present in low volume fractions through September–October. The proportion of adipogranular cells (ADG) gradually decreased through winter and into early spring, the months of early- to mid-gametogenesis. Volume fractions of these nutritive cells generally reached low values (approaching a minimum volume fraction of zero) during March, April, and May (e.g., Berth 4 (B4) 1981–1982) prior to spawning. The ADG cells generally increased in June to a maximum summer peak in July or August and were variable in fall and early winter with a second peak occasionally observable in September–October to January. Vesicular connective tissue (VCT) volume fractions VCT also showed decreases through the winter but remained relatively high compared to ADG cells. The VCT cells usually reached minimum values between April and June and increased in the following months, with peaks often occurring in August and again in January. Minimum proportions of

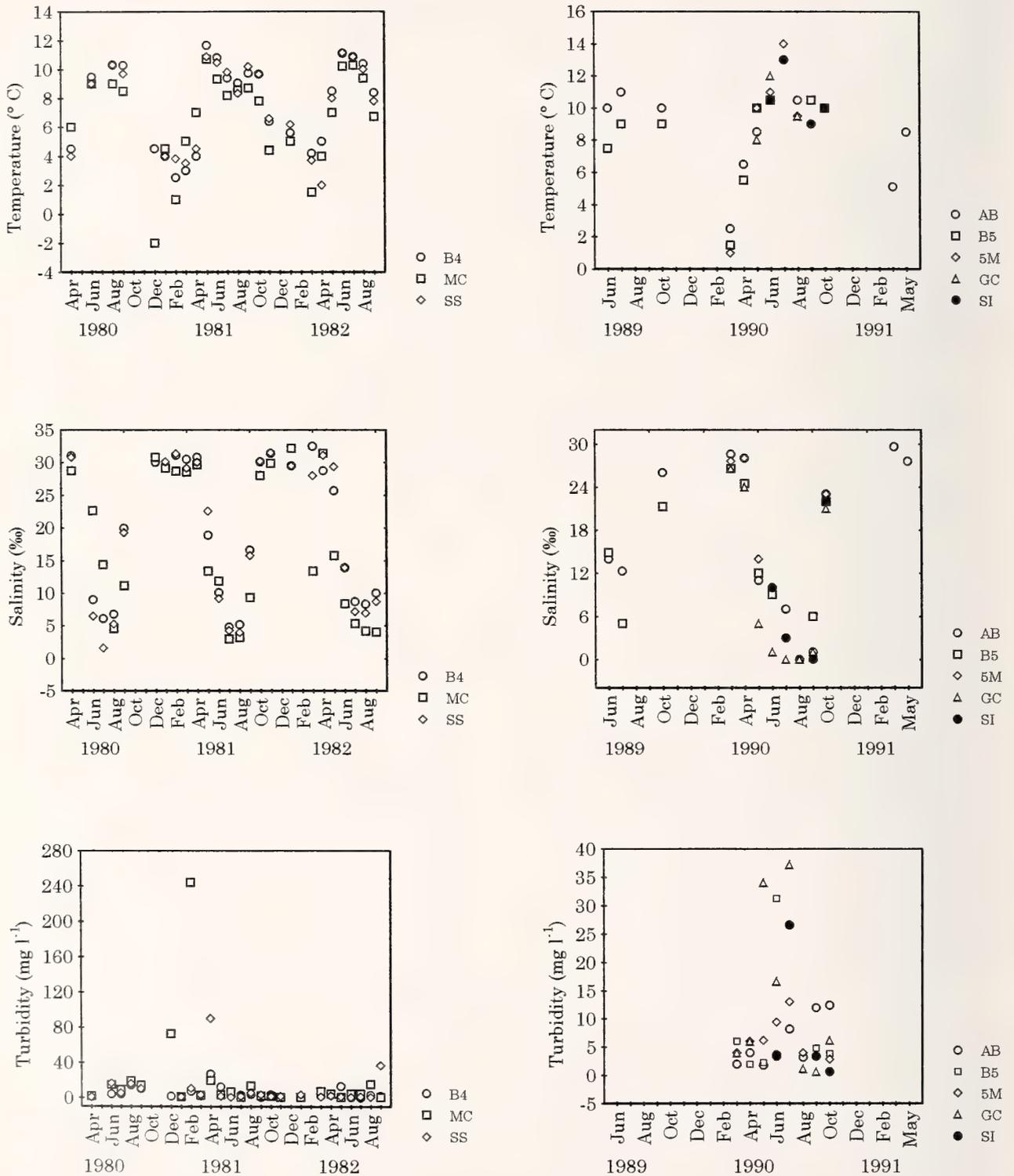


Figure 2

Physical data for all sites sampled in Port Valdez from March 1980 to September 1982 and April 1989 to May 1990. Data for 1991 is courtesy of the Solomon Gulch Fish Hatchery Valdez, Alaska. Symbols represent values at time of sampling.

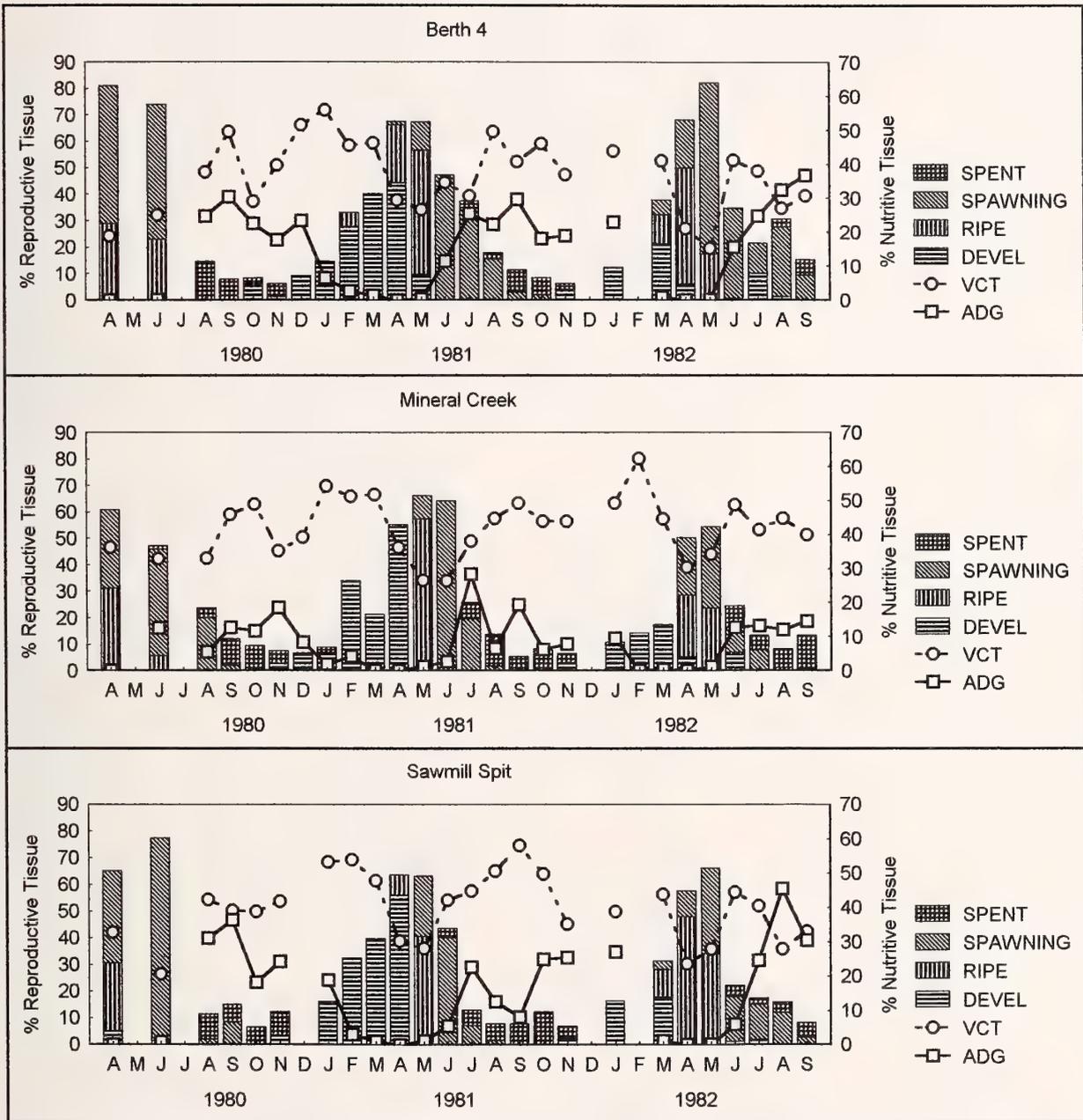


Figure 3

Volume fractions of cell categories for the 1980–1982 study period. The vertical axes are % volume fraction for the reproductive and nutritive tissues.

VCT cells generally occurred about two months later than minimum values for ADG cells. Decreased VCT cell volumes generally coincided with increased volume fractions of ripe and spawning follicles.

Some statistical differences were observed in data from both study periods. Comparisons between sites sampled in 1980–1982, using two way rank ANOVA with factor and

treatment as time and location, demonstrated significant differences for the gametic tissue ($P < 0.001$) and VCT tissues categories ($P = 0.005$). The multiple comparisons demonstrated that B4 had significantly higher quantities of mean reproductive tissues ($P < 0.05$) and lower quantities of mean VCT tissues than the Mineral Creek (MC) and Sawmill Spit (SS) sites. SS demonstrated significantly

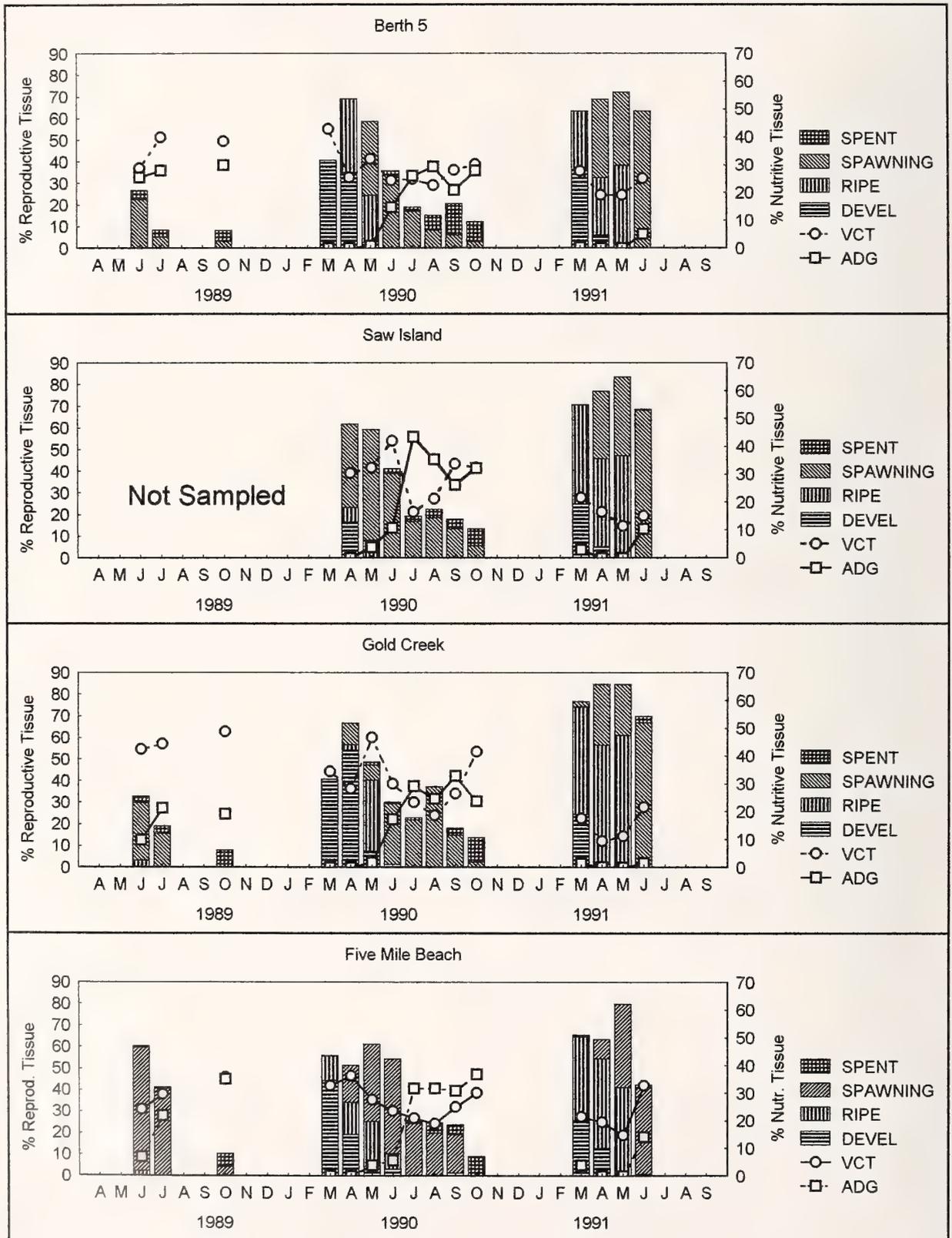


Table 1

Pearson product moment coefficients of correlation (r) and coefficients of determination (r^2) between total gametic and total nutritive tissue volume fractions. The negative r values signify that total nutritive cell volume fractions decrease as total gametic volume fractions increase. n = sample size.

Site	Months	n	r	r^2	P
Berth 4	Nov. 80–Sep. 81	120	−0.842	0.709	<0.001
Berth 4	Nov. 81–Sep. 82	94	−0.839	0.704	<0.001
Mineral Creek	Nov. 80–Sep. 81	113	−0.699	0.489	<0.001
Mineral Creek	Nov. 81–Sep. 82	85	−0.582	0.339	<0.001
Sawmill Spit	Nov. 80–Sep. 81	104	−0.836	0.699	<0.001
Sawmill Spit	Nov. 81–Sep. 82	95	−0.816	0.666	<0.001
Berth 5	Mar. 90–Oct. 90	109	−0.905	0.819	<0.001
Berth 5	Mar. 91–Jun. 91	54	−0.912	0.832	<0.001
Five Mile Beach	Mar. 90–Oct. 90	111	−0.940	0.884	<0.001
Five Mile Beach	Mar. 91–Jun. 91	55	−0.894	0.799	<0.001
Gold Creek	Mar. 90–Oct. 90	109	−0.915	0.837	<0.001
Gold Creek	Mar. 91–Jun. 91	58	−0.928	0.861	<0.001
Saw Island	Apr. 90–Oct. 90	103	−0.926	0.857	<0.001
Saw Island	Mar. 91–Jun. 91	56	−0.966	0.933	<0.001

higher quantities of mean reproductive tissues than MC. Two way rank ANOVA comparisons for the 1989–1991 study showed no significant differences. *A priori* comparisons of gametic tissue and nutritive cell data between sites within and those outside the terminal area for the 1990–1991 study period, showed no differences with the Mann-Whitney rank sum test ($P = 0.87$ and 0.93 , respectively). Significant negative correlation values between increases in reproductive-tissue volume fractions and decreases in total nutritive storage cell fractions for sites in 1980–1982 and 1989–1991 indicate a moderate to strong relationship (Table 1). The coefficients of determination (r^2) for the 1989–1991 study were generally higher than those of the 1980–1982 study, accounting for 79.9% to 93.3% of the variation between the reproductive and nutritive storage cycles for sites in 1989–1991 versus 33.9% to 70.9% for sites in the 1980–1982 study. Mussels from MC demonstrated much lower coefficients of determination, accounting for 48.9% and 33.9% of the variation between the reproductive and nutritive storage cycles for the periods November 1980–September 1981 and November 1981–September 1982, respectively.

DISCUSSION

Development of *Mytilus trossulus* gametes in Port Valdez begins in autumn (Figures 3,4) and continues throughout winter when mussels are frequently exposed to freezing

air temperatures during low tides (Hood et al., 1973; Feder & Keiser, 1980). Ripe follicles are apparent in March–April as surface-water temperatures increase to about 5°C. Spawning begins in late spring, is heaviest in May and June (when surface-water temperatures range between 5° to 10°C, salinity approaches 0‰, and turbidity is high: Feder & Keiser, 1980; Figure 2) and continues throughout the summer. After spawning commences, proportions of adipogranular cells (ADG) cells increase to a summer maximum in July, similar to observations by Lowe et al. (1982) and Emmett et al. (1987). However, unlike the results of Lowe et al. (1982) and Emmett et al. (1987), proportions of vesicular connective tissues (VCT) cells did not always follow that pattern. The summer increase and peak in VCT cells were sometimes delayed as much as 2 months, possibly in response to continued gametogenesis and/or shell growth. The delay in VCT cell renewal coincides with months of highest shell growth rates (Feder & Keiser, 1980). The late fall/winter maximum in the ADG and VCT cycles may represent storage of nutrients from the fall bloom.

Differences in the reproductive biology of mussels from Port Valdez attributable to hydrocarbons were not apparent during either study period. Shaw et al. (1986) demonstrated that mussel tissue from *M. trossulus* at the marine terminal in 1980–1982 had hydrocarbon concentrations elevated above that of mussels from shores 3 km away. Feder & Shaw (1994) demonstrated no differences in pe-

Figure 4

Volume fractions of cell categories for the 1989–1991 study period. The vertical axes are % volume fraction for the reproductive and nutritive tissues.

roleum hydrocarbon concentrations for mussels within and outside the marine terminal area from 1989 to 1993, likely a result of changes in ballast water treatment methods that significantly decreased hydrocarbon output. During the 1980–1982 study period, reproductive tissues of mussels from the Berth 4 (B4) site did not demonstrate adverse effects of the elevated concentrations but instead, demonstrated significantly higher volume fractions of reproductive tissue than the other two sites. As well, in the 1989–1991 study, proportions of reproductive tissues at the Berth 5 (B5) and Saw Island (SI) sites were not significantly different ($P < 0.05$) from the other sites. If a sublethal response to hydrocarbons was present, it was minor and masked by variability within the reproductive and nutritive storage cycles at the B4, B5, and SI sites and by the differences in cycles between sites. Observations by Lobel et al. (1990) suggest that *M. trossulus* may be able to tolerate greater body burdens of pollutants than *M. edulis*, possibly contributing to the lack of observed response.

Although stress-related changes in the reproductive and nutritive storage cycles of mussels adjacent to the marine terminal were not observed, modification of these cycles occurred for mussels at Mineral Creek (MC), a site remote from the marine terminal. At B4, mussels occur on rock outcroppings that expose them to greater water movement and better food resources than on the gently sloping beaches at MC and SS (see discussion in Rodhouse et al., 1984). In contrast, MC, the site with the lowest proportion of active reproductive tissue, is a low-profile beach exposed to silt-laden, glacial melt-waters from nearby Mineral Creek. The overall mean surface-water temperature at MC was significantly lower than at B4 and Sawmill Spit (SS) ($P = 0.04$ and $P = 0.06$, respectively, with a t-test), and turbidity was higher and salinity lower at MC than at B4 ($P = 0.06$ and $P = 0.08$). The lower proportions of reproductive tissue and lower coefficients of determination at MC (Table 1) indicate less association between the reproductive and nutritive storage cycles. One possible explanation for this decoupling is that an increased proportion of nutrient resources is required for metabolic needs within the silt-stressed environment of MC, leaving less available for general reproductive activities. The general trend of lower coefficients of determination in 1980–1982, compared to 1989–1991, likely reflects the inclusion, in the latter period, of only months when the reproductive and nutritive cycles are closely coupled rather than a response to stress.

Mussels sampled in Port Valdez during 1991 demonstrated higher volume fractions of gametic tissue in early spring (Figure 4) compared to 1990. Two way rank ANOVA, with the factor and treatment as location and time (the reverse of previous designs), showed significantly higher levels of reproductive tissue ($P < 0.05$) in April and May of 1991 than in April to June 1990. The higher proportions of reproductive tissue in 1991 suggest a response to an

increased food resource (see discussions in Newell et al., 1982; Fell & Balsamo, 1985).

The year-long reproductive cycle for *M. trossulus* from Port Valdez differs from cycles of mussels for other populations along Pacific coasts. The reproductive cycle for *M. trossulus*, at Vancouver Island, British Columbia (Emmett et al., 1987) begins with gamete development in March, has a summer to autumn spawning period, and follicles are quiescent during winter. In Port Valdez, mussels use a more “conservative” reproductive strategy (Bayne, 1976; Seed & Suchanek, 1992) with gametogenesis continuing through the winter. Moore & Reish (1969), studying mussels in Southern California (a mixed population of *M. galloprovincialis* Lamarck, 1819, and *M. trossulus*; McDonald et al., 1991), observed development and spawning during the cooler winter months (October to February)—the reverse of the reproductive cycle in Port Valdez—when water temperature fell below 18–20°C. As temperatures increased above 18°C in spring, spawning ceased. Suguira (1959) demonstrated a reproductive pattern for *M. galloprovincialis* (originally described as *M. edulis*; McDonald et al., 1991) along the Western Pacific coast near Tokyo similar to that observed by Moore & Reish (1969). Sustained water temperatures above 18–20°C appear to be the upper limit for reproduction of *Mytilus* along the Pacific Coast. Summer water temperatures often reach these critical temperatures in temperate areas of the Pacific (Moore & Reish, 1969). These critical temperatures were occasionally observed by Emmett et al. (1987) but were never observed during the study period in Port Valdez. There is no evidence of a critical lower temperature value for gametogenic development in *M. trossulus* in Port Valdez where exposure to extreme temperature conditions (air temperatures to at least –10°C and water temperatures to at least 0°C) is common. Gametogenic differentiation at temperatures close to 0°C was described for subtidal mussels in the Baltic by Kautsky (1982).

Similarities were observed between European *M. edulis* and Pacific populations of *M. trossulus*. *Mytilus* in Britain (Seed, 1976; Lowe et al., 1982; Seed & Suchanek, 1992) and those in the subarctic environment of Port Valdez follow a conservative reproductive strategy in spite of great differences in the environmental regimes between the two areas. In the two mussel populations, gametogenesis begins in autumn and continues through winter when food resources are limited. The strategy is conservative in that nutrient reserves are stored in summer for use for gametogenesis during winter in contrast to an opportunistic strategy of utilizing food resources when available. Thus, subtidal Baltic Sea mussels (Kautsky, 1982) and Newfoundland mussels (Thompson, 1984) demonstrate an opportunistic reproductive strategy, as also observed for mussels from Vancouver, British Columbia (Emmett et al., 1987), where gametogenic development stops in winter when food is limited. Although Seed & Suchanek (1992) indicated that food availability is the primary factor con-

trolling reproductive strategy, it is apparent that *Mytilus* spp., can utilize either conservative or opportunistic strategies.

In summary, the aspects of the reproductive biology of *M. trossulus* from Port Valdez presented here demonstrate features similar to *M. edulis* elsewhere and follow the conservative reproductive strategy of Bayne (1976). The reproductive biology of mussels examined in this study was not influenced by proximity to the marine terminal. However, stress on mussels at the Mineral Creek site was likely due to the influence of glacially derived, silt-laden water. It is apparent that *M. trossulus* populations in the northern fjordic environment of Port Valdez are resilient to natural and anthropomorphic disturbances.

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New Species of Neritid Gastropods from Cretaceous and Lower Cenozoic Strata of the Pacific Slope of North America

by

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Abstract. Ten new species of neritid gastropods are described from the fossil record of the Pacific slope of North America. *Nerita* (*Amphinerita*) *eos* sp. nov., from northern California, is of Early Cretaceous (Hauterivian) age and is the earliest record of *Amphinerita*. *Nerita* (*Amphinerita*) *vacca* sp. nov., from northern California, is of Late Cretaceous (Turonian) age. *Nerita* (*Bajanerita*?) *larix* sp. nov., from Washington, is of middle early Eocene ("Capay") age. *Nerita* (subgenus?) *salsa* sp. nov., from northern California, is of Turonian age.

Otostoma lucanus sp. nov., from southern California, is of Turonian age, and *Otostoma?* *atopos* sp. nov., from northern California, is of late Early Cretaceous (Albian) age.

Corsania (*Corsania*) *allisoni* sp. nov., from Baja California, Mexico, is of Albian age. *Corsania* (*Januncia*) *rhoga* sp. nov., from northern California, is of early Paleocene age, and *Corsania* (*J.*) *susana* sp. nov., from southern California, is of late Paleocene age. *Corsania* (*J.*) *oraria* sp. nov., a Washington species of middle early Eocene age, is the youngest record of this genus and subgenus and the first record of them in the Eocene of the Pacific coast of North America.

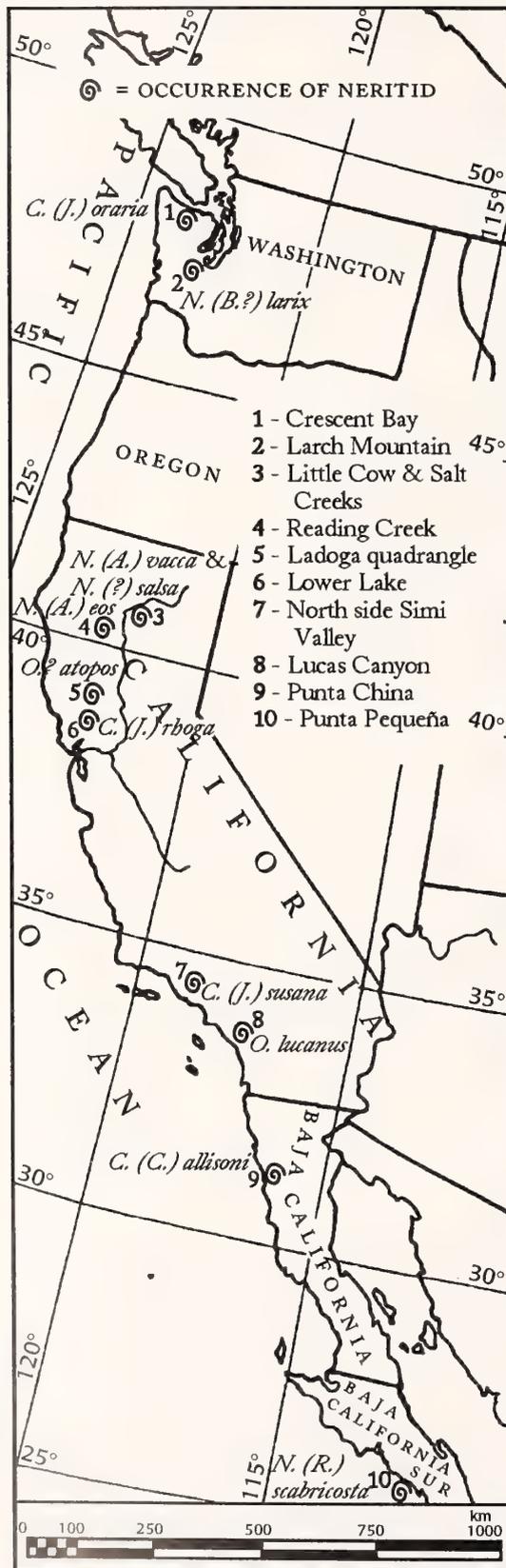
Although neritids are of sufficiently uncommon occurrence north of Baja California to make them of limited biostratigraphic importance, their thermophilic tendencies make them useful in recognizing periods of warmer climate.

INTRODUCTION

The gastropod family Neritidae has a geologic range from Triassic to Recent (Keen & Cox, 1960; Tracey et al., 1993), but members of this family are uncommon to rare in the rock record. This scarcity is due, in large part, to the preference of these gastropods for living in rocky shoreline habitats, which are usually sites of erosion rather than deposition. In addition, many of the fossil neritid specimens, especially the smooth-shelled ones whose apertures are filled with hardened rock matrix, are overlooked because they resemble naticid gastropods. The apertures of

neritids, however, are quite distinct, but normally require very careful and time-consuming cleaning.

Mesozoic neritids from the Pacific coast of North America are rare for the above reasons. In addition, the record is not continuous because neritids, which are warm-water gastropods, only lived in this area during periods of warm climate. The neritid's discontinuous record parallels that of other thermophilic mollusks, such as the record of the bivalve *Plicatula*, which has been recently studied by Squires & Saul (1997). While examining the extensive collection of Cretaceous and Cenozoic fossils at the Natural History Museum of Los Angeles County, we came across impor-



tant new finds of neritids, as well as undescribed neritids that had been discovered by the late paleontologists W. P. Popenoe and E. C. Allison. These new neritids are the basis of this report. The geographic distribution of each new species is shown in Figure 1, and the geologic range of each is shown in Figure 2. Today, the northernmost record of a neritid on the Pacific coast of North America is *Nerita (Ritena) scabricosta* Lamarck, 1822, which ranges from Punta Pequeña at Bahía San Juanico (26°15'N) on the outer coast of Baja California Sur, Mexico, to Ecuador (Keen, 1971).

Abbreviations used are: CIT, California Institute of Technology (collections now stored at LACMIP); CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California Museum of Paleontology (Berkeley); UCLA, University of California, Los Angeles (collections now stored at LACMIP).

SYSTEMATIC PALEONTOLOGY

Family NERITIDAE Rafinesque, 1815

Subfamily NERITINAE Rafinesque, 1815

Genus *Nerita* Linnaeus, 1758

Type species: *Nerita peloronta* Linnaeus, 1758, by subsequent designation (Montfort, 1810); Recent, South Florida, West Indies, and Bermuda.

Subgenus *Amphinerita* Martens, 1887

Type species: *Nerita umlaasiana* Krauss, 1848, by subsequent designation (Baker, 1923); Recent, South Africa.

Discussion: *Amphinerita* is closely allied to and part of the same clade as subgenus *Linnerita* Vermeij, 1984, and the most diagnostic feature used to distinguish between the two is the type of sculpture on the operculum (Vermeij, 1984). *Amphinerita* differs from most species of *Linnerita* by having an elevated spire, a smooth shell, and a parietal callus that is not transversely wrinkled (Vermeij, 1984). In addition, in our study of modern specimens of these two taxa, we observed that *Linnerita* can have small spiral wrinkles adjacent to the inner lip teeth. *Amphinerita* has a fossil record extending back to the Late Cretaceous (Wenz, 1938; Keen & Cox, 1960), whereas subgenus *Linnerita* has no known fossil record (Vermeij, 1984).

Amphinerita has a sharp-edged inner lip with a nearly

Figure 1

Index map for occurrences of new species of neritids from Washington to Baja California.

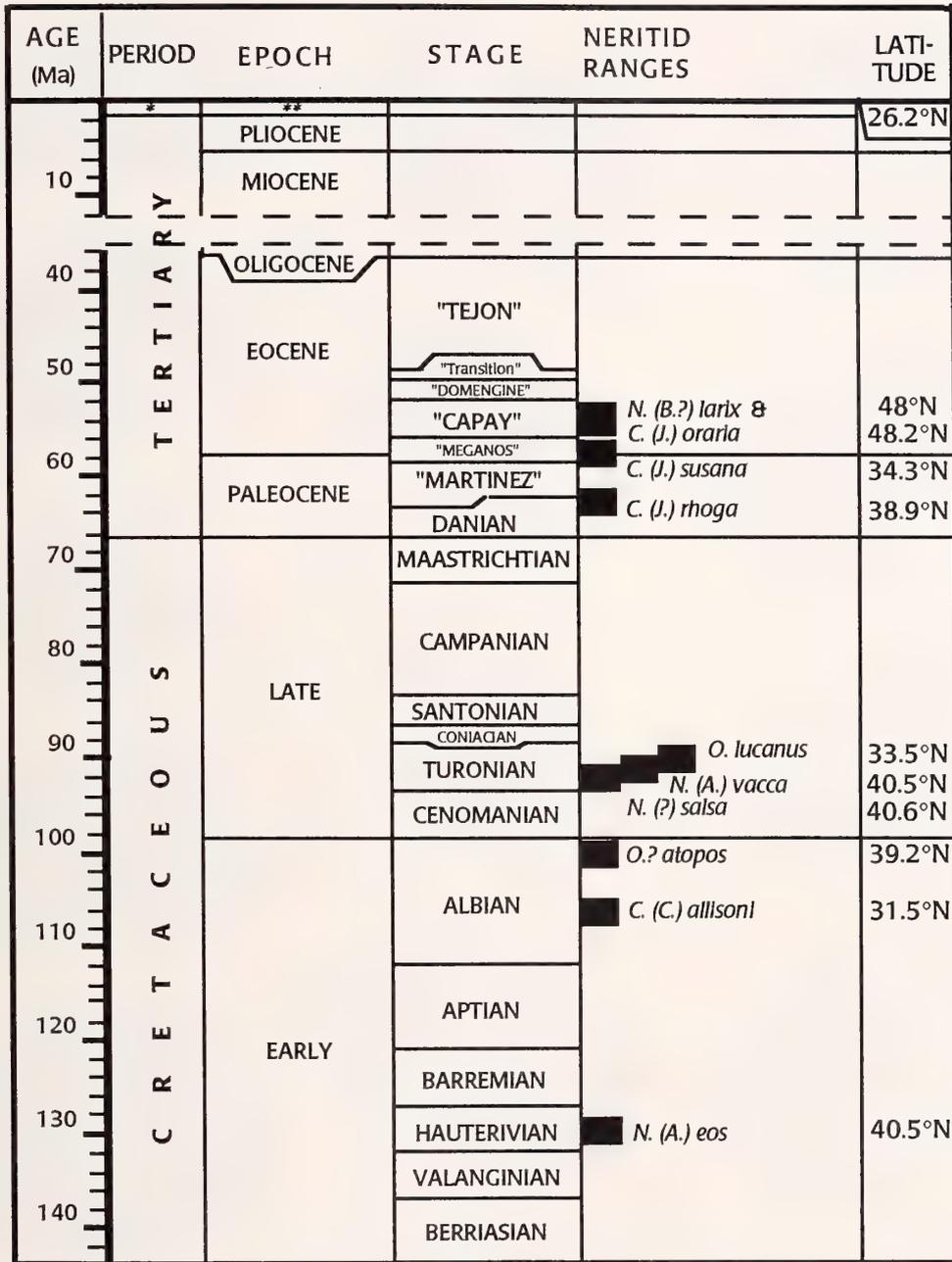


Figure 2

Time ranges of the new species of neritids. * = Quaternary; ** = Pleistocene.

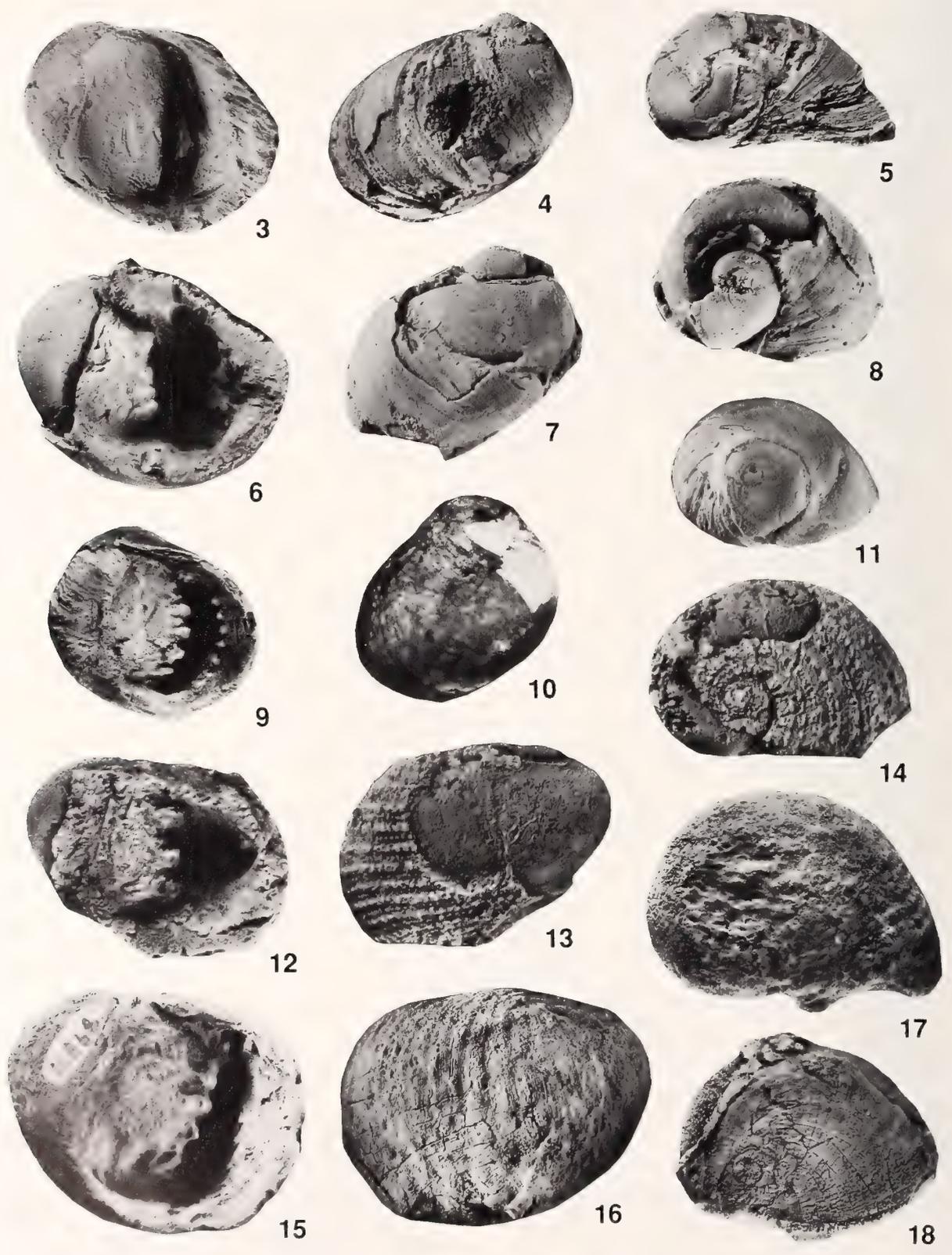
straight trend; its edge is commonly somewhat concave and finely toothed medially.

Nerita (Amphinerita) eos Saul & Squires, sp. nov.

(Figures 3-5)

Diagnosis: An *Amphinerita* with broad, flat, and smooth deck and smooth inner lip.

Description: Shell small, obliquely ovate, globose, broader than high, thin-shelled, consisting of 2½ whorls; spire moderately elevated; body whorl rapidly expanding with rounded shoulder. Body whorl relatively smooth, except for some irregularly spaced growth rugae, especially near outer lip. Growth lines closely spaced and prosocline. Aperture moderately large, sub-ovate. Deck wide, smooth, and flat. Posterior end of deck with shallow but prominent



groove. Trend of inner lip very slightly sinuous, nondentate.

Dimensions of holotype: Height 7.5 mm, width 11.4 mm.

Holotype: LACMIP 7880.

Type locality: LACMIP loc. 26600, latitude 40°35'30"N, longitude 122°54'28"W.

Distribution: Budden Canyon Formation, Ogo Member, Trinity Alps, Trinity County, northern California (LACMIP loc. 26600).

Geologic age: Early Cretaceous (Hauterivian).

Discussion: Only a single specimen was found. It is complete and shows overall good preservation. The apertural area is well preserved. The shell is missing on the spire, and the sutural area between the spire and body whorl is poorly preserved. The teleoconch exterior is somewhat weathered.

The new species most closely resembles *Nerita ovoides* Geinitz (1871–1875:pl. 57, fig. 4a, b) from strata in Germany that Gignoux (1950:421) correlated to the early Late Cretaceous (Cenomanian). The new species differs from *N. ovoides* by having a slightly more elevated spire, a longer inner lip, and a straighter abapical side of the deck.

The new species superficially resembles *Neritina incompta* White (1879:308–309, pl. 7, figs. 6–6c) from Upper? Cretaceous rocks in Wyoming. The exact age of these rocks is uncertain (Erickson, 1974:162). The new species differs from *N. incompta* by having a much wider deck area.

For a comparison of *N. (A.) eos* with *N. (A.) vacca* sp. nov., see "Discussion" under the latter.

The operculum of the new species is not known, as is the case for most extinct neritids, but the new species is assigned to subgenus *Amphinerita* based on the presence of a moderately elevated spire, a smooth shell, and a parietal callus without axial wrinkles. There are growth rugae on the body whorl of *N. (A.) eos*, but they are quite unlike the close-spaced, regularly spaced, and rather broad

axial wrinkles on the living species *N. (Linnerita) antiquata* Recluz, 1853, which has the best developed axial wrinkles of any species of *Linnerita*.

Associated fauna at the type locality of *N. (A.) eos* includes the shallow-marine bivalves *Yaadia* and *Pholadomya*. A Hauterivian age is indicated by ammonites found nearby along Reading Creek (Imlay, 1960).

The new species is the earliest record of *Amphinerita*. Previously, this subgenus was only known from the Late Cretaceous (Wenz, 1938). The new species is the earliest record of genus *Nerita* from the west coast of North America and, as far as we know, the earliest record of this genus anywhere in the world.

Nerita (Amphinerita) eorex Vokes (1939:180–181, pl. 22, figs. 24, 26, 29) from shallow-marine rocks in the middle Eocene Domengine Formation of central California (Vokes, 1939; Kappeler et al., 1984, table 2) is the only previously reported *Amphinerita* from the fossil record of the Pacific coast of North America. Vokes's species has five subequal, relatively large teeth (strength decreasing posteriorly) and a very low spire, and is not an *Amphinerita*. His species, as well as *Nerita* cf. *N. (Amphinerita) eorex* Vokes of Squires (1984:16, fig. 6a) from the middle lower Eocene ("Capay Stage") part of the Llajas Formation in Simi Valley, southern California, are judged by us to be juvenile stages (less than 10 mm high) of *Velates perversus* (Gmelin, 1791), a nearly cosmopolitan species that is also found in "Capay Stage" and possibly "Domengine Stage" strata of southern California and Baja California Sur, Mexico (Woods & Saul, 1986; Squires, 1987; Squires & Demetrio, 1992). The growth stages of *V. perversus* involve a change from tightly coiled juvenile whorls with a globose-naticiform shape, a subangulate shoulder, fewer teeth, and a much thinner callus on the inner lip to reduced-coiled adult whorls with a very extensive callus and a patelliform shape (Woods & Saul, 1986; Squires, 1987; Savazzi, 1992). These features are like those observed on *N. (A.) eorex* and *N. cf. N. (A.) eorex*. *Velates perversus* is very similar to *V. californicus* Vokes (1935:384–385, pl. 26, figs. 3–8). The juvenile stage of *V. perversus* differs from *V. californicus* in

Explanation of Figures 3 to 18

Specimens are coated with ammonium chloride, unless otherwise stated. Figures 3–5. *Nerita (Amphinerita) eos* Saul & Squires, sp. nov., holotype LACMIP 7880, LACMIP loc. 26600, height 7.5 mm, width 11.4 mm, ×5. Figure 3: apertural view. Figure 4: abapertural view. Figure 5: apical view. Figures 6–8. *Nerita (Amphinerita) vacca* Saul & Squires, sp. nov. Figure 6: paratype LACMIP 7882, LACMIP loc. 10751, apertural view, height 10 mm, ×3.8. Figures 7–8: holotype LACMIP 7881, height 11.6 mm, width 12.5 mm, ×3.1. Figure 7: abapertural view. Figure 8: apical view. Figures 9–11. *Nerita (Bajanerita?) larix* Saul & Squires, sp. nov., holotype LACMIP 7883, CSUN loc. 1563, height 9 mm, width 10.3 mm, ×3.8. Figure 9: apertural view. Figure 10: abapertural view, uncoated. Figure 11: apical view. Figures 12–14. *Nerita* (subgenus?) *salsa* Saul & Squires, sp. nov. Figures 12–13: holotype LACMIP 7884, LACMIP loc. 10773, height 6 mm, ×5.6. Figure 12: apertural view. Figure 13: abapertural view. Figure 14: paratype LACMIP 7885, LACMIP loc. 10760, apical view, width 5 mm, ×9. Figures 15–18. *Ostostoma lucanus* Saul & Squires, sp. nov. Figures 15–17: holotype LACMIP 7886, LACMIP loc. 16868, height 23.3 mm, width 30.3 mm, ×1.7. Figure 15: apertural view. Figure 16: abapertural view. Figure 17: apical view. Figure 18: paratype LACMIP 7887, apical view, width 18 mm, ×2.4.

that *V. perversus* has a subangulate shoulder rather than a rounded one. In addition, the adult stage of *V. perversus* has dentition expressed only as projections (in some cases bifurcating) of the inner lip edge, whereas *V. californicus* has much stronger and better developed dentition (Woods & Saul, 1986). *Nerita* (*A.*) *eorex* and *N. cf. N. (A.) eorex* have a subangulate shoulder like *V. perversus*. Saul (1983a) reported *V. californicus* from the lower Eocene part of the "Meganos Stage" of the upper 100 m of the Santa Susana Formation on the south side of Simi Valley, southern California. Squires (1991) tentatively identified this species from the same rocks and corroborated the age, based on calcareous nannofossil data.

Etymology: The species name is derived from *eos*, Greek, meaning dawn or early.

Nerita (Amphinerita) vacca Saul & Squires, sp. nov.

(Figures 6–8)

Diagnosis: An *Amphinerita* with three small teeth on inner lip and posterior portion of inner lip prominently bulged.

Description: Shell small (up to 11.6 mm high), obliquely ovate, globose, thick shelled, two whorls; spire moderately elevated; body whorl rapidly expanding with rounded shoulder. Body whorl smooth. Growth lines prosocline. Aperture moderately large, sub-circular. Deck callus smooth. Inner lip with three small teeth; trend of inner lip straight on anterior half, posterior portion prominently semi-triangular and protruding. Outer lip thickened and showing tendency to be flared. Interior of outer lip smooth.

Dimensions of holotype: Height 11.6 mm, width 12.5 mm.

Holotype: LACMIP 7881.

Type locality: LACMIP loc. 10751, latitude 40°38'47"N, longitude 122°12'30"W.

Paratype: LACMIP 7882; height 10 mm (incomplete), width 12.6 mm; same locality as holotype.

Distribution: Redding Formation, Melton Sandstone Member, Little Cow Creek valley, Shasta County, northern California (LACMIP loc. 10751).

Geologic age: Late Cretaceous (Turonian).

Discussion: Two specimens were found. Only the holotype has the spire preserved. Both specimens are missing shell on the body whorl, and both have incomplete outer lips.

The new species most closely resembles *Nerita (Amphinerita) picea* Récluz, 1841, an extant species that has been reported (Kay, 1979) as the dominant nerite along shorelines in the Hawaiian Islands. The new species differs from *N. (A.) picea* by not having any fine spiral ribs. The operculum of the new species is not known, but the new species is assigned to subgenus *Amphinerita* rather than to the closely allied subgenus *Linnerita*, based on the presence

of a more elevated spire, a smooth shell, and no transverse wrinkles on the deck area near the inner lip teeth.

The new species differs from *Nerita (Amphinerita) eos* by having teeth on the inner lip and a bulging, semi-triangular area on the posterior portion of the inner lip.

The new species was found in strata that were correlated to the Turonian Stage by Jones et al. (1978). The locality (LACMIP 10751 = CIT 1265) of the new species is part of a series of CIT localities plotted on a generalized geologic map and included in a megafaunal list within the report by Jones et al. (1978). They did not report the new species.

Etymology: The species is named for its type locality in Little Cow Creek valley, Latin, *vacca* meaning cow.

Subgenus *Bajanerita* Squires, 1993

Type species: *Nerita (Bajanerita) californiensis* (White, 1885), by original designation; Late Cretaceous, Baja California, Mexico.

Discussion: *Bajanerita* has an inner lip with a convex trend, and this is one of the main distinguishing features of this subgenus. The new species described below has this feature and also the following features of *Bajanerita*: elevated spire, smooth body whorl, many equal-sized teeth on the interior of the outer lip, and a divaricate color pattern. The new species, however, has certain characteristics that are not known for *Bajanerita*. These are the following: four teeth on the inner lip, narrow teeth on the inner lip, a swollen callus, and a thickened outer lip. The new species might belong to *Bajanerita* or belong to a closely allied new subgenus. We are very hesitant to name a new subgenus based on a single specimen.

Nerita (Bajanerita?) larix Saul & Squires, sp. nov.

(Figures 9–11)

Diagnosis: A moderately high-spined shell with four, narrow teeth on the inner lip, a thickly swollen callus, and a thickened outer lip.

Description: Shell small (up to 9 mm high), sub-rhomboid, convex, consisting of approximately 2½ whorls; spire elevated, blunt body whorl rapidly expanding, early whorls nearly hidden by body whorl; suture between spire and body whorl impressed. Body whorl smooth. Growth lines prosocline, especially near suture. Color pattern intricately divaricate. Aperture moderately large, sub-circular; apertural opening narrow. Deck callus swollen and smooth. Trend of inner lip convex; inner lip with four equal teeth, narrow and widely spaced. Outer lip thickened, with about seven small, equal-sized teeth on its inner margin.

Dimensions of holotype: Height 9 mm, width 10.3 mm.

Holotype: LACMIP 7883.

Type locality: CSUN 1563 [= LACMIP loc. 16655], latitude 47°59'03"N, longitude 123°8'12"W.

Distribution: Upper part of Crescent Formation, Larch Mountain, Black Hills, Thurston County, southwestern Washington (CSUN loc. 1563).

Geologic age: Middle early Eocene ("Capay Stage").

Discussion: Only the holotype is known, but it is well preserved.

The new species resembles *Nerita vokesi* Durham (1944: 156, pl. 17, figs. 11, 12) from UCMP loc. A-1802 in the Quimper Formation, Discovery Bay, Jefferson County, Washington. Durham (1944:117) assigned the beds at this locality to his *Molopophorus stephensoni* Zone. Armentrout (1975) assigned this zone to the uppermost Eocene part of his Galvinian Molluscan Stage. The new species differs from *N. vokesi* in the following features: an inner lip with a convex rather than a straight trend, larger shell size, a more? elevated spire, and, apparently, a convex callus. Although Durham (1944) reported that *N. vokesi* has a sharp and smooth outer lip, these features are not observable on the type specimens. The only type specimen that shows the aperture is a worn-down specimen that is essentially only a cross section of the aperture. We have not been able to locate any other specimens of this species that fully show all the details of the spire, the aperture, and the callus. Until such specimens are found, the subgenus assignment of *N. vokesi* cannot be positively determined.

As mentioned above, the new species has some of the characteristics of subgenus *Bajanerita*, which is known only as the species *N. (B.) californiensis* (White, 1885:pl. 5, figs. 7, 8; Squires, 1993, fig. 2.1-2.8). Although *N. (B.) californiensis* has been reported (Squires, 1993) from the Upper Cretaceous (upper Campanian to lower Maastrichtian) Rosario Formation at Punta Banda, Baja California, Mexico, our study of the LACMIP collection revealed that this species is also present at LACMIP loc. 24137 in the Upper Cretaceous Jalama Formation, Santa Barbara County, southern California. Dailey & Popenoe (1966) assigned the age of this formation to the late Campanian, or possibly early Maastrichtian. The new species differs from *N. (B.) californiensis* by having a slightly higher spire, four rather than three inner lip teeth, narrower inner lip teeth, a thicker callus, fewer outer lip teeth, and a thickened outer lip.

Etymology: The species is named for Larch Mountain; from *larix*, Latin, meaning larch.

Nerita (subgenus?)

Discussion: The new species described below has the main morphologic characteristics listed in Keen & Cox (1960) that generally apply to genus *Nerita*; namely, a sturdy shell, spirally ribbed, and a well-developed inner lip deck area. The new species, however, does not match with any of the descriptions of the known subgenera of *Nerita*. We are hesitant to name a new subgenus to accommodate the new

species because it has somewhat poor preservation, especially of the outer lip and callus areas.

Nerita (subgenus?) *salsa* Saul & Squires, sp. nov.

(Figures 12-14)

Diagnosis: A *Nerita* with barely elevated to flat spire, noded spiral ribs, adult inner lip with three squarish teeth, and a smooth callus.

Description: Shell small (up to 6 mm high), neritiform, thin-shelled, consisting of approximately two whorls; spire lowly elevated to flat; body whorl rapidly expanding with a tabulate shoulder. Body whorl covered with evenly spaced and noded primary spiral ribs, becoming slightly coarser toward base of whorl. Interspaces with a single, noded secondary spiral rib. Aperture moderately large, subquadrate. Deck callus moderately thick and smooth. Trend of inner lip straight; inner lip on juvenile specimens (< 4 mm height) with one tooth, located posteriorly; inner lip on larger specimens with three, slightly subequal squarish and widely spaced teeth; posteriormost tooth the most projecting. Outer lip thickened, at least anteriorly.

Dimensions of holotype: Height 6 mm, width 7 mm.

Holotype: LACMIP 7884.

Type locality: LACMIP loc. 10773, latitude 40°40'52"N, longitude 122°11'50"W.

Paratype: LACMIP 7885, height 4 mm, width 5 mm, LACMIP loc. 10760.

Distribution: Redding Formation, Bellavista Sandstone Member, Shasta County, northern California (LACMIP locs. 10760 and 10773).

Geologic age: Late Cretaceous (Turonian).

Discussion: Five specimens were found. Four are from LACMIP loc. 10773, but only two of these show moderately good preservation. A single specimen was found at LACMIP loc. 10760, and it is poorly preserved. Only the holotype shows the inner lip well, but the posterior portion of the aperture is poorly preserved. None of the specimens has the outer lip intact, except the paratype, which has only the anteriormost part present. Shell is missing on the spire area of most of the specimens.

The new species is unlike any known neritid species.

The new species was found in strata that were correlated to the Turonian Stage by Jones et al. (1978). The two localities (LACMIP 10760 = CIT 1438; LACMIP 10773 = CIT 1217) where the new species is present are part of a series of CIT localities plotted on a generalized geologic map and included in a megafaunal list within the report by Jones et al. (1978). They did not report the new species.

Etymology: The species is named for Salt Creek; from *salsus*, Latin, meaning salted.

Genus *Otostoma* d'Archiac, 1859

Type species: *Nerita rugosa* Hoeninghaus, 1830, by indication (Douvillé, 1904); see Squires & Saul (1993) for a thorough discussion of the complex history of the type species of *Otostoma*; Late Cretaceous (Maastrichtian), Netherlands.

Otostoma lucanus Saul & Squires, sp. nov.

(Figures 15–18)

Diagnosis: A medium-sized, thick-shelled *Otostoma* with moderately wide-spaced, coarse axial ribs on body whorl shoulder and five squarish teeth on inner lip.

Description: Shell medium (up to 23.3 mm high), globose, thick-shelled, consisting of two to three whorls; spire flat; body whorl rapidly expanding with rounded shoulder. Body whorl with numerous, coarse axial ribs, obsolete? toward the base of whorl; axial ribs moderately wide-spaced with ribs narrower than the interspaces. Aperture large, sub-circular. Deck wide and smooth; deck callus present in medial and parietal areas. Inner lip with five coarse, squarish teeth, becoming smaller anteriorly. Outer lip thickened.

Dimensions of holotype: Height 23.3 mm, width 30.3 mm.

Holotype: LACMIP 7886.

Type locality: LACMIP loc. 16868, latitude 33°33'N, longitude 117°31'29"W.

Paratype: LACMIP 7887, height 12.2 mm, width 18 mm, same locality as holotype.

Distribution: Ladd Formation, Baker Canyon Member, Orange County, southern California (LACMIP loc. 16868).

Geologic age: Late Cretaceous (Turonian).

Discussion: Two specimens were found. Although the holotype is a worn specimen with a poorly preserved spire, the aperture is well preserved. The paratype is poorly preserved, except for the spire area.

The new species is most similar to *Otostoma ponticum* Archiac (1859:figs. 2, 2a, 3; Noetling, 1898:54–55, pl. 14, figs. 3, 3a, 3A, 4, 4a, 4A) from Upper Cretaceous rocks of Turkey and western Pakistan. The new species differs from *O. ponticum* by having wider spaced and coarser axial ribs and no tendency for cancellate ornamentation.

Although *Otostoma* is best known from the Old World Tethyan region, it achieved cosmopolitan warm-water distribution. Its earliest appearance is clouded, in part because the bounds of the genus have been drawn differently by various workers. Keen & Cox's (1960) report of *Otostoma* from rocks of Late Jurassic age reflected their inclusion of *Lysoma* White, 1883, in *Otostoma*. Sohl (1965) adamantly considered *Lysoma*, which has a non-dentate inner lip, clearly distinct from *Otostoma* with its dentate

inner lip. Kase's (1984) report of *Otostoma* from strata of late Aptian age in Japan reflected his inclusion in *Otostoma* of the roughly sculptured species herein assigned to *Corsonia*. Undoubted *Otostoma* of Albian age from Texas, *O. marcouana* (Cragin, 1895) and *O. elpasensis* (Stanton, 1947), have been discussed by Stanton (1947); and *Otostoma* species of Albian age have been reported from Tunisia (Thomas & Peron, 1889) and Portugal (Choffat, 1902). Squires (1995) reported the youngest record of *Otostoma* to be late early to early middle Eocene and from southern California (see below).

The only other confirmed Cretaceous record of *Otostoma* from the Pacific coast of North America is *Otostoma aethes* Squires & Saul (1993:figs. 2–4) from uppermost Cretaceous or possibly lowermost Paleocene strata on the south side of Lake Nacimiento, San Luis Obispo County, California. The new species differs from *O. aethes* by having a circular aperture rather than a quadrate one, five rather than seven teeth on the inner lip, axial ribs, and no indication of spiral ribs.

The youngest record of *Otostoma* is *Otostoma bisculptata* (Hanna, 1927:pl. 57, figs. 4, 7; Squires, 1995: figs. 2–6) from upper lower to lower middle Eocene ("Domengine Stage") of southern California. The new species differs from *O. bisculptata* by having fewer and more widely spaced axial ribs and coarser axial ribs. The inner lip of *O. bisculptata* is not known.

The type locality of the new species is equivalent to locality 7 of Stevenson (1948), which plots in the Baker Canyon Member of the Ladd Formation on the geologic map by Morton & Miller (1973). Associated megafauna at this locality includes the following: the bivalves *Glycymeris pacificus* (Anderson, 1902), *Ostrea* sp., *Alleinacin* [*As-tarte*] *sulcata* (Packard, 1922), *Lima* (*Limatula*) cf. *L. (L.) suciensis* Whiteaves, 1903, unidentified rudistids, and the gastropod *Anchura* (*Helicaulax*) *tricolora*? Saul & Popenoe, 1993. Based on comparison to paleontologic work by Saul (1982), this fauna is of Turonian age and of shallow-water origin. Furthermore, the presence of *Otostoma* and rudistids indicates subtropical, warm-water conditions, which are known to be especially associated with these types of mollusks (Kauffman & Sohl, 1974; Sohl, 1987).

Etymology: The species is named for Lucas Canyon.

Otostoma? atopos Saul & Squires, sp. nov.
(Figures 19–21)

Diagnosis: Small, globose, low-spined, body whorl without axial ridges; deck area broad, flat, and smooth; inner lip with six moderately prominent teeth.

Description: Shell small (up to 7 mm high), subquadrate, broader than high, thin-shelled, consisting of 2½ whorls; spire moderately elevated; body whorl rapidly expanding with tabulate shoulder. Suture between spire and body whorl impressed? Body whorl with closely spaced growth rugae in vicinity of aperture; growth lines procline. Ap-

erture moderately large, quadrate. Deck wide, smooth, and flat, except near inner lip area. Inner lip with six moderately strong teeth. Teeth equidistant, except for more closely spaced anteriormost one. Teeth approximately same strength, except for slightly weaker posteriormost one and somewhat shorter anteriormost one. Outer lip thin.

Dimensions of holotype: Height 7 mm, width 10.4 mm.

Holotype: LACMIP 7888.

Type locality: LACMIP loc. 24369, latitude 39°16'N, longitude 122°20'15"W.

Distribution: Reworked clasts in the Late Cretaceous Venado Formation, Colusa County, northern California (LACMIP loc. 24369).

Geologic age: Late Early Cretaceous (late Albian-early Cenomanian).

Discussion: Only a single, small, possibly immature specimen was found. It is complete and shows overall good preservation, with excellent preservation of the apertural area. The shell is missing on the spire and on the area adjacent to the inner lip callus. The sutural area between the spire and body whorl is poorly preserved.

The sculpture of the inner lip of the new species closely resembles that found on species of *Ostostoma*. For example, the inner lip of *Ostostoma equinum* (Bezançon, 1870) (Cossman & Pissarro, 1910:pl. 6, fig. 40–2) from the Eocene of the Paris Basin, France, is close to that of the new species, except that the most anterior inner lip tooth of the new species is not markedly smaller than the other five teeth. The new species cannot be positively assigned to genus *Ostostoma* because the new species shows no evidence of axial sculpture, a feature that is diagnostic of *Ostostoma*. The presence of growth rugae on the body whorl in the vicinity of the aperture of the new species might be the barest suggestion of axial ribbing, but poor preservation prevents positive determination.

The new species differs from *Ostostoma lucanus* sp. nov. by being much smaller, having an elevated spire, six rather than five teeth on the inner lip, and having no definite evidence of axial ribs.

The new species was found at LACMIP loc. 24369 in reworked clasts contained within younger rocks. Brown & Rich (1960, 1967) studied the stratigraphy of the area in the vicinity of the type locality and reported that the clasts, which are Early Cretaceous (late Albian-early Cenomanian) in age, were redeposited during the Late Cretaceous as part of a submarine-slump. The type locality of the new species plots in map unit 8b of Brown & Rich (1961). Ingersoll & Dickinson (1981) correlated this unit with submarine-fan rocks of the lower Turonian Venado Formation. Fauna associated with the new species in the slump block are the shallow-marine bivalves *Idonearca truncata* Gabb, 1964, and "*Trigonia*," as well as the shallow-marine gastropods *Euspira mariana* Murphy & Rodda, 1960, and

Turritella petersoni Merriam, 1941. The bivalve *Idonearca truncata* is indicative of late Albian or earliest Cenomanian age. For a thorough discussion of the age of the megafauna of this unit, see Saul (1978).

Etymology: The species name is derived from *atopos*, Greek, meaning out-of-place.

Genus *Corsania* Vidal, 1917

Type species: *Corsania douvillei* Vidal, 1917, by original designation; late Early Cretaceous (Aptian), Cors, Lérída, Spain.

Subgenus *Corsania* s.s.

Corsania (*Corsania*) ***allisoni*** Saul & Squires, sp. nov.

(Figures 22–24)

?*Semineritina apparatus* (Cragin) of Allison, 1955:414, pl. 40, fig. 18.

Ostostoma (*Lyosoma*) *japonica* (Nagao, 1934). Allison, 1955: 414, pl. 40, figs. 11, 12.

Corsania japonica (Nagao) of Allison. Woods & Saul, 1986: 640, fig. 5.7.

?*Ostostoma japonicum* (Nagao) of Buitrón, 1986:20, 22, pl. 1, fig. 1.

Diagnosis: A *Corsania* having a lowly elevated spire with axial ribs, a concave upper body whorl bordered by tuberculate angulations, and noded spiral ribs on remaining part of body whorl.

Description: Shell medium (up to 15.6 mm high), broader than high, consisting of 2½ whorls; spire lowly elevated; body whorl rapidly expanding. Penultimate whorl with approximately 12 closely spaced and prominent axial ribs. Body whorl large and separated from penultimate one by a shallowly grooved suture. Ramp broad, bordered posteriorly by a raised and noded spiral angulation. Ramp concave with one to two faintly noded, spiral threads. Periphery of body whorl strongly angulate and tuberculate. Below periphery, medial part of body whorl concave and ornamented by three noded and regularly spaced spiral ribs. Anterior border of concave area delimited by a swollen spiral band with nodes. Anteriormost region of body whorl with one to two weakly spiral ribs. Aperture subcircular. Deck area strongly swollen and smooth with a thin deck callus. Inner lip with six small but distinct teeth, the middle four the strongest. Teeth extend only a short distance onto deck. Outer lip thickened, at least posteriorly. Growth lamellae distinct, consisting of numerous prosocline lines.

Dimensions of holotype: Height 15.6 mm, width 18.8 mm.

Holotype: UCMP 33409.

Type locality: UCMP loc. A-8317, latitude 31°31'18"N, longitude 116°39'10"W.



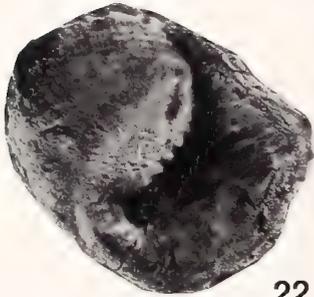
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Distribution: Upper member of the Alisitos Formation, Baja California, Mexico (UCMP loc. A-8317).

Geologic age: Late Early Cretaceous (middle Albian).

Discussion: Although this species was reported as common at its type locality, only a single specimen is available for study. Careful cleaning by the senior author revealed the aperture, which was first illustrated in Woods & Saul (1986:fig. 5.7).

Corsania (*C.*) *allisoni* is the earliest *Corsania* on the Pacific coast of North America. Allison (1955:pl. 40, figs. 11, 12), who discovered this species, identified it as *Ostotoma* (*Lyosoma*) *japonica* (Nagao, 1934:237, pl. 34, figs. 19–23; Kase, 1984:90–91, pl. 9, figs. 1–10; pl. 10, figs. 6, 8, 13), known from the Aptian to Albian stages of Japan. Allison's figured specimen, however, is not the same as the Japanese species (Kase, 1984; Woods & Saul, 1986; Squires & Saul, 1993). Also mentioned in Woods & Saul (1986) and Squires & Saul (1993) was that neither Allison's figured specimen nor "*Ostotoma*" *japonicum* (Nagao) belong to *Ostotoma*; both belong instead to the genus *Corsania*.

The new species is most closely related to *Corsania* (*C.*) *japonica* (Nagao, 1934), but the new species differs by being smaller and having spiral ribs on the body whorl anterior to the periphery, as well as having axial ribs on the penultimate whorl.

The new species resembles *C.* (*C.*) *douvillei* Vidal (1917; Cossmann, 1925:203, pl. 7, figs. 1–3), which is the type species of typical *Corsania* and is from upper Lower Cretaceous (Aptian) strata of Cors, Lérida, Spain. The new species differs from *C.* (*C.*) *douvillei* by having much weaker ornamentation.

The new species is unlike the two new species of *Corsania* (*Januncia*) mentioned in this paper in that on *C.* (*C.*) *allisoni*, the inner lip area is not set off from the deck area, and the inner lip teeth are smaller and finer.

The minute and incomplete specimen of *Semineritina* *apparata* (Cragin) of Allison (1955:414, pl. 40, fig. 18) is, most likely, the axially sculptured penultimate whorl of a specimen of *Corsania* (*C.*) *allisoni*. The incomplete spec-

imen, whose apertural area is embedded in matrix, is only 3 mm in diameter, but has the same dimensions as the penultimate whorl of the holotype of *C.* (*C.*) *allisoni*. The two specimens were also found at the same locality; namely, UCMP loc. A-8317. The type locality of *Semineritina* *apparata* (Cragin, 1893:227, pl. 46, fig. 14), a species that Stanton (1947:61, pl. 47, figs. 14, 15) identified as *Nerita?* *apparata* (Cragin), is the Edwards Limestone (middle Albian) of eastern Texas. The axial sculpture on Cragin's species, which belongs in genus *Ostotoma*, appears to be more sharply elevated than that on the specimen of *Semineritina* *apparata* (Cragin) of Allison.

Buitrón (1986:20, 22, pl. 1, fig. 1) reported *Ostotoma japonicum* (Nagao) from strata of late Aptian to early Albian age from the western part of Jalisco, Mexico. These specimens are poorly preserved internal molds that might be *Corsania* (*C.*) *allisoni*, but positive identification awaits future collection of better preserved specimens.

Cossmann (1925), Wenz (1938), and Keen & Cox (1960) considered *Corsania* to be a subjective junior synonym of *Ostotoma*, but, as pointed out by Woods & Saul (1986), *Ostotoma* have a more roundly globose shape and sculpture that is predominantly axial. The geologic range of typical *Corsania* is not well established but is tentatively late Early Cretaceous (Aptian) to late Paleocene (Thanetian), utilizing the work by Woods & Saul (1986). *Corsania* (*C.*) *allisoni* is one of the earliest representatives of *Corsania*. *Corsania* (*C.*) *douvillei* from Aptian strata of Spain and *Corsania* (*C.*) *japonica* Nagao, 1934, from Aptian to Albian strata of Japan are the earliest.

The strata at the type locality of the new species are middle Albian in age and consist of fossiliferous biohermal limestone interbedded with volcanic breccia. Some of the more abundant associated megafossils are shallow-marine, warm-water caprinid rudistid bivalve oysters, nerineid gastropods, hermatypic corals, club-spined cidaroid echinoids, holecypoid echinoids, and large benthic foraminifera (Allison, 1955, 1974).

Etymology: The specific name is in honor of the late Edwin C. Allison who discovered this species.

Explanation of Figures 19 to 33

Specimens coated with ammonium chloride. Figures 19–21. *Ostotoma?* *atopos* Saul & Squires, sp. nov., holotype LACMIP 7888, LACMIP loc. 24369, height 7 mm, width 10.4 mm, $\times 4.7$. Figure 19. apertural view. Figure 20: abapertural view. Figure 21: apical view. Figures 22–24. *Corsania* (*Corsania*) *allisoni* Saul & Squires, sp. nov., holotype UCMP 33409, UCMP loc. A-8317, height 11.1 mm width 13.3 mm, $\times 3.5$. Figure 22: apertural view. Figure 23: abapertural view. Figure 24: apical view. Figures 25–27. *Corsania* (*Januncia*) *rhoga* Saul & Squires, sp. nov., holotype LACMIP 7889, LACMIP loc. 7047, height 18 mm (incomplete and crushed specimen), width 36 mm, $\times 2.8$. Figure 25: apertural view, anterior portion of aperture missing. Figure 26: abapertural view, anterior portion of body whorl missing. Figure 27: apical view. Figures 28–30. *Corsania* (*Januncia*) *susana* Saul & Squires, sp. nov. Figures 28–29: holotype LACMIP 7890, CSUN loc. 969, height 21, width 24.7, $\times 1.6$. Figure 28: apertural view. Figure 29: abapertural view. Figure 30: paratype LACMIP 7891, CSUN loc. 973, apical view, width 24.3 mm, $\times 1.6$. Figures 31–33. *Corsania* (*Januncia*) *oraria* Saul & Squires sp. nov., holotype LACMIP 6442, LACMIP loc. 6160, height 12.3 mm, width 23.4 mm, $\times 2.2$. Figure 31: apertural view. Figure 32: abapertural view. Figure 33: apical view.

Subgenus *Januncia* Woods & Saul, 1986

Type species: *Corsania (Januncia) janus* Woods & Saul, 1986, by original designation; late Paleocene?, Baja California Sur, Mexico.

Corsania (Januncia) rhoga Saul & Squires, sp. nov.

(Figures 25–27)

Diagnosis: A *Januncia* with a strongly noded angulate shoulder and a very prominent tuberculate angulation near middle of body whorl, with remaining part of teleoconch covered by closely spaced spiral rows of very strong pustules.

Description: Shell medium (up to 18 mm high, incomplete), broader than high, thick-shelled, and robust, consisting of 2½ whorls; spire flat with about six spiral beaded to pustulate ribs; body whorl rapidly expanding. Body whorl shoulder strongly noded and angulate, nodes largest toward aperture, ramp broad and concave with three pustulate spiral ribs. Middle part of body whorl with a very prominent tuberculate angulation; large tubercles elongate, extending a short distance anteriorly, and prosocline. Anterior to prominent angulation, body whorl covered by closely spaced spiral rows of very strong pustules. Aperture large, inner lip area depressed and delineated by a ridge; inner lip area with at least four robust and very long teeth. Outer lip thick.

Dimensions of holotype: Incomplete and crushed specimen, height 18 mm, width 36 mm.

Holotype: LACMIP 7889.

Type locality: LACMIP loc. 7047, latitude 38°54'16"N, longitude 122°36'45"W.

Distribution: Lake County, northern California (LACMIP loc. 7047).

Geologic age: Early Paleocene (late? Danian).

Discussion: Only a single specimen was found, and it is badly crushed. It is difficult to distinguish the spire from the shoulder area of the body whorl. The anterior third of the body whorl is missing. The inner lip is well preserved, but the anteriormost part is missing.

The new species is very similar to *C. (J.) persica* (Douvillé, 1904:347, pl. 49, figs. 1–12; Cossmann, 1925:203, pl. 7, figs. 15–18), which is the earliest known species of *Januncia* and is from Maastrichtian (Cossmann, 1925) or Danian strata (Eames in Davies, 1975:84) of Luristan, western Iran. The new species differs from *C. (J.) persica* by having at least four rather than three teeth on the inner lip.

Corsania (J.) rhoga is much more similar to *C. (J.) susana* sp. nov. than to *C. (J.) oravia* sp. nov. *Corsania (J.) rhoga* differs from *C. (J.) susana* by having a sculptured spire and very strong and closely spaced spiral rows of

pustules between the angulations on the body whorl, rather than weak and widely spaced rows of nodes.

Subgenus *Januncia* differs from *Corsania* sensu stricto in having the inner portion of the inner lip strongly depressed. The new species appears to have this feature and, apparently, there is a ridge on the inside of the aperture.

In addition to the new species of *Corsania* mentioned in this paper, the only other *Corsania* reported from the Pacific coast of North America is *C. (Januncia) janus* Woods & Saul (1986:figs. 5.1–5.6) from upper Paleocene? strata east of Bahía Sebastian Vizcaino, Baja California Sur, Mexico. The new species differs from *C. (J.) janus* by having an angulate profile rather than a globose shape, prominent carinae, much stronger tubercles, and stronger and longer teeth on the inner lip.

The beds that include the type locality of *C. (J.) rhoga* were mapped as part of the Martinez Formation by Dickerson (1914) and Brice (1953). Both workers reported the presence of *Turritella pachecoensis* Stanton, 1896, in these strata. In the course of our study, however, we detected a specimen of *Turritella* from LACMIP loc. 7047 with a wide pleural angle and sculpture more suggestive of *Turritella peninsularis quaylei* Saul, 1983a. This subspecies is indicative of an early Paleocene (possibly late Danian) age (Saul, 1983b).

Etymology: The species is derived from *rhoga*, Greek, meaning rough.

Corsania (Januncia) susana Saul & Squires, sp. nov.

(Figures 28–30)

Diagnosis: A *Januncia* with a strongly noded angulation on the shoulder, middle, and anterior parts of body whorl (middle one the strongest and tuberculate), and two to three weaker noded spiral ribs between adjacent angulations.

Description: Shell medium (up to 24.5 mm high), broader than high, thick-shelled, consisting of about two whorls; spire flat to slightly concave, smoothish with two rows of very small nodes, obsolete toward the aperture; body whorl rapidly expanding. Body whorl shoulder strongly noded and angulate, nodes largest toward aperture; ramp broad and concave with two spiral ribs bearing small nodes. Middle of body whorl with a very prominent tuberculate angulation. Anterior part of body whorl with a noded angulation. Interspace between middle and anterior angulation with two to three spiral ribs with nodes, somewhat spirally elongate on larger specimens. Aperture moderately large, inner lip area depressed and set off from the convex, thick, and smooth deck callus; inner lip with six narrow and long teeth. Growth lines prosocline.

Dimensions of holotype: Height 21 mm, width 24.7 mm.

Holotype: LACMIP 7890.

Type locality: CSUN 969 [= LACMIP loc. 16894], latitude 34°18'34"N, longitude 118°41'32"W.

Paratypes: LACMIP 7891, height 20 mm, width 24.3 mm, CSUN loc. 973 [= LACMIP loc. 16895]; LACMIP 6441 (unfigured), height 24.5 mm, width 37.9 mm, CSUN loc. 966 [= LACMIP loc. 16893].

Distribution: Uppermost part of Santa Susana Formation, north side of Simi Valley, southern California (CSUN locs. 966, 969, 973).

Geologic age: Early Eocene ("Meganos Stage").

Discussion: Three specimens were found. Only the holotype shows the inner lip, which is prominently set off from the deck area.

The new species is most similar to *Corsania? peruviana* (Olsson, 1934:58–59, pl. 4, fig. 8) from the Monte Grande Formation in the Amotape region, Talara basin, northwestern Peru. This formation is of Late Cretaceous (Maastrichtian) age, according to Zuñiga & Cruzado (1979). The new species differs from *C.? peruviana* in the following features: three angulations on the body whorl rather than two, ornamentation on the interspaces between the angulations of the body whorl, and less elongate nodes on the shoulder of the body whorl. The aperture is not known for *C. peruviana*.

The new species does not have the pervasive pustulate appearance of *C. (J.) rhoga*.

The three localities where the new species was found are in the upper 100 m of the Santa Susana Formation. The lithology at the three localities is the same and consists of gray, silty, very fine-grained sandstone. The dominant megafossil at the localities is the gastropod *Turritella andersoni susanae* Merriam, 1941 [= *T. andersoni* n. subsp. of authors]. Along with a few other megafossils, the turritellid is present in thin, lensoidal storm-lag accumulations. *Turritella andersoni susanae* is indicative of the early Eocene part of the "Meganos Stage" (Squires, 1991). Saul (1983a) also assigned the upper 100 m of the Santa Susana Formation on the north side of Simi Valley to this stage.

The type locality of the new species is in the immediate vicinity of where the articulated holotype of the bivalve *Arca (Arca) filewiczi* Squires, 1991, was found. The specimen is from a lens containing *T. andersoni susanae*, and the fossils in the lens represent a transported assemblage in a relatively shallow-offshore environment (Squires, 1991).

Etymology: The new species is named for the Santa Susana Formation.

Corsania (Januncia) oraria Saul & Squires, sp. nov.

(Figures 31–33)

Diagnosis: A *Januncia* with a smooth, rounded shoulder and a prominent noded angulation near middle of body

whorl, two to three noded spiral ribs in the area between the shoulder and the angulation, and remaining part of body whorl with weak to obsolete spiral ribs.

Description: Shell medium (up to 15.5 mm high), subquadrate, thick shelled, consisting of about two whorls; spire flat and smooth; body whorl rapidly expanding. Body whorl shoulder smooth and rounded, ramp broad and slightly concave to flattish, with one to two noded spiral ribs. Middle of body whorl with noded spiral angulation. Anterior to angulation, body whorl with weak spiral ribs, obsolete toward base of body whorl. Aperture moderately large, circular. Inner lip area prominently depressed and set off from the prominently swollen, thick, and smooth deck callus; inner lip area shelflike and transversely crossed by six prominent and long teeth, the posteriormost and anteriormost ones smaller than the other four. Growth lines prosocline.

Dimensions of holotype: Height 12.3 mm, width 23.4 mm.

Holotype: LACMIP 6442.

Type locality: LACMIP loc. 6160, latitude 48°9'52"N, longitude 123°42'15"W.

Paratype: LACMIP 6443 (unfigured), height 16 mm, width 24.6 mm, LACMIP loc. 30188.

Distribution: Crescent Formation, western Washington (LACMIP locs. 6160 and 30188).

Geologic age: Middle early Eocene ("Capay Stage").

Discussion: Two specimens were found. The paratype has a poorly preserved inner lip.

The new species is similar to *Corsania carolina* (Stoliczka, 1868:341, pl. 23, figs. 13, 14) from the "Arrialoor" Group of southern India. These strata are of Campanian to middle Maastrichtian in age, according to Acharyya & Lahiri (1991). The new species differs from *C. carolina* by having less swollen spiral ribs and nodes rather than tubercles. The deck area is not known for *C. carolina*.

The new species is also similar to *Corsania? peruviana* (Olsson, 1934:58–59, pl. 4, fig. 8) from the Monte Grande Formation in the Amotape region, Talara basin, northwestern Peru. This formation is of Maastrichtian age, according to Zuñiga & Cruzado (1979). The new species differs from *C.? peruviana* by being smaller and having more numerous and weaker spiral ribs with much weaker nodes. The aperture is not known for *C. peruviana*.

The new species resembles *Corsania (Corsania) rinctus* (White, 1887:195, pl. 15, figs. 10–12) from lower Paleocene strata of Maria Farinha, Province of Pernambuco, eastern Brazil. White (1887) considered these strata to be Cretaceous in age, but Davies (1975:133) assigned them an early Paleocene age. The new species differs from *C. (C.) rinctus* by having much weaker sculpture, especially on the periphery and on the anterior half of the body whorl.

The new species is the youngest known record of *Januncia*, and the revised geologic range of this subgenus is latest Cretaceous (Maastrichtian) or early Paleocene (Danian) (Woods & Saul, 1986) to the middle early Eocene ("Capay Stage"). The previously youngest species was *Corsania (Januncia) janus* Woods & Saul (1986:figs. 5.1–5.6) from upper Paleocene? strata east of Bahía Sebastian Vizcaino, Baja California Sur, Mexico. The new species differs by having an angulate profile rather than a globose shape and weaker spiral ribs on the anterior one-half of the body whorl.

The type locality of the new species is in greenish tuffaceous conglomerate containing pebble to boulder-size clasts of basalt. Associated megafossils are large limpets, bivalves, solitary scleractinian corals, and encrusting bryozoans. Berthiaume (1938) assigned the Crescent Formation in the vicinity of the type locality to the middle early Eocene ("Capay Stage").

Etymology: The species name is derived from *oraria*, Latin, meaning from the coast.

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- (1350 ft.), near head of small tributary on E side of Chivo Canyon, 31 m (100 ft.) W and 122 m (400 ft.) N of SE corner of section 30, T. 3 N, R. 17 W, U.S. Geological Survey, 7.5-minute, Santa Susana Quadrangle, 1951 (photorevised 1969), Ventura County, north side of Simi Valley, southern California. Upper part of Santa Susana Formation. Age: Early Eocene (“Meganos”). Collector: R. L. Squires, 1 March, 1986.
- CSUN 1563 [= LACMIP 16655]. At elevation of 680 m (2230 ft.), exposed in roadcut on NE side of logging road, 300 m N and 50 m E of SW corner of section 1, T. 17 N, R. 4 W, and 500 m S32° of Larch Mountain, latitude 47°59′03″N, longitude 123°8′12″W, U.S. Geological Survey, 7.5-minute, Capitol Peak Quadrangle, provisional edition 1986, Thurston County, Washington. Crescent Formation. Age: Middle early Eocene (“Capay”). Collectors: J. L. & G. H. Goedert, 1992.
- LACMIP 6160. East side of Crescent Bay at seacliff on S side of “Tongue Point,” S side of Strait of Juan de Fuca, 914 m (3000 ft.) N and 320 m (1050 ft.) W of SE corner of section 21, T. 31 N, R. 8 W, latitude 48°0′52″N, longitude 123°42′15″W, U.S. Geological Survey, 7.5-minute, Joyce Quadrangle, 1950 (photorevised 1979), Clallam County, western Washington. Crescent Formation. Age: Middle early Eocene (“Capay”). Collector: J. L. Goedert, 8 July, 1981.
- LACMIP 7047 [= CIT 868]. A thin but richly fossiliferous layer of limonite-stained white sandstone, 0.9 km (0.75 mi.) E of Lower Lake, 366 m (1200 ft.) S from bridge over Copsey Creek, in gully on W side of creek, SE/4 of NE/4 of section 11, T. 12 N, R. 7 W, latitude 38°54′16″N, longitude 122°36′45″W, U.S. Geological Survey, 7.5-minute, Lower Lake Quadrangle, 1975, Lake County, northern California. Martinez Formation. Age: Early Paleocene (late? Danian). Collectors: D. W. Scharf and W. P. Popenoe, 26 August, 1930.
- LACMIP 10751 [= CIT 1265]. Right bank of Little Cow Creek, about 15 m (50 ft.) from creek, 1181 m (3875 ft.) N42°E of SW corner of section 9, T. 32 N, R. 3 W, latitude 40°38′47″N, longitude 122°12′30″W, U.S. Geological Survey, 15-minute, Millville Quadrangle, 1953, Shasta County, northern California. Redding Formation, Melton Sandstone Member. Age: Late Cretaceous (Turonian). Collector: W. P. Popenoe, 15 April, 1937.
- LACMIP 10760 [= CIT 1438]. Highest sandstone bed under lava in gully on N side of Little Cow Creek, about 0.4 km (¼ mi.) NE of Wilsey Ranch House, near NE corner of SW ¼ of section 31, T. 33 N, R. 2 W, U.S. Geological Survey, 15-minute, Millville Quadrangle, 1953, Shasta County, northern California. Redding Formation, Bellavista Sandstone Member. Age: Late Cretaceous (Turonian). Collector: W. P. Popenoe, 19 March, 1940.
- LACMIP 10773 [= CIT 1217]. In bed of Salt Creek at bend in stream, a short distance upstream from fence across stream, and about 2.4 km (1 ½ mi.) above mouth of the creek. Blocky, much-jointed sandstone, section 3,

APPENDIX

LOCALITIES CITED

- CSUN 966 [= LACMIP 16893]. At elevation of 529 m (1735 ft.), on E side of dirt road, 792 m (2600 ft.) E and 152 m (500 ft.) S of NW corner of section 32, T. 3 N, R. 17 W, U.S. Geological Survey, 7.5-minute, Santa Susana Quadrangle, 1951 (photorevised 1969), Ventura County, north side of Simi Valley, southern California. Upper part of Santa Susana Formation. Age: Early Eocene (“Meganos”). Collector: R. L. Squires, 28 February, 1986.
- CSUN 969 [= LACMIP 16894]. At elevation of 381 m (1250 ft.), on E side of Chivo Canyon, 343 m (1125 ft.) W and 107 m (350 ft.) N of SE corner of section 30, T. 3 N, R. 17 W, latitude 34°18′34″N, longitude 118°41′32″W, U.S. Geological Survey, 7.5-minute, Santa Susana Quadrangle, 1951 (photorevised 1969), Ventura County, north side of Simi Valley, southern California. Upper part of Santa Susana Formation. Age: Early Eocene (“Meganos”). Collector: R. L. Squires, 1 March, 1986.
- CSUN 973 [= LACMIP 16895]. At elevation of 412 m

- T. 32 N, R. 3 W, latitude 40°40'52"N, longitude 122°11'50"W, U.S. Geological Survey, 15-minute, Millville Quadrangle, Shasta County, 1953, northern California. Redding Formation, Bellavista Sandstone Member. Age: Late Cretaceous (Turonian). Collector: W. P. Popenoe and Ahlroth, 9 July, 1936.
- LACMIP 16868 [= Locality 7 of Stevenson, 1948]. In uppermost part of Baker Canyon Member in friable conglomerate intercalated with coarse sandstone, at 820 ft. elevation, section 17, T. 7 S, R. 6 W, latitude 33°33'N, longitude 117°31'29"W, U.S. Geological Survey, 7.5-minute, Cañada Gobernadora Quadrangle, 1968, south side of Lucas Canyon, east side of Ortega Highway 74, southern Santa Ana Mountains, Orange County, southern California. Ladd Formation, Baker Canyon Member. Age: Late Cretaceous (Turonian). Collector: Robert E. Stevenson, circa 1946.
- LACMIP 24137 [= UCLA loc. 4137]. Approximately 0.4 km (0.25 mi.) E of Jalama Road in canyon on N side of Jalama Creek, 1219 m (4,000 ft.) N and 4694 m (15,400 ft.) W of SE corner of the unsurveyed U.S. Geological Survey Lompoc Hills Quadrangle, 1959, Santa Barbara County, southern California. Jalama Formation. Age: Late Cretaceous (late Campanian, or possible early Maastrichtian). Collector: W. P. Popenoe, 1938.
- LACMIP 24369. Latitude 39°16'N, longitude 122°20'15"W, NW ¼, SW ¼ section 5, T. 16 N, R. 4 W, U.S. Geological Survey, 15-minute, Lodoga Quadrangle, 1943, Colusa County, northern California. A reworked clast in the Late Cretaceous (Turonian) Venado Formation. Age of reworked clast: Late Early Cretaceous (late Albian or earliest Cenomanian). Collector: T. P. Harding, May, 1955.
- LACMIP 26600. Fossils from dark to light gray mudstone with minor coarse sandstone cropping out in stream banks almost due south of collapsed house in section 29 on S side of road between Brown's Creek and Reading Creek across Blanchard Flat, latitude 40°35'30"N, longitude 122°54'28"W, 96 m (317 ft.) S and 595 m (1954 ft.) W of northeast corner of section 32, T. 32 N, R. 9 W, U.S. Geological Survey, 15-minute, Weaverville Quadrangle, 1953, Trinity Alps, Trinity County, northern California. Budden Canyon Formation, Ogo Member. Age: Late Cretaceous (late Hauterivian). Collectors: L. R. and R. B. Saul, 10 August, 1979.
- LACMIP 30188. West side of Crescent Bay, S side of Strait of Juan de Fuca, E one-half of section 20, T. 31 N, R. 8 W, U.S. Geological Survey, 7.5-minute, Joyce Quadrangle, 1950 (photorevised 1979), Clallam County, western Washington, western Washington. Crescent Formation. Age: Middle early Eocene ("Capay"). Collector: T. Susuki, 1950s.
- UCMP A-1802. On beach 0.4 km N of Woodman's Station (= Woodman Wharf), Discovery Bay, SW ¼ of NE ¼ of section 8, T. 29 N, R. 1 W, U.S. Geological Survey, 7.5-minute, Port Townsend South Quadrangle, 1981, southwestern Quimper Peninsula, Jefferson County, western Washington. Lower part of Quimper Sandstone. Age: Latest Eocene. Collector: W. L. Effinger?, circa middle 1930s.
- UCMP A-8317. In poorly sorted dark volcanic breccia overlying the third caprinid limestone downward from top of Punta China section, along the shore line of Punta China, latitude 31°31'18"N, longitude 116°39'10"W, approximately 2 km S of mouth of Río de Santo Tomás, northwestern Baja California, Mexico. Alisitos Formation, upper member. Age: Late Early Cretaceous (middle Albian). Collector: E. C. Allison, circa 1952.

Protection of the Nudibranch *Aeolidia papillosa* from Nematocyst Discharge of the Sea Anemone *Anthopleura elegantissima*

by

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Abstract. The nudibranch *Aeolidia papillosa* is resistant to being harmed by the nematocysts of its prey, the sea anemone *Anthopleura elegantissima*. This study tested whether the epidermal mucous coat of *A. papillosa* elicits lower levels of nematocyst discharge by *A. elegantissima* than other non-anemone-eating gastropods, the nudibranchs (*Phidiana crassicornis* and *Cadlina luteomarginata*) and a shelled gastropod (*Lithopoma gibberosum*). Mucous samples were collected from each species of gastropod on glass coverslips, and they were put in contact with the tentacles of anemones. The density of nematocysts discharged in response to each sample was enumerated. Relatively low densities of nematocysts were discharged by *A. elegantissima* in response to mucus of *A. papillosa* and a negative control (no mucus); high nematocyst densities were found in mucous samples from non-anemone-eating gastropods. This suggests that the mucous coating of *A. papillosa* has specific properties that provide protection for the nudibranch from being stung during predatory encounters with *A. elegantissima*. The response of *A. elegantissima* to contact with whole gastropods was also tested. Individuals of *A. papillosa* appeared to be stung by anemones upon initial contact, which caused the nudibranchs to retreat. However, there was no visible harm to the nudibranchs, and they returned to attack and eat the anemones. The two other nudibranch species were stung and consumed by the anemones, and the *L. gibberosum* retreated into its shell for protection. Thus, *A. papillosa* was the only gastropod species that remained unharmed during encounters with *A. elegantissima* and whose mucus did not elicit strong nematocyst discharge.

INTRODUCTION

The aeolid nudibranch *Aeolidia papillosa* (Linnaeus, 1761) is a well-known predator of sea anemones (Grosvenor, 1903; Graham, 1938; Edmunds, 1966; Salvini-Plawen, 1972; Waters, 1973; Edmunds et al., 1976). It occurs intertidally, usually among colonies of *Anthopleura elegantissima* (Brandt, 1835), which is its main food source (Waters, 1973). Harris (1970) observed that when *A. papillosa*

fed on *A. elegantissima*, the nudibranch would seize the column of the anemone with its jaws and use the radula to tear the tissue. Although the nudibranch appears to be stung during the initial stage of a predatory encounter with an anemone, the nematocysts and toxins do not have a debilitating effect on the nudibranch (Grosvenor, 1903; Edmunds, 1966). Most aeolid nudibranchs have a buccal cavity lined with a chitinous cuticle that protects their digestive tract from nematocysts (Graham, 1938). Edmunds (1966) also suggested that the epidermal vesicles of the nudibranchs probably protect them from being stung. Russell (1942) reported that *A. papillosa* produces a copious amount of mucus when feeding on anemones. This

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mucus was observed mainly around the mouth region and was assumed to prevent the anemone's nematocysts from harming the nudibranch. Grosvenor (1903) suggested that the mucus can act either as a buffer or as a preventive substance that interferes with nematocyst discharge. Salvini-Plawen (1972) inferred that the hyperviscosity of nudibranch mucus, or its enzymatic secretions, may prevent the discharge of nematocysts. However, none of these studies have definitively shown that the mucus of *Aeolidia* reduces the nematocyst discharge of its anemone prey.

The objective of the present study was to test whether the mucus of *A. papillosa* elicits fewer nematocysts to discharge in *A. elegantissima* than the mucus of non-anemone-eating gastropods. Two nudibranchs, *Cadlina luteomarginata* (MacFarland, 1905) and *Phidiana crassicornis* (Eschscholtz, 1831), and a snail, *Lithopoma gibberosum* (Dillwyn, 1817), were tested. The dorid *C. luteomarginata* feeds on sponges such as *Halichondria* and *Myxilla* in the low intertidal (Behrens, 1980). The aeolid nudibranch *P. crassicornis* feeds mainly on hydroids such as *Obelia* (Behrens, 1980). *Lithopoma gibberosum* is a large turban snail that feeds on algae but is not known to feed on cnidarians (Morris, 1966). Forced encounters between the gastropods and the anemones were staged to determine if the gastropods would be stung and harmed.

MATERIALS AND METHODS

The study was conducted at the Bamfield Marine Station on the west coast of Vancouver Island, British Columbia, Canada. Three individuals of *A. elegantissima* were collected from the rocky intertidal zone and kept in a sea table with running water. The anemones were 2.5 cm, 2.7 cm, and 3.2 cm in diameter. Three individuals of each gastropod species (*A. papillosa*, *C. luteomarginata*, *P. crassicornis*, and *L. gibberosum*) were collected from the intertidal zones surrounding the marine station. The nudibranchs were maintained in separate clear cylinders (diameter = 4.8 cm, length = 7.4 cm) covered with a fine meshed material. The cylinders were then placed in an aquarium (31.2 × 62.1 × 31.2 cm) supplied with flowing seawater. All individuals were fed natural prey items.

Mucous samples were collected from each of the gastropods by placing a glass coverslip against their body wall until there was a visible coating of mucus. The coverslip was then put in contact with the tentacles of an anemone for 3 seconds. The coverslip was then stained with methylene blue (5%), placed on a slide, and then the slide was viewed under a Laborlux 11 microscope (× 400) equipped with a video camera and video monitor. An acetate sheet was placed over the image on the monitor, and the outer edge of each nematocyst aggregation was traced. The number of nematocysts within the traced areas was counted. The surface area (mm²) of each nematocyst aggregation was calculated using a Summa-Sketch II digitizer and MacMeasure 2.25 for the Macintosh. Nematocyst density (#/μm²) was then calculated.

Mucous samples ($n = 5$) from each of the four gastropod species were tested with each of the three *A. elegantissima*, resulting in 15 tests per gastropod species. The mucus from the varying gastropod species was presented to the anemones in a randomized fashion over the time period of 2 weeks. A negative control for nematocyst discharge was conducted by placing a clean coverslip against the tentacles of an anemone for 3 seconds. The mean densities of the nematocyst aggregations produced in response to the mucus from each gastropod species was compared with a One-way Analysis of Variance using the SAS microcomputer package JMP®. The data were \ln transformed to meet the assumptions of equal variances and normality. A pairwise comparison of individual means was then done with Tukey's HSD test.

The response of the sea anemones to contact with the whole animals was also tested. A sea anemone was placed in a large glass viewing bowl with an individual of one of the four species of gastropods. The nudibranch or snail was placed near the anemone and was allowed to either contact the anemone's tentacles on its own or it was directed into the tentacles. This test was repeated twice with each of the four gastropod species and the blank coverslip control. The responses of the anemones and gastropods were recorded.

RESULTS

There was a significant difference in the nematocyst densities discharged by *Anthopleura elegantissima* in response to mucus from the different species of gastropods (Figure 1; $F = 152.78$, $P < 0.0001$). The mean nematocyst densities discharged in response to the negative control (0.78 nematocysts/μm²) and mucus of *A. papillosa* (1.76 nematocysts/μm²) were considerably less than the nematocyst discharged in response to mucus from the other three gastropod species. The mucus of *C. luteomarginata* and *P. crassicornis* elicited the highest density of nematocyst discharge (13.78 and 16.34 nematocysts/μm², respectively). All means were significantly different from each other except those for the mucus of *C. luteomarginata* and *P. crassicornis* (Figure 1).

Interactions between *A. elegantissima* and each of the gastropods were also observed. In both trials with *A. papillosa*, the nudibranchs approached the anemones and initially contacted the tentacles with their cerata. The anemones retracted in response to this contact but then re-extended their tentacles. The nudibranchs also retracted after their initial contact, but then approached the anemones, again crawling onto the oral disk, projected their mouth, and began ingesting the anemone. No visible harm to the nudibranchs was observed.

When *C. luteomarginata* was placed inside a glass bowl with an anemone, the nudibranch quickly went to the opposite side of the container. The nudibranch was then forced to contact the anemone's tentacles, and it was adhered to and captured. In trial 1 the nudibranch was com-

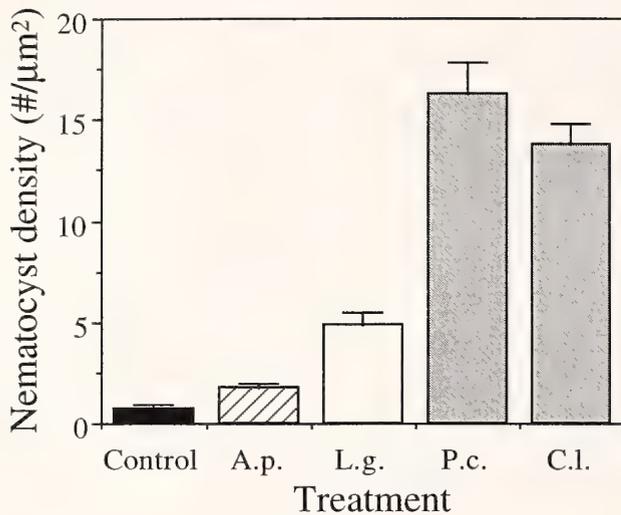


Figure 1

Nematocyst discharge of *Anthopleura elegantissima* in response to the mucus of different gastropod species and a clean coverslip (control). Bars with different patterns are significantly different (Tukey's HSD test, $P < 0.0001$). Control = clean coverslip control; A.p. = *A. papillosa*; L.g. = *L. gibberosum*; P.c. = *P. crassicornis*; C.l. = *C. luteomarginata*.

pletely consumed by the anemone. However, in trial 2 the anemone held the nudibranch for approximately 4 minutes and then retracted its tentacles, releasing the nudibranch.

In tests with *P. crassicornis*, the nudibranchs moved immediately to the opposite side of the glass bowl from the anemones. When the nudibranchs were forced into contact with the anemone, the anemones stung the nudibranchs and ingested them. The anemones then retracted their tentacles as in a typical feeding response. In one of the trials, the nudibranch crawled out of the anemone's mouth after 3 minutes, having autotomized all of its cerata. In trials with *L. gibberosum*, it also moved to the opposite side of the container from the anemone. However, in both trials, the snails, when placed near the tentacles of the anemone, retreated into their shells. No tentacles adhered to the shell of *L. gibberosum*.

DISCUSSION

The primary defense of aeolid nudibranchs against being stung by anemones is considered to be their ability to secrete copious amounts of viscous mucus (Edmunds, 1966; Waters, 1973). Whether the mucus acts primarily as a shield and prevents discharged nematocysts from reaching the epidermis of the nudibranch (Waters, 1973), or if it actually prevents nematocyst discharge has not been determined. The results of the present study showed that the mucus of *A. papillosa* elicited significantly lower densities of nematocyst discharge from the tentacles of *A. elegantissima* than the mucus of the other gastropod species tested.

This suggests that the mucus of *A. papillosa*, a predator of *A. elegantissima*, is significantly less stimulatory than the mucus of the other, non-anemone-feeding gastropods. Other researchers have suggested that the mucus of *Aeolidia* may elicit lower nematocyst discharge than other mollusks (Grosvenor, 1903; Graham, 1938; Edmunds, 1966; Edmunds et al., 1976; Salvini-Plawen, 1972), but this was not demonstrated quantitatively. However, since *A. papillosa* is stung by some other species of sea anemones (Edmunds, 1966; Waters, 1973; Edmunds et al., 1976), its mucus does not provide comprehensive protection from all cnidarian prey species. Since *A. papillosa* is known to feed principally on *A. elegantissima*, it would be advantageous to be protected from this species of prey.

The response of *A. elegantissima* to contact with the whole organism supported the results from the mucous tests. *A. papillosa* was not strongly adhered to by the tentacles of the anemone. The nudibranch was also able to eat the anemone with no visible harm to itself. In contrast, the tentacles of *A. elegantissima* adhered to both of the other nudibranch species. This is in accordance with the mucous tests where relatively high densities of nematocysts were discharged by *A. elegantissima* in response to these same nudibranch species.

In a study such as this, it would have been more appropriate to have a double-blind experiment in which the researcher did not know which mucous sample was being presented to the anemone. This would eliminate any discrepancies in the presentation of the coverslip to the anemone. Also, the nematocyst density of the negative control may be underestimated simply due to the absence of mucus, which because of its physical viscosity will cause retention of fired nematocysts.

The theory of mucous coat protection of aeolid nudibranchs to their cnidarian prey is analogous to the protection of anemonefishes from the stinging tentacles of their host anemones. Anemonefishes have a mucous coating that protects them from being stung by symbiotic species of anemones (reviews by Mariscal, 1971; Fautin, 1991). Glass rods coated with anemonefish mucus do not elicit nematocyst discharge when put in contact with the tentacles of host anemones (Lubbock, 1980). However, the mucus from other species of coral reef fishes elicits high levels of nematocyst discharge from the same anemones. A similar result was found in the present study when glass coverslips coated in *A. papillosa* mucus elicited low levels of nematocyst discharge, but other gastropod species elicited high levels of discharge. Thus, both symbionts and predators have adapted their mucous coating to provide protection from cnidarians.

Early studies of the protection of anemonefishes from sea anemones concluded that the fishes acquire protection from the cnidae of anemones through a behavioral process called "acclimation" (reviews by Mariscal, 1971; Fautin, 1991). However, recent studies have shown that at least some species of anemonefishes do not need to go through

acclimation behavior before they are protected from their hosts (Miyagawa & Hidaka, 1980; Miyagawa, 1989; Elliott et al., 1994). The fishes are considered to have innate protection, which results from processes taking place during normal development, and not as a result of contact with chemical, visual, or mechanical stimuli from sea anemones (i.e., the protection mechanism has a genetic basis and is not acquired through experience). Whether *A. papillosa* also produces its own protective mucous coating, or acquires it through acclimation is not known. In the present study, when *A. papillosa* first contacted *A. elegantissima*, it retracted as if it were stung. However, after a few moments, the nudibranch was able to contact the anemone and consume it without being harmed. The nudibranch may have modified its mucous coat in response to the first encounter with the anemone by either secreting substances into its mucus or by incorporating substances from the anemone. Alternatively, the nudibranchs may produce their own protective mucous coat during normal development, and thus be innately protected. Studies with nudibranchs that have had no contact with anemones would be required to determine if nudibranchs are innately protected or if they must acclimate to become protected from anemones.

The actual mechanism that protects anemonefishes from being stung is also unknown. Whether substances in the mucous coat of anemonefishes inhibit the discharge of nematocysts, or whether their mucus lacks stimulatory chemicals has yet to be determined. Similarly, further research is needed on the chemical composition of the external mucous coats of nudibranchs and the biochemical mechanism(s) that prevent nematocyst discharge in sea anemones.

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A Synthesis and Review of the Expanding Range of the Asian Freshwater Mussel *Anodonta woodiana* (Lea, 1834) (Bivalvia: Unionidae)

by

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Abstract. The freshwater mussel *Anodonta woodiana* is native to eastern Asia. In recent years, it was discovered in fish hatcheries in Romania, Hungary, France, and several Indonesian islands. It also was collected in the wild in the Dominican Republic and Costa Rica. These occurrences are believed to be the result of the incidental introduction of exotic fishes imported for food, as foraging fishes, or for mosquito control, which bore parasitic glochidia of the mussel. These hosts are grass, common, bighead, and silver carp; Nile tilapia; and mosquitofish. Because these fishes are imported throughout the world, *Anodonta woodiana* may eventually be found in additional countries. It has the potential to escape and compete with native freshwater mussels wherever it is introduced.

INTRODUCTION

Accidental introductions of aquatic mollusks have become more common with the increase in traffic and speed of transoceanic crossings. Transport in ballast water has been implicated in the North American invasion by the zebra mussels *Dreissena polymorpha* (Pallas, 1771) and *D. bugensis* (Andrusov, 1897) from Europe (Hebert et al., 1989; Rosenberg & Ludyanskiy, 1994), and the marine gastropod *Philine auriformis* Suter, 1909, from New Zealand (Gosliner, 1995). The brackish-water bivalve *Mytilopsis leucophaeta* (Conrad, 1831) was introduced from North America to the Netherlands, France, and Belgium; and the Caribbean *Mytilopsis sallei* (Récluz, 1849) was introduced to Visakhapatnam in India, and Fiji (Marelli & Gray, 1983). Numerous marine exotics in Hawaii were traced to Barge YO-146, which carried mollusks on its hull from Guam; other Hawaiian exotics may have arrived on other ships during World War II (Burgess, 1995). The estuarine bivalves *Corbicula largillierti* (Philippi, 1811), *C. fluminea* (Müller, 1774), and *Limnoperna fortunei* (Dunker, 1857) were introduced to Argentina as food items (Darrigran & Pastorino, 1993). *Corbicula fluminea* was similarly introduced to North America as a food item, and has since spread throughout much of the continent (Mills

et al., 1993). Exotic thiarid freshwater gastropods were introduced repeatedly to North America through the aquarium trade, and many have escaped to the wild (Murray, 1971).

Unionacean bivalves, "freshwater mussels," also were transported to areas outside their normal range by the activities of man. The Indonesian *Pseudodon vondembuschianus* (Lea, 1840) was introduced to Singapore, presumably as glochidia on exotic fishes (Ng et al., 1993). *Anodonta anatina* (Linnaeus, 1758) may be a recent arrival in Ireland (Ross & McCarthy, 1991; Lucey, 1995). The eastern North American *Pyganodon grandis* (Say, 1829) was found in Arizona, probably as the result of the release of infected fishes (Taylor, 1966). But no unionacean has been introduced as widely as *Anodonta woodiana* (Lea, 1834).

DISCUSSION

Biology

Anodonta woodiana is a native of southeastern Russia, China, Cambodia, Thailand, Malaysia, and Taiwan (Dudgeon & Morton, 1983; Chang, 1991). A form or subspecies also occurs in Japan and has been given the subspecific name *japonica* Martens, 1874. Other subspecific taxa have been proposed, such as *calipygos* Kobelt,

1879, and *lauta* Martens, 1877, but the status of these is unclear. Dudgeon & Morton (1983) discussed the taxonomy of this variable species, which also has been placed in *Cristaria*, *Pletholophus*, and *Sinanodonta*. Considering the changing status of anodontine higher taxa, this species is referred to here conservatively as an *Anodonta*. It is a large species, reaching lengths of 26 cm. Like most anodontines, it grows quickly and can tolerate a variety of habitats (Dudgeon & Morton, 1983; Kiss & Pekli, 1988; Kiss, 1990b). Most anodontines that have been investigated were able to parasitize a wide range of host fishes (Trdan & Hoeh, 1982), including exotics. Kiss (1990a) believed *A. woodiana* could parasitize any freshwater fish. The potential thus exists for anodontines, and *A. woodiana* in particular, to become established outside their native range if given the opportunity.

Reported potential fish hosts for *Anodonta woodiana* include *Metzia takakii*, *Puntius semifasciolatus*, *Rhinogobius brunneus*, *Rhodeus tabira*, *Zacco platypus*, *Z. temmincki*, and *Acheilgnathus morioka*. More importantly, the following commercially exported species are suspected as hosts: black carp (*Mylopharyngodon piceus*), grass carp (*Ctenopharyngodon idella*), silver or mud carp (*Hypophthalmichthys molitrix*), bighead carp (*Aristichthys nobilis*), common carp (*Cyprinus carpio*), western mosquitofish (*Gambusia affinis*), and Nile tilapia (*Oreochromis niloticus*) (Habe, 1975; Dudgeon & Morton, 1983, 1984; Péto, 1984; Girardi & Ledoux, 1989; Kondo, 1987, 1989; Sárkány-Kiss, 1986). These fishes were, and still are being introduced outside their native range for food, control of aquatic vegetation, hatchery water quality maintenance, mosquito control, or as aquarium fishes.

Introductions

Anodonta woodiana was introduced in Hungary to the Szarvas hatchery on exotic food and foraging fishes imported from the Amur River, and later from Krasnodar, Russia, between 1963 and 1965 (Pétró, 1984; Kiss, 1990a). The Amur River is part of the natural range of *A. woodiana*. The origin of the Russian fishes was not determined. The imported fishes included grass, silver, and bighead carp. *Anodonta woodiana* has since been recorded from the Szazhlombatta hatchery as well. Mussels or infested fishes have escaped the hatcheries, and *A. woodiana* was established in six localities in Hungary as of 1988, including the Tisza River at Szeged and Szentes, the Körös River at Biharugra, and the Danube River (Kiss & Pétró, 1992).

In 1982, *A. woodiana* appeared in a hatchery at l'Étang des Gravières à Fonvieille near Arles, France (Girardi & Ledoux, 1989). Introduced common and grass carp were procured that year from Hungarian hatcheries in Hortobagy, Szazhlombatta, and Szarvas. As described above, the latter two hatcheries were infested at that time with the mussels carried by fishes imported from the Amur River (Pétró, 1984; Kiss & Pétró, 1992). *Anodonta woodiana* therefore had survived through at least several gen-

erations in these Hungarian hatcheries to infest fishes exported to France 19 years later.

Sárkány-Kiss (1986) documented the introduction of *A. woodiana* into Romania. In 1959, 54,000 young-of-year, and in 1960, 22,555 larvae of grass carp were imported from the Yangtze River basin via Moscow into the Experiment Station at Nucet. Like the Amur, the Yangtze River is part of the natural range of this mussel. A similar import took place in 1962 into Cefa-Oradea and Nucet, again. Adult *A. woodiana* were collected in fish ponds in 1979 at Cefa-Oradea. Grass, silver, and bighead carp were introduced, all hosts for *A. woodiana*. It is likely that *A. woodiana* was or is present at the Moscow hatchery as well, but there was no information available.

Anodonta woodiana was introduced from Taiwan into the Inland Fisheries Research Institute at Bogor, West Java, in 1969 on silver carp and/or Nile tilapia. Mussels themselves were released in 1972 into the Bogor Botanical Garden ponds. This species subsequently was introduced on fishes into other sites in Java, Sumatra, Manado in North Sulawesi, Kendari in Southeast Sulawesi, Lombok Island in the Nusa Tenggara Islands, and Moluccas (Djajasmita, 1982; Dharmas, 1992).

In 1994, E. Keferl collected *A. woodiana* at Laguna de Arenal, a hydroelectric impoundment at San Luis, Costa Rica. The mussel did not occur there until blue tilapia, *Oreochromis aureus*, and Nile tilapia, *Oreochromis niloticus*, were introduced as food fishes (Keferl, 1995; in litt., 1996). The fishes were imported from an agriculture project in the Guanacaste region near Lomas Barbudal Reserve, which in turn may eventually have received the fishes from Taiwan.

Hispaniola has no native unionids (Johnson, 1981). In 1982, Padre J. Cicero and G. Grullón P. (1982) first recognized that an exotic anodontine occurred in the Dominican Republic in a hatchery at Nigua near Santo Domingo, but identified it as *Anodonta* [= *Pyganodon*] *grandis* Say, 1829, a North American species. Gomez et al. (1986) also reported that an *Anodonta* sp. was "recently introduced" into the Dominican Republic and was present in these carp and tilapia ponds at the Ministry of Agriculture in Nigua. Subsequently, G. Duffy and M. Kohl independently collected specimens of this species in the wild in Santo Domingo (Watters & Kohl, 1995). Specimens sent to the author were identified as *A. woodiana* based upon comparisons with material from China and Sulawesi. Additional specimens also were identified as this species by malacologists R. Johnson, Museum of Comparative Zoology, Cambridge, Massachusetts, and H. Lee, Jacksonville, Florida (Duffy, written communication, 1995). The mussel was recorded from several places: Rio Yuna in the El Seibo region; the impoundment of Presa de Rincón near Bonao (Duffy, written communication, 1995); and Byaguana (F. Richardson, written communication, 1995). Numerous exotic fish species have been introduced into the Dominican Republic, including species believed to host *A. woodiana*: common, grass, and silver carp, Nile tilapia,

and mosquitofish. It is likely that these fishes were imported via Panama from Taiwan. Unfortunately, the original import manifests for the Dominican Republic were destroyed in a fire in 1994 (F. Richardson, written communication, 1995). The import of these fishes, whatever their source, resulted in the introduction of *A. woodiana* to the Dominican Republic, where it has escaped to the wild.

There is no doubt that *A. woodiana* is being accidentally translocated to new areas outside its normal range by the shipping of host fishes. Saline solutions used for transporting fishes, usually 0.5% or less, may be insufficient to destroy attached glochidia. Bruno et al. (1988) treated Atlantic salmon infested with *Margaritifera margaritifera* (Linnaeus, 1758) glochidia with saline water at 5.4, 10.1, and 24.3% for 1, 3, and 9 hours, and at 33.3% for 24 hours. No significant glochidial mortality was observed in any treatment. Bathing fishes in 0.5 mg/l⁻¹ CuSO₄ for 1 hour, or 5 mg/l Nuvan® for 1 hour followed by 1 mg/l Roccal® for 1 hour, also did not significantly affect glochidial mortality. Because *A. woodiana* may require several weeks to metamorphose, depending on water temperature, there is ample time to move infested fishes great distances. The fact that *A. woodiana* has colonized hatcheries and successfully infested exported fishes years after its initial introduction indicates that hatcheries can act as sources of repeated release of this exotic mussel.

Similar Species

Presently there are no records of *A. woodiana* in North America, which has a diverse but imperiled unionid fauna. However, it may exist undetected in hatcheries or adjacent rivers, confused with native species. *Anodonta woodiana* resembles *Utterbackia suborbiculata* (Say, 1831) from the Mississippi River system, and *Anodonta* sp. from the Pearl River of Louisiana (Vidrine, 1993: pl. 1, fig. M). The latter appears to represent an undescribed species. It differs from those species in the following ways: the umbo protrudes above the hinge line, whereas in *U. suborbiculata* it is flush; the beak sculpture consists of coarse, linear or slightly concentric ribs without prominent nodules, whereas in *U. suborbiculata* and *Anodonta* sp. the sculpture is fine, concentric but nodulous. It is often more brightly colored, with dark green rays, whereas *U. suborbiculata* and *Anodonta* sp. are typically tan or yellowish, rayless, or with very fine brown or green rays. *Utterbackia suborbiculata* and *Anodonta* sp. are consistently round in profile, whereas *A. woodiana* is variable in outline, from round to elongate. *Pyganodon grandis* has very different beak sculpture composed of fine double loops. The European unionids *Anodonta anatina* (Linnaeus, 1758) and *Pseudanodonta complanata* (Rossmässler, 1835) also have double-looped beak sculpture, and *Anodonta cygnea* (Linnaeus, 1758) has fine concentric beak sculpture (Fechter & Falkner, 1990). The glochidium of *A. woodiana* was illustrated by Inaba (1941) and Bykhovskaya-Pavlovskaya (1962), but consis-

tent differences from other anodontine glochidia (Wiles, 1975; Rand & Wiles, 1982) have not been identified.

Implications for Native Freshwater Mussels

Where introduced, it is believed that *A. woodiana* is using native fishes as hosts (Djajasasmita, 1982; Dudgeon & Morton, 1983, 1984). However, its natural hosts, grass and common carp are found as exotics, wild throughout much of North America, including nearly all of the contiguous United States; and silver and bighead carp, and Nile tilapia, occur wild in several southern states. Common carp was introduced into the United States in 1831 (Page & Burr, 1991). Grass carp was introduced to Arkansas and Alabama in 1963, silver carp to Arkansas in 1973, and bighead carp to Arkansas in 1972. Culture of Nile tilapia is allowed by permit, and triploid grass carp are stocked by several states in the United States (Howells, 1992; S. Ross, personal communications 23 August 1994). Blue tilapia is annually stocked in Alabama ponds (Page & Burr, 1991). If *A. woodiana* enters North America, it may therefore use not only native hosts, but wild exotic hosts as well.

It is suspected that unionids compete for hosts (Rashleigh, 1995). So far, *A. woodiana* has been introduced to areas having few or no native unionids. It is not known what impact an introduction would have on North America's several hundred native species. The introduction of an anodontine capable of infesting native and exotic fishes may diminish the chances of native unionids' survival, many of which are already rare or endangered. Simulations have shown that such an exotic may locally drive some types of native mussels to extirpation by monopolizing suitable hosts, both native or exotic. Populations of the exotic may become larger than those of the native species by orders of magnitude (Watters, in press). Given the history of this species' invasion elsewhere, and the continued farming and exporting of its hosts, it is likely that *A. woodiana* eventually will invade North America and other countries.

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A Worldwide Review of the Food of Nudibranch Mollusks. Part I. Introduction and the Suborder Arminacea

by

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Abstract. The prey items of 33 of the approximately 166 species of the suborder Arminacea are presented here along with instructions for accessing a larger electronic publication which gives all of the information on the food of nudibranchs on a worldwide basis as drawn from an extensive literature search.

INTRODUCTION TO THE SERIES

This paper is the initial paper in a series that will review the food of nudibranchs on a worldwide basis. This review is based on the published literature and is not the result of the investigations of the authors. Each of the papers will be an abstracted version of a much larger database that contains all of the available information on the food of nudibranchs extracted from an extensive search of the literature. This database is much too large to publish in its entirety in hard copy. It will, however, be available electronically as the first electronic publication of *The Veliger*. The exact genus and species of the food item(s) and the exact citation for that food item can be brought up by accessing the database. The full compilation (McDonald & Nybakken, 1997) is available in electronic form via anonymous FTP from ucmp1.Berkeley.Edu as PostScript (/pub/mollusca/food 001.ps through food 005.ps), Word Perfect (/pub/mollusca/food 001.wpf through food 005.wpf), and ASCII (/pub/mollusca/food 001.asc through food 005.asc) files. To retrieve these documents, open an FTP connection to ucmp1.Berkeley.Edu (128.32.146.3).

At the request for login enter "anonymous." At the request for password, enter your e-mail address (e.g., jsmith@veliger.amu.edu). At the prompt, change directory to /pub/mollusca (command = cd/pub/mollusca), set file transfer mode to binary (command = bin), and retrieve the desired file (command = get "filename.*"). At the end of your FTP session, close the connection (command = close) and quit. The database provides the name of each food item and references for every time that the item is mentioned in the literature. If you choose to cite the master electronic paper in a subsequent publication of your own, the citation should read something like this:

McDonald, Gary & James Nybakken. 1997. A world-wide review of the food of nudibranchs. *The Veliger* 40: Supplement: 1-000. Available in electronic form via anonymous FTP from ucmp1.Berkeley.Edu as PostScript (/pub/mollusca/food 001.ps through food 005.ps), Word Perfect (/pub/mollusca/food 001.wpf through food 005.wpf), and ASCII (/pub/mollusca/food 001.asc through food 005.asc) files

Table 1
Summary of the Food of the Suborder Arminacea

Family	Genus	Species	Food
Heterodoridae	<i>Heterodoris</i>	<i>robusta</i>	Alcyonaria (<i>Anthothela</i>)
Doridomorphidae	<i>Doridomorpha</i>	<i>gardineri</i>	<i>Heliopora</i>
Arminidae	<i>Armina</i>	<i>californica</i>	Pennatulacea (<i>Ptilosarcus</i> , <i>Renilla</i>)
		<i>loveni</i>	Pennatulacea (<i>Virgularia</i>)
		<i>maculata</i>	Pennatulacea (<i>Pennatula</i>); soft corals
		<i>mulleri</i>	Pennatulacea (<i>Renilla</i>)
		<i>tigrina</i>	Pennatulacea (<i>Renilla</i>)
		<i>striatus</i>	on stoloniferans (<i>Clavularia</i> , <i>Tubipora</i>)
		<i>convolvula</i>	Gorgonacea (<i>Muricea</i>)
		<i>souleyeti</i>	cheilostome ascophoran bryozoans
		<i>aurantiaca</i>	cheilostome ascophoran bryozoans
		<i>ferruginosa</i>	bryozoans (<i>Mucropetraliella</i>)
<i>sanguinea</i>	bryozoans (<i>Mucropetraliella</i>)		
<i>sp.</i>	cheilostome, anascan bryozoans		
Dironidae	<i>Dirona</i>	<i>albolineata</i>	gastropod mollusks and anascan bryozoans
		<i>aurantia</i>	anascan bryozoans, cheilostome bryozoans, hydroids, gammarid amphipods, caprellid amphipods
		<i>picta</i>	cheilostome anascan bryozoans, hydroids
Zephyrinidae	<i>Bonisa</i>	<i>nakaza</i>	cheilostome ascophoran bryozoans
		<i>affinis</i>	cheilostome anascan bryozoans
		<i>rubiginosa</i>	cheilostome anascan bryozoans
	<i>Janolus</i>	<i>barbarensis</i>	cheilostome anascan bryozoans, hydroids
		<i>capensis</i>	cheilostome anascan bryozoans
		<i>cristatus</i>	cheilostome anascan bryozoans
		<i>eximius</i>	<i>Orthoscuticella</i>
		<i>hyalinus</i>	cheilostome anascan bryozoans and hydroids (<i>Tubularia</i>)
		<i>longidentatus</i>	cheilostome anascan bryozoans
		<i>mokohinau</i>	cheilostome anascan bryozoans
		<i>novozelandicus</i>	cheilostome anascan bryozoans
		<i>praeclara</i>	cheilostome anascan bryozoans
		<i>mucroniferus</i>	on sponge or diet unknown
<i>formosa</i>	thecate and athecate hydroids		
<i>rebus</i>	scleractinian corals of the genus <i>Porites</i>		
Heroidae	<i>Proctonotus</i>	<i>Hero</i>	
Pinufiidae	<i>Pinufius</i>		

Because the food items of nudibranchs encompass a wide range of invertebrate taxa, because our search has included both old and new literature, and because we are not taxonomic experts on these various taxa consumed by nudibranchs, we have been unable to verify the current proper scientific name of many of the prey items. Therefore, in the database, the name of the prey is as given in the original reference. In the case of the nudibranchs, however, we have researched the literature and have listed the species under the most currently acceptable name. In the database, we have indicated if a different name for the nudibranch was used in the original publication. In all cases, the *Traite de Zoologie* is the basis of the classification used for the nudibranchs with some minor modifications based on more recently published literature.

The current database is based on literature published through June of 1996. A decision on how often to update the database has not yet been made.

It should be noted that in the database the distinction is made between a nudibranch being "on" a prey and the

actual consumption of the prey. We feel this is an important distinction that will avoid erroneous attributing of food habits.

The total number of papers in this series is estimated to be seven. Each will give a summary table of the nudibranch species and the generalized food group that it preys upon (or the exact food if the animal is a specialist on a single taxon) and discuss the trends and/or peculiarities of the nudibranch taxon. Literature citations will be limited to those that discuss the nudibranch group as a whole.

INTRODUCTION TO THE ARMINACEA

The suborder Arminacea is one of the smallest in the Order Nudibranchia. The number of species worldwide, according to our search of the literature, is about 166, but this figure should be considered only an approximation as we have not checked out junior synonyms or names which might not have appeared in the Zoological Record. This group is, according to Thompson & Brown (1984), one of

the most difficult to define and recognize visually by external features. According to Boss (1982), Thompson & Brown (1984) and McDonald & Nybakken (1980), all arminaceans lack rhinophoral sheaths, have the anus displaced forward, either lateral or dorsal, and tend to lack oral or cephalic tentacles. The major papers describing the taxonomy of the suborder are those of Odner (1934, 1939). In this paper we provide food data on 33 species.

RESULTS AND DISCUSSION

As can be seen from Table 1, the arminaceans have a somewhat varied diet, and the suborder includes both specialists and generalists. In the families Heterodorididae and Arminidae, the species tend to prey upon some sort of octocoral. Among the Arminidae, there seems to be a specialization among the different genera for different orders of octocorals with *Armina* specializing in pennatulids, while *Dermatobranchus* feeds on stoloniferans, and *Histiomena* consumes gorgonians.

The two specialist families are the Doridomorphidae and the Pinufiidae, the former feeding apparently only on the blue coral *Heliopora*, while the latter feeds on scleractinian corals of the genus *Porites*.

The remainder of the families tend to consume either bryozoans or hydroids. Among the bryozoan predators, the tendency is to consume cheilostomes, primarily the anascan types. *Dirona albolineata* is somewhat unusual in that the species preys on mollusks in addition to bryozoans. An-

other odd species is *Proctonotus mucroniferus* which was reported to occur on sponges by Alder & Hancock (1845-55), but Thompson & Brown (1984) said that the diet is unknown.

Rudman (1982) reported that *Doridomorpha gardineri* has symbiotic zooxanthellae as does *Pinufius rebus*, and both may well prove to be dependent upon these symbionts for at least part of their energy requirements.

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Range Expansion of an Alien Invader—the Nudibranch Mollusk *Doridella obscura* Verrill, 1870 (Opisthobranchia: Corambidae) in the Black Sea

by

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Abstract. An annotated list of the Black Sea locations of the alien nudibranch *Doridella obscura* Verrill, 1870 (native to the brackish-water environment of the Atlantic coast of North America) is given. This species was most likely introduced to the Black Sea in the veliger stage via ballast water discharge in the 1980s and 1990s. Two sample sites from the northeastern coast of the Black Sea (Bolshoy Utrish and Gelendzhik), as well as one from the Crimean coast (Inkerman, Sevastopol Bay), are new for the Black Sea. The environmental factors most strongly influencing the process of colonization and establishment of *D. obscura* in the new surroundings are discussed. The numerous egg masses of *D. obscura* observed in the field (Inkerman, November, 1992) indicate that the Black Sea population of this species already represents a self-maintaining, proliferating population, and not merely a pseudopopulation sustained exclusively by constant transoceanic immigration of veliger larvae by ship ballast waters.

INTRODUCTION

In the Black Sea, the small, cryptic, shallow-water dorid nudibranch *Doridella obscura* Verrill, 1870 (a native of the brackish-water environment of the Atlantic coast of North America) first was reported from Laspi Bay, southern coast of Crimea (Roginskaya & Grintsov, 1990). A single specimen was discovered by the second author (V.G.) on a mussel collector, which had been in place from the end of September 1988 through mid-January 1989. It has been suggested that this species may have been introduced into the Black Sea in the veliger stage via ballast water discharge.

Soon after our publication appeared, Black Sea samples of this exotic mollusk (sent for examination by various researchers concerned about the changes in Black Sea benthos communities) were received by the first author (I.R.). The “unusual mollusks” in these samples, identified by the first author as *D. obscura*, were collected in the late

1980s and early 1990s from Varna Bay, the Bolshoy Utrish Cape region (near Anapa), Blue Bay (near Gelendzhik), and Sevastopol Bay (Table 1). Some of them were collected at considerably earlier dates than the first documented record of the species.

In 1993 three new Black Sea localities of *D. obscura* (Odessa, Varna, Burgas), as well as one from Kertch Strait, were documented by Sinegoub (1993).

Although it seemed probable that this alien species, occasionally introduced into the Black Sea, has now attained a rather wide geographic range along the coastline of the sea, and perhaps has even become a permanent inhabitant of this body of water, the possibility of a pseudopopulation could not be ignored. Only in November 1992, when the second author had an opportunity to observe numerous egg masses of *D. obscura* in the field (Inkerman, Sevastopol Bay), did we become convinced that this species had established itself in the Black Sea.

The purpose of the present paper is to follow the dy-

Table 1
Collection data for *Doridella obscura* in the Black Sea.

N	Loc.	n	Body length (mm)		Date	Habitat	Depth (m)	Collector	Reference
			range	\bar{x}					
1	Varna Bay (Bulgaria)	4	—	—	07/20/86	<i>Rapana</i> epibiosis	2	Sinegoub	Sinegoub, 1993, 1994
		3	2.5–3.1	—	08/07/86	<i>Rapana</i> epibiosis	No data	Sinegoub	This study
2	Burgas Bay (Bulgaria)	3	—	—	06/26/87	<i>Rapana</i> epibiosis	1–2	Sinegoub	Sinegoub, 1993, 1994
		23	2.1–4.1	2.7 ± 0.8	03/89	<i>Rapana</i> epibiosis	No data	No data	This study
3	Bolshoy Utrish Cape region	27	0.7–4.0	2.3 ± 0.9	1989	Artificial reefs' fouling	No data	Besossov	Roginskaya, Grintsov, 1995; this study
4	Laspi Bay (near Sarych Cape)	1	4.5	—	12/23/88–01/89	Mussel collector	15	Grintsov	Roginskaya, Grintsov, 1990
5	Blue Bay (near Gelendzhik)	1	2.8	—	09/91	<i>Cystoseira barbata</i> epibiosis	No data	Reznichenko	Roginskaya, Grintsov, 1995; this study
6	Inkerman, Sevastopol Bay	40	2.3–3.6	2.8 ± 0.4	11/92	bryozoans, encrusting mussels, and barnacles	0.3	Grintsov	Roginskaya, Grintsov, 1995; this study
6a	300 m from Inkerman	rare	—	—	1991	bryozoans	No data	—	Nikolaenko, personal communication
7	Odessa Bay	3	—	—	09/17/91	Concrete hydro-technical constructions' fouling, dominated by mussels	0.7–1.5	Sinegoub	Sinegoub, 1993, 1994
8	Kertch Strait	1	—	—	10/21/89	mussel epibiosis	5	Sinegoub	Sinegoub, 1993, 1994

Abbreviations: N—number of sampling stations (localities) referred to in the map (Figure 1) and in the annotated checklist of localities. Loc.—locations of the samples. n—number of specimens. \bar{x} —body length: mean ± standard deviation.

namics of colonization by *D. obscura* of the new localities far beyond the usual geographic range of this species. The environmental factors most strongly influencing the process of accommodation of *D. obscura* in the Black Sea are discussed.

MATERIALS AND METHODS

Material for this study came from several sources (Table 1). The samples for external examination and laboratory dissection included 94 adults of *D. obscura* from five sampling localities along the coastline of the Black Sea (Table 1, locs. 1–3, 5, 6). Measurements of the specimens were made using a stereomicroscope MBS-I. New Black Sea records of *D. obscura* (locs. 3, 5, 6), as well as literature data and additional information from personal communications (locs. 4, 6a, 7, 8) are combined in Table 1. Representative specimens from three localities (locs. 1, 3, 6) are deposited in the Zoological Museum of Moscow State University, Russia: loc. 1—Varna, 1 specimen, no. Lc 22842; loc. 3—Bolshoy Utrish, 2 specimens, no. Lc 22841; loc. 6—Inkerman, Sevastopol Bay, 3 specimens, no. Lc 22843.

RESULTS

The distribution of the immigrant nudibranch *Doridella obscura* in the Black Sea is shown in the map of locations of sampling stations (Figure 1).

Table 1 summarizes what is known up to now about the recorded distribution of *D. obscura* in the Black Sea, dates of collection, habitat character, and size of specimens. The annotated checklist of localities of the immigrant *D. obscura* was compiled based on the data from Bulgarian, Russian, and Ukrainian areas of the Black Sea (Figure 1). The new localities for *D. obscura* are designated by a single asterisk.

(loc. 1) **Varna Bay, Bulgaria** (45°38'N, 25°36'E), western coast of the Black Sea.

Three specimens, preserved length 2.5–3.1 mm, collected in July–August 1986 from *Rapana thomasiana* Crosse epibiosis, were received from Dr. I. S. Sinegoub (see also Sinegoub, 1993, 1994). According to Sinegoub (1994), associated fauna in the fouling included *Nereis succinea* Leuckart (Polychaeta), *Conopeum seurati* (Cann) (Bryozoa), *Balanus improvisus* Darwin (Cirripedia), and *Mytilaster lineatus* Gmelin (Bivalvia). Depth 2 m, sandy bottom.

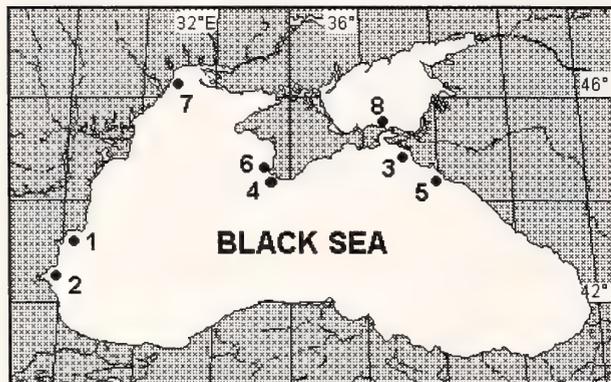


Figure 1

Map of the Black Sea showing the localities where introduced *Doridella obscura* have been observed. The sampling stations are indicated by black circles. The numbers are those referenced in Table 1 and in the annotated checklist of localities. 1. Varna Bay, Bulgaria; 2. Burgas Bay, Bulgaria; 3. Bolshoy Utrish Cape region, Russia; 4. Laspi Bay (near Sarych Cape), Ukraine; 5. Blue Bay (near Gelendzhik), Russia; 6. Inkerman, Sevastopol Bay, and 6a. 300 m from Inkerman, Ukraine; 7. Odessa Bay, Ukraine; 8. Kertch Strait, Ukraine.

(loc. 2) Burgas Bay, Bulgaria (42°30'N, 27°29'E), western coast of the Black Sea.

A representative series of 23 fixed specimens ranging from 2.1–4.1 mm in length, mean 2.7 ± 0.8 mm, collected (per attached label) in March 1989, and received from Professor Ya. I. Starobogatov. Collector name and substrate characteristics are absent. Dr. Sinogub (1993, 1994) reported three specimens of *D. obscura* in Burgas Bay 21 June 1987 in *Rapana thomasiana* epibiosis, from a depth of 1–2 m, sandy bottom, and the same faunal composition as in loc. 1.

***(loc. 3) Bolshoy Utrish Cape region, Russia** (44°45'N, 37°23'E), northeastern coast of the Black Sea.

A representative series of 27 specimens ranging in length from 0.7–4.0 mm (preserved), with mean 2.3 ± 0.9 mm, collected throughout 1989, from barnacles in the fouling of artificial reefs. Associated fauna: colonial hydroids (*Obelia*) and encrusting bryozoans. Collector: V. Besnossov. Received from L. A. Rittikh.

(loc. 4) Laspi Bay (near Sarych Cape), Ukraine (42°23'N, 33°44'E), southern coast of Crimea.

One specimen, 4.5 mm in length (preserved), was collected at a depth of 15 mm from a mussel collector placed at a depth of 17 m, which had been in place from 23 December 1988 through January 1989. Associated fauna: the hydroid *Obelia longissima* (Pallas), *Electra crustulenta* (Pallas) (Bryozoa), and barnacles *Balanus improvisus* (Roginskaya & Grintsov, 1990).

***(loc. 5) Blue Bay (near Gelendzhik), Russia** (44°33'N, 38°05'E), northeastern coast of the Black Sea.

One living specimen, 2.8 mm long, collected by Dr. O. G. Reznichenko from the alga *Cistoseira barbata*, encrusted by bryozoans and barnacles, in September 1991. This specimen later was transported by Dr. Reznichenko to Moscow where we were able to observe it in aquaria for more than a week.

***(loc. 6) Inkerman, Sevastopol Bay, Ukraine** (44°37'N, 33°22'E), southern coast of Crimea.

An established population, including a total of 40 adults of *D. obscura*, ranging from 2.3–3.6 mm preserved, mean 2.8 ± 0.4 mm, and numerous (~30) egg masses, collected by the second author in November 1992, at a depth of about 30 cm from the surface (water temperature 12°C, salinity 10–12‰). The egg masses, attached to the colonies of bryozoans, encrusting mussels, and barnacles, were observed alongside the adult *D. obscura*. The egg masses that were found in the field were arranged in the form of low, flat spiral coils (3 mm diameter) and, typically for *D. obscura*, twisted in a clockwise direction (Franz, 1967). The spawns found in the field were identical to the egg ribbons of *D. obscura* released by seven captured animals in aquaria (water temperature 13–15°C).

***(loc. 6a) 300 m from loc. 6 Inkerman, Sevastopol Bay, Ukraine**, southern coast of Crimea.

According to Dr. T. N. Nikolaenko (personal communication), rare specimens of *D. obscura* were observed on bryozoans throughout the year 1991. Dr. Nikolaenko kindly placed at our disposal the list of the six most common bryozoans she had discovered in this location in 1991: *Bowerbankia caudata* (Hinks, 1877), *B. gracilis* (Leydy, 1855), *Conopeum seurati* (Canu, 1928), *Membranipora crustulenta* (Pallas, 1766), *Electra monostachys* (Busk, 1853), *Laeralia pallasiana* (Moll, 1803).

(loc. 7) Odessa Bay, Ukraine (46°28'N, 30°44'E), northwestern coast of the Black Sea.

Three specimens of *D. obscura* were collected by Sinogub (1993, 1994) 17 September 1991 in the fouling of concrete hydrotechnical constructions (dominated by mussels), at a depth of 0.7–1.5 m.

(loc. 8) Kertch Strait, Ukraine (45°15'N, 36°33'E)

On 21 October 1989, one specimen of *D. obscura* was collected by Dr. Sinogub in the mussel biocoenosis, at a depth of 5 m (northern part of the Kertch Strait) bottom salinity 11.2‰, water temperature 14°C.

DISCUSSION

Until the late 1980s, *Doridella obscura*, as well as other members of the family Corambidae, was completely unknown from the Black Sea (Valkanov, 1957; Swennen, 1961; Golikov & Starobogatov, 1972; Chukhchin, 1984;

Marinov, 1990). But after our first confirmed record of *D. obscura* in Laspi Bay (Roginskaya & Grintsov, 1990), we received several simultaneous reports about the spread of this species within the last decade in the Black Sea.

Was it possible that this cryptic nudibranch species had simply been overlooked by collectors? This possibility cannot be excluded. However, another explanation seems more probable: that is, the intensification of direct marine traffic from the western Atlantic to the Black Sea resulting in increased transatlantic transport of larvae of coastal invertebrates with ship ballast water (Vinogradov & Shushkina, 1993). Could it be a mere coincidence that all the samples of *D. obscura* in the Black Sea were discovered after the beginning of the transport of United States and Canadian corn to the USSR in the 1980s? We consider the ballast waters (discharged into Black Sea ports) of transoceanic corn freighters arriving directly from USA harbors the most likely vector for the veligers of this common Western Atlantic nudibranch (Roginskaya & Grintsov, 1990).

A very important argument in favor of this assumption is the ability of veligers of *D. obscura* to delay metamorphosis and to survive during periods of low phytoplankton production. Veligers that were starved at the beginning of the pelagic phase and did not receive food (*Isochrysis galbana*) until 5 to 9 days after hatching, metamorphosed only on the 14th to 18th day, even in the presence of metamorphosis-inducing substrate (Perron & Turner, 1977). This is sufficient time for a ship to cruise the Atlantic.

The far-ranging locations of the records of *D. obscura* along the coastline of the Black Sea, the constantly increasing number of records, and especially the numerous egg masses of this species observed in the field, suggest that this species has become established in the Black Sea. The Black Sea population of *D. obscura* can no longer be considered a pseudopopulation, sustained only by constant immigration of veligers, originating from the Western Atlantic and crossing the ocean by means of human activity, but as a self-maintaining, proliferating population.

The successful accommodation of the brackish-water *D. obscura* is favored by the suitable environmental parameters in the Black Sea, e.g., low environmental salinity (14–15‰), up to 18.4‰ near the coasts of Crimea, the Caucasus, and in the shallow waters of the northwestern part of the sea; and even 5–10‰ in estuaries (Shalyapin, 1990). The fluctuations of Black Sea shallow-water temperatures (from 2–3°C [and even below 0°C], up to 23°C [Shalyapin, 1990]) remain within the species' known physiological tolerance limits. In its native habitat, *D. obscura* is known to spawn from June until cold weather (even at water temperature of 5°C [Franz, 1967]), and the larvae of *D. obscura* remain viable at temperatures ranging from 1.5°C to 28°C (Perron & Turner, 1977).

The short embryonic period of *D. obscura* (the hatching of pelagic veligers with turbo-spiral larval shells, measuring $100 \times 150 \mu\text{m}$, took place at the Inkerman Laboratory after a 4-day embryonic stage, at a water temperature of

13–15°C [Roginskaya & Grintsov, 1995]), as well as the occurrence in the shallow water of the Black Sea of the colonial bryozoan *Electra crustulenta* (Pallas) (Roginskaya & Grintsov, 1990; Nikolaenko, personal communication), promote the colonization of the region by this species. *Electra crustulenta*, co-occurring with *D. obscura* along the Atlantic coast of North America, not only serves as habitat for juveniles and significant substrate and primary prey for adult *D. obscura*, but also appears to be the main environmental cue inducing the metamorphosis of the veligers of this mollusk (Perron & Turner, 1977).

It is still uncertain when and where the initial introduction of the veligers of *D. obscura* took place. Probably the veligers were released with ship ballast waters simultaneously in several Black Sea ports harboring transoceanic ships. The theory of multiple introduction is supported by the concentration of most records of *D. obscura* near major Black Sea ports. Further study is needed to settle the matter. To date, the Varna record in 1986 (Sinigoub, 1993, 1994) is the earliest in the Black Sea.

We are now witnessing the rapid spread of *D. obscura* along the coastline of the Black Sea. The larvae of *D. obscura*, constantly released from ship ballast waters (as the egg masses of *D. obscura* at the Atlantic coast of North America are found for most parts of the year [Franz, 1967; Perron & Turner, 1977]), as well as those hatched from the native Black Sea egg masses, could be dispersed by circular currents along the whole perimeter of the Black Sea. Information on the occurrence of *D. obscura* at more southern coasts of the Black Sea would be helpful in understanding the degree of colonization of the shallow-water environment of the Black Sea by this species.

The record of one specimen of *D. obscura* in the northern part of the Kertch Strait (loc. 8) leads us to predict the spread of this species to the brackish water Sea of Azov.

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Microscopic Growth of Bivalve Shells and its Computer Simulation

by

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Abstract. Microscopic features of bivalve shells in radial and vertical sections were examined both empirically and theoretically. Many of the examined 72 species, all of which are extant, indicated inclination and curving in the growth directions of aggregated biomineral units as the result of geometric selection. The shape of the growth front formed by the aggregated units determines the profile of internal microgrowth increments. The rate of relative crystal growth generally decreases with the elongation of the structural unit, in association with the curvature of the elongation front of the structural units and internal microgrowth increments. The geometric pattern of the shell microstructures is reasonably well represented by computer simulations under the condition when the elongation of the structural units declines at a fixed lateral expansion rate throughout crystal growth. This result suggests anisotropy of decline of crystal growth derived from an inhibition of crystal elongation.

INTRODUCTION

Previous studies of hard tissue construction have focused mainly on the physicochemical process of biomineralization or growth kinematics of macroscopic morphology. Many efforts have been made in the field of biomineralogy (e.g., Wada, 1961; Crenshaw, 1972; Weiner & Traub, 1984) and theoretical morphology (e.g., Raup, 1966; Bayer, 1978; Okamoto, 1988) of molluscan shells, but both approaches were developed independently without strong interactions between them. However, the understanding of the shell formation requires not only empirical knowledge of the relationship between biological factors and shell morphology but also recognition of rule or algorithm linking the factors and geometry.

The process of shell construction should be regarded as an integrated system, that is, related to both biomineralogical nature and geometric limitation. Particularly in the construction of the marginally growing shell microstructure, interaction among crystals is an essential character of the kinematics of microscopic growth. Understanding of the interaction system and kinematics of crystals and/or units of mineral aggregates is a first step in synthesizing the system of shell construction, and requires geometric analysis of the microscopic feature.

The purpose of this paper is two-fold: to recognize the kinematic process of microstructural construction of bivalve shells, and to predict the mode of control of the geometric profile of microgrowth increments. For this pur-

pose, computer simulation of the growth kinematics at the microscopic order is attempted, and the results are compared with the microscopic observation of actual specimens. The Bivalvia are particularly suitable for this study because their shell microstructure has been well studied (e.g., Bøggild, 1930; Taylor et al., 1969; Uozumi & Suzuki, 1981; Carter & Clark, 1985).

NOTES ON SHELL MICROSTRUCTURE IN BIVALVES

This paper basically follows the nomenclature of Carter et al. (1991) for the terminology of shell microstructure. The bivalve shell consists of a number of columnar, fibrous or sheetlike units, i.e., prisms or lamellae, each of which is not a single crystal but an aggregation of numerous small crystals. Such a bundle of mineral aggregation (prism, lamella, etc.) is tentatively designated as a "structural unit."

According to Carter et al. (1991), the prismatic structure consists of parallel, adjacent structural units (first order prisms) and can be subdivided into simple (Figure 1A), fibrous (Figure 1B), and composite prismatic (Figure 1C) structures based on their appearance. The composite prism consists of second-order diverging units toward the depositional surface (Figure 1C). The first-order prisms elongate horizontally or vertically. In the present paper, the informal term "columnar prismatic structure" which includes both simple and vertical-type composite prismatic structures are used. Foliated structure consists of more or

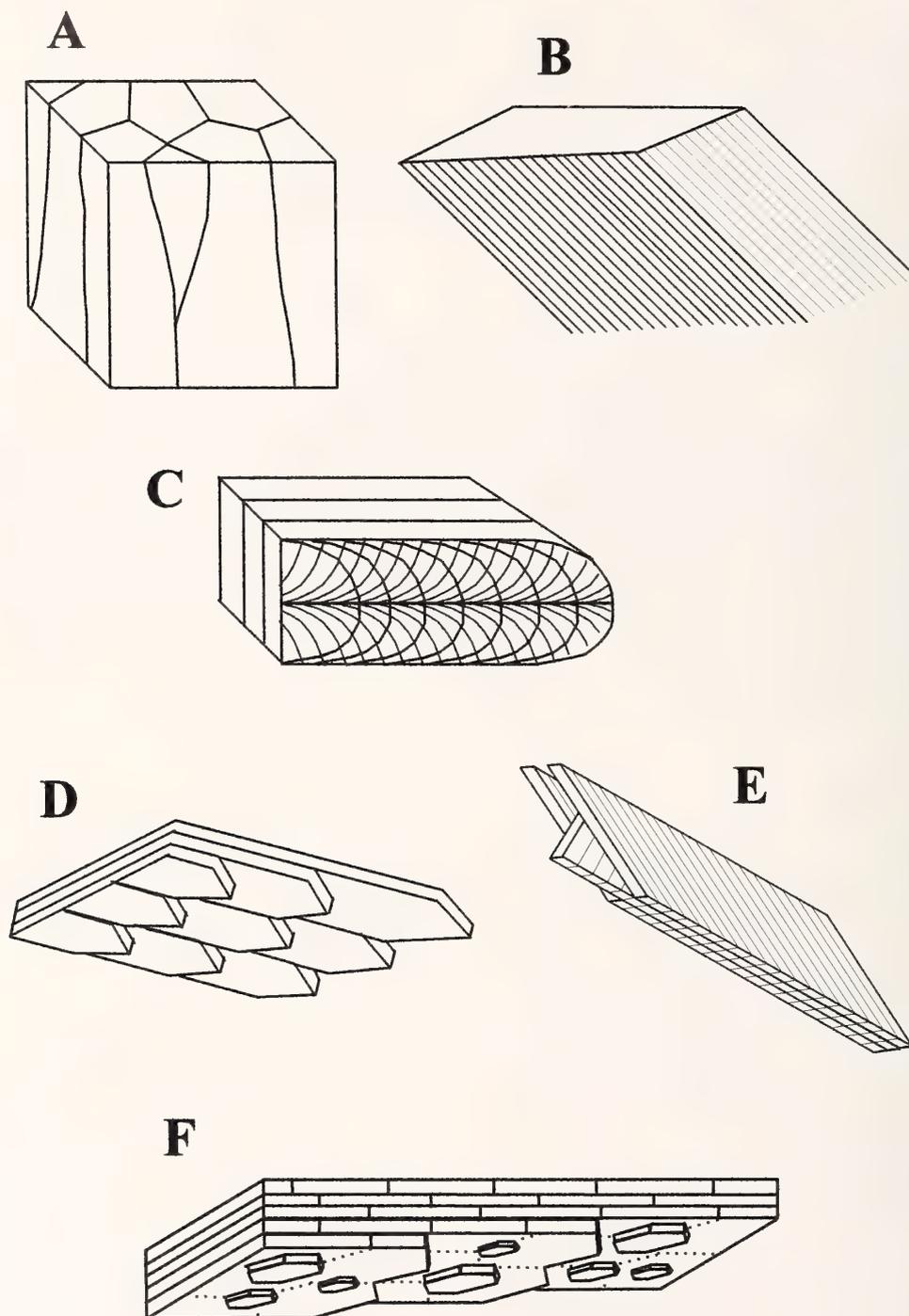


Figure 1

Schematic diagram of the shell microstructure. A. simple prismatic structure. B. fibrous prismatic structure. C. horizontal-type composite prismatic structure. D. foliated structure. E. crossed lamellar structure. F. nacreous structure. Terminology after Carter et al. (1991).

less mutually parallel calcitic blades or laths arranged in laminae dipping at a generally uniform angle and in the same general direction over large portions of the depositional surface (Figure 1D). The crossed lamellar structure consists of mutually parallel rods, laths, or blades aggregated into first-order lamellae. The second-order lamellae in adjacent first-order lamellae show two dominant dip directions, and they alternate regularly between adjacent first-order lamellae (Figure 1E). The first-order lamellae are radiating or vertically arranged. The nacreous structure consists of polygonal to rounded tablets arranged in mutually parallel laminae (Figure 1F). The homogeneous structure lacks clear first-order structural arrangement except for accretion banding.

MATERIALS AND METHODS

A total of 72 species of extant bivalves was studied. A summary of their classification and the locality of collection are given in Table 1. Each species was represented by one or a few specimens. Most specimens were collected, either alive or dead, at various localities in the northwestern Pacific region by the author, but some were selected from collections housed in the University Museum, University of Tokyo (UMUT).

For observation in thin section, a single valve of each shell was cut vertical to the outer shell surface in the radial direction, embedded in epoxy resin, and polished with graded powder. The polished surface was etched with 5% acetic acid for 2 minutes, washed, dried in air, coated with platinum vanadium, and then observed by scanning electron microscopy (SEM) (Hitachi S-2400). For observation of the initial stage of crystal growth, the shell edge adjacent to the periostracum was carefully removed by hand from the shell under a binocular microscope, mounted inner surface uppermost without etching, and coated with platinum vanadium prior to observation with SEM. An acetate peel was also prepared for each specimen by pressing a sheet of triacetylcellulose film onto the etched surface while it was flooded with acetone (Kennish et al., 1980). The resulting preparation was observed by ordinary light microscopy (Olympus AHBT).

For estimating the ratio of the growth rate of the structural unit versus shell accretion rate, growth increments both along a represented elongating structural unit and along the outer shell surface at the pallial attachment was measured on an acetate peel of the outer shell layer (Figure 2) in each specimen (35 species) using a digital micrometer attached to a profile projector (Nikon Model V-16D) with the magnification at $\times 100$ (Figure 2). Specimens examined possess various kinds of shell microstructure in the outer shell layer (Table 2), and some of them include nacreous and homogeneous structures which lack the elongating structural units in the inner part of the outer shell layer. In nacreous or homogeneous shell, growth increments are measured along the imaginary elongating unit which intersects the internal microgrowth increments at 90° .

For the computer simulation, a program written in N-88 BASIC was carried out with a personal computer (NEC PC-9821 Xp) interfaced with a CRT (SANYO CMT-B15M6) and an ink-jet printer (Canon BJC-600J).

RESULTS

Shell Microstructure

In order to understand the growth process of the shell, microscopic observations were made in all species examined. SEM observations at the surface of crystal growth at the shell edge show incipient hemispheres of the first-order lamellae (Carter et al., 1991) on the inner surface of the periostracum of *Geloina papua* (Lesson, 1832) and *Pseudocardium sachalinense* (Schrenck, 1862); both species have crossed lamellar shell structure (Figure 3A). In *Periglypta puerpera* (Linnaeus, 1771), second- or third-order units of an incipient lamella appear to be more or less spherulitic. In *Tapes philippinarum* Adams & Reeve, 1850, many small hemispherical second-order prisms occur at the growing front of the first-order composite prisms (Figure 3B). A spherulitic texture is also recognized in a second-order composite prism in *Codakia tigerina* (Linnaeus, 1758), *Katelsysia japonica* (Gmelin, 1791), and *Dosinia japonica* (Reeve, 1850). These characters of structural units at the initial stage of formation of the crossed lamellae and the composite prisms are similar to those of the columnar and fibrous prisms described by Ubukata (1994). These observations indicate that at the initial stage of crystal growth, the first-order units of the crossed lamellae and the second-order units of the composite prisms both grow in a similar way to the first-order units of the columnar and fibrous prisms.

Geometric selection of the first-order lamellae was recognized in the radiating type crossed lamellar outer shell layer of *Arca navicularis* Bruguière, 1789, *Barbatia amygdaluntortum* (Röding, 1798), *Begonia semiorbiculata* (Linnaeus, 1758) (Figure 3C), *Cardita leana* Dunker, 1860, *Chama brassica* Reeve, 1847, *Gafrarium tumidum* Röding, 1798, and *Corbula erythrodon* Lamarck, 1818. In these species, the density of the first-order lamellae on the inner shell surface is generally much less than that on the outer shell surface of the crossed lamellar shell layer. In the horizontal type of crossed lamellar and composite prismatic structures of *Codakia tigerina*, *Paphia amabilis* (Philippi, 1847), *Tridacna crocea* Lamarck, 1819, *Mercenaria simpsoni* (Gould, 1861), *Dosinia japonica*, *Callista brevisiphonata* Carpenter, 1865, and *Katelsysia japonica*, first-order lamellae or second-order prisms radiate from the longitudinal axis toward the depositional surface, and the elongation axes of the structural units are often curved and inclined toward the ventral margin in the radial and vertical shell section (Figure 3D, E). The size of the structural unit generally increases as each unit elongates in radial direction. These geometric patterns of the crossed-lamellar and horizontal composite prismatic structures in the radial

Table 1

List of species utilized in this study.

Family	Species	Locality
Archidae	<i>Arca navicularis</i> Bruguiere, 1789	Shikanoshima, Fukuoka, western Japan
	<i>A. boucardi</i> Jousseau, 1894	Morozaki, Aichi, central Japan
	<i>Barbatia amygdalumtortum</i> (Röding, 1798)	Iriomote Is., Okinawa, southwest Japan
	<i>Anadara antiquata</i> (Linnaeus, 1758)	Honda Bay, Palawan, southwest Philippines
Glycymerididae	<i>Glycymeris ezoensis</i> (Sowerby, 1886)	Sarufutsu, Hokkaido, northern Japan
Mytilidae	<i>Mytilus grayanus</i> Dunker, 1853	Samani, Hidaka, northern Japan
	<i>M. galloprovincialis</i> Lamarck, 1819	Yokohama, Kanagawa, central Japan
	<i>M. californianus</i> Conrad, 1837	Neah Bay, Washington, USA
	<i>Septifer bilocularis</i> (Linnaeus, 1758)	Turtlecove Is., Palau
Pteriidae	<i>Modiolus modiolus</i> (Linnaeus, 1758)	Samani, Hokkaido, northern Japan
	<i>Pinctada margaritifera</i> (Linnaeus, 1758)	Ishigaki Is., Okinawa, southwest Japan
Isognomonidae	<i>Isognomon perna</i> (Linnaeus, 1758)	Iriomote Is., Okinawa, southwest Japan
Malleidae	<i>Malleus regula</i> (Forsk., 1775)	Iriomote Is., Okinawa, southwest Japan
Pinnidae	<i>Pinna muricata</i> Linnaeus, 1758	Honda Bay, Palawan, southwest Philippines
	<i>Atrina kinoshitai</i> Habe, 1953	Amakusa, Nagasaki, western Japan
Limidae	<i>Lima vulgaris</i> Link, 1807	Turtlecove Is., Palau
Ostreidae	<i>Crassostrea lineata</i> (Röding, 1798)	Iriomote Is., Okinawa, southwest Japan
	<i>Crassostrea gigas</i> (Thunberg, 1973)	Misaki, Kanagawa, central Japan
Plicatulidae	<i>Plicatula muricata</i> Sowerby, 1873	Misaki, Kanagawa, central Japan
Pectinidae	<i>Chlamys farreri</i> (James & Preston, 1904)	Morozaki, Aichi, central Japan
	<i>C. vesiculosus</i> Dunker, 1877	Misaki, Kanagawa, central Japan
	<i>C. swifti</i> (Bernardi, 1858)	Wakkanai, Hokkaido, northern Japan
	<i>Patinopecten yessoensis</i> (Jay, 1857)	Wakkanai, Hokkaido, northern Japan
Spondyliidae	<i>Spondylus squamosus</i> Schreibers, 1793	Iriomote Is., Okinawa, southwest Japan
	<i>S. barbatus</i> Reeve, 1856	Sagami Bay, Kanagawa, central Japan
Unionidae	<i>Unio biwae</i> Kobelt, 1879	Biwa Lake, Shiga, central Japan
	<i>Lanceolaria oxyrhyncha</i> (Martens, 1861)	Biwa Lake, Shiga, central Japan
	<i>Cristaria plicata</i> (Leach, 1815)	Biwa Lake, Shiga, central Japan
	<i>Lamprotula rochechoarti</i> (Heude, 1885)	Tung-t'ing Lake, China
Trigoniidae	<i>Neotrigonia margaritacea</i> (Lamarck, 1804)	French Is., Australia
Lucinidae	<i>Codakia tigrina</i> (Linnaeus, 1758)	Panglao Is. Cebu, southern Philippines
	<i>Cardita leana</i> Dunker, 1860	Misaki, Kanagawa, central Japan
Carditidae	<i>Begonia semiorbicularis</i> (Linnaeus, 1758)	Honda Bay, Palawan, southwest Philippines
	<i>Megacardita ferruginosa</i> (Adams & Reeve, 1850)	Misaki, Kanagawa, central Japan
	<i>Chama brassica</i> Reeve, 1847	Honda Bay, Palawan, southwest Philippines
Astartidae	<i>Tridonta alaskensis</i> (Dall, 1903)	Etorofu Is., Hokkaido, northern Japan
Cardiidae	<i>Fragum unedo</i> (Linnaeus, 1758)	Iriomote Is., Okinawa, southwest Japan
	<i>Nemocardium samarangae</i> Makiyama, 1934	Misaki, Kanagawa, central Japan
	<i>Laevicardium mutica</i> Reeve, 1844	Morozaki, Aichi, central Japan
Tridacnidae	<i>Tridacna crocea</i> Lamarck, 1819	Honda Bay, Palawan, southwest Philippines
Mactridae	<i>Mactra chinensis</i> Philippi, 1846	Wakkanai, Hokkaido, northern Japan
	<i>Pseudocardium sachalinense</i> (Schrenck, 1862)	Wakkanai, Hokkaido, northern Japan
Solenidae	<i>Solen gordonis</i> Yokoyama, 1920	Misaki, Kanagawa, central Japan
Tellinidae	<i>Tellina venulosus</i> Schrenck, 1861	Sarufutsu, Hokkaido, northern Japan
Psammobiidae	<i>Gari elongata</i> Lamarck, 1818	Iriomote Is., Okinawa, southwest Japan
Glossidae	<i>Meiocardia tetragona</i> (Adams & Reeve, 1850)	Misaki, Kanagawa, central Japan
Corbiculidae	<i>Corbicula sandai</i> Reinhardt, 1878	Biwa Lake, Shiga, central Japan
	<i>Geloina papua</i> (Lesson, 1832)	Iriomote Is., Okinawa, southwest Japan
Veneridae	<i>Venus foveolata</i> (Sowerby, 1853)	Shima, Mie, central Japan
	<i>Venus toreuma</i> Gould, 1850	Danvers, Massachusetts, USA
	<i>Periglypta puerpera</i> (Linnaeus, 1771)	Honda Bay, Palawan, southwest Philippines
	<i>Circe scripta</i> (Linnaeus, 1758)	Sagami Bay, Kanagawa, central Japan
	<i>Gafrarium tumidum</i> Röding, 1798	Iriomote Is., Okinawa, southwest Japan
	<i>Callanaitis disjecta</i> (Perry, 1771)	Australia
	<i>Anomalocardia brasiliensis</i> (Gmelin, 1791)	Brazil
	<i>Mercenaria stimpsoni</i> (Gould, 1861)	Wakkanai, Hokkaido, northern Japan
	<i>M. mercenaria</i> (Linnaeus, 1758)	Danvers, Massachusetts, USA
	<i>Protothaca euglypta</i> (Sowerby, 1914)	Misaki, Kanagawa, central Japan
	<i>P. jedoensis</i> (Lischke, 1874)	Misaki, Kanagawa, central Japan

Table 1
Continued.

Family	Species	Locality
	<i>Timoclea micra</i> (Pilsbry, 1904)	Shikanoshima, Fukuoka, western Japan
	<i>Meretrix petechialis</i> Lamarck, 1818	Morozaki, Aichi, central Japan
	<i>Callista brevisiphonata</i> Carpenter, 1865	Wakkanai, Hokkaido, northern Japan
	<i>Saxidomus purpuratus</i> (Sowerby, 1852)	Morozaki, Aichi, central Japan
	<i>Tapes philippinarum</i> Adams & Reeve, 1850	Misaki, Kanagawa, central Japan
	<i>Katelysia japonica</i> (Gmelin, 1791)	Iriomote Is., Okinawa, southwest Japan
	<i>Paphia amabilis</i> (Philippi, 1847)	Sagami Bay, Kanagawa, central Japan
	<i>P. euglypta</i> (Philippi, 1847)	Sagami Bay, Kanagawa, central Japan
	<i>Dosinia japonica</i> (Reeve, 1850)	Misaki, Kanagawa, central Japan
	<i>Clementia vatheleti</i> Mabilie, 1901	Shima, Mie, central Japan
	<i>Cyclina sinensis</i> (Gmelin, 1791)	Ariake, Saga, Japan
Corbulidae	<i>Corbula erythrodon</i> Lamarck, 1818	Morozaki, Aichi, central Japan
Cuspidariidae	<i>Cuspidaria hindsiana</i> (Adams, 1864)	Misaki, Kanagawa, central Japan
	<i>C. nobilis</i> (Adams, 1864)	Misaki, Kanagawa, central Japan

and vertical section are also similar to those of the columnar and fibrous prismatic structures in *Malleus regula* (Forskål, 1775), *Isognomon perna* (Linnaeus, 1758), *Unio biwae* Kobelt, 1879, and *Mytilus grayanus* Dunker, 1853, described by Ubukata (1994), although the arranging pattern of crossed-lamellae is often disturbed. This fact shows that the geometric patterns of the first-order lamellae and second-order composite prisms also depend upon competition for space among structural units during growth.

In the crossed-lamellar and the horizontal composite prismatic shell structures, the elongation axes of the structural units and the internal microgrowth increments in radial and vertical sections intersect at 90° in the initial stage of crystal growth, as in the columnar prismatic shell

(Ubukata, 1994). In *Tapes philippinarum*, *Paphia euglypta* (Philippi, 1847), *Paphia amabilis*, and *Dosinia japonica*, the elongation axes of lamellae or prisms occasionally become slightly reclined to the microgrowth increments as crystals grow toward the inner surface (Figure 3D, E). On the other hand, in the foliated shell structure of *Chlamys vesiculosus* Dunker, 1877, *Chlamys swifti* (Bernardi, 1858), and *Patinopecten yessoensis* (Jay, 1857), foliated blades are remarkably inclined or almost parallel to the increments throughout crystal growth (Figure 3F). The obliquity of microstructural units to the increments is also common in the fibrous prismatic shells of *Mytilus galloprovincialis* Lamarck, 1819, *Mytilus grayanus*, and *Modiolus modiolus* (Linnaeus, 1758) (Ubukata, 1994). In nacreous and ho-

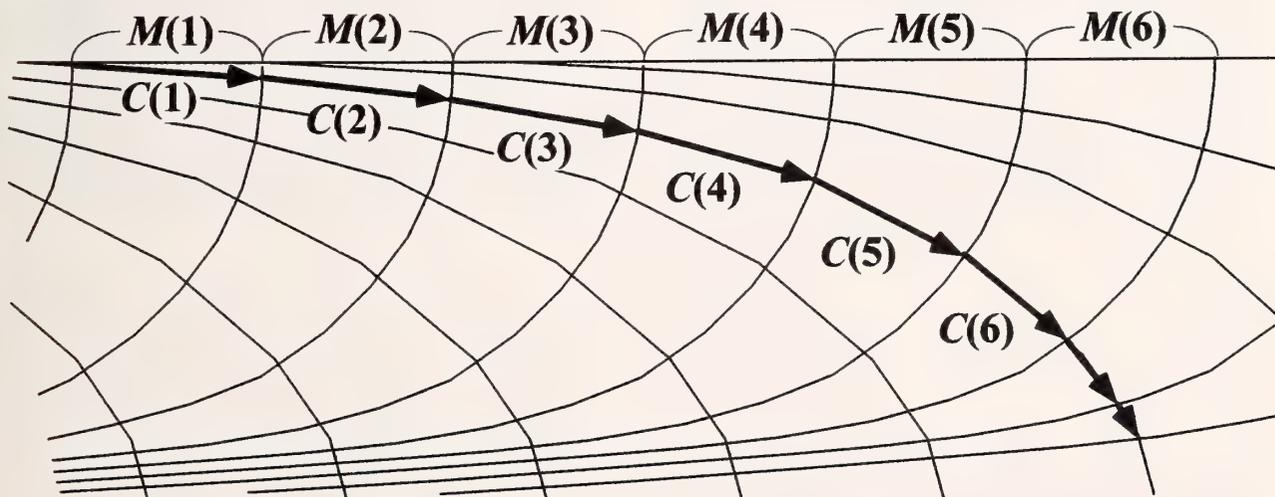


Figure 2

Schematic diagram of the outer layer of a bivalve shell along the maximum growth axis, showing the measurements of the extent of shell accretion $M(S)$ along the outer surface, and the extent of structural unit elongation $C(S)$ along a structural unit situated around the pallial attachment, where S is an integer representing the growth step.

Table 2

Results of the least squares analysis of the growth curves of the structural units. *A* and *B* are constants in the equation (1). The value of *r* represents the index of fitness. The numbers in the left column show the label of species utilized in measurements (see Figure 6).

Label	Species	UMUT no.	<i>A</i>	<i>B</i>	<i>r</i>	Microstructure of Outer Shell Layer
1	<i>Callista brevisiphonata</i>	27340	0.666	0.205	0.995	horizontal composite prism + crossed lamellar
2	<i>Codakia tigerina</i>	27341	1.099	0.801	0.995	horizontal composite prism + crossed lamellar
3	<i>Gafrarium tumidum</i>	27342	1.885	1.666	0.994	vertical crossed lamellar + homogeneous
4	<i>Anadara antiquata</i>	27343	1.317	0.845	0.992	vertical crossed lamellar
5	<i>Fragum unedo</i>	27344	0.559	0.492	0.995	horizontal crossed lamellar
6	<i>Protothaca jodoensis</i>	27345	1.314	0.750	0.998	horizontal composite prism + crossed lamellar
7	<i>Mercenaria stimpsoni</i>	27346	1.734	1.365	0.999	horizontal composite prism + homogeneous
8	<i>Pinctada margaritifera</i>	27347	1.129	3.348	0.997	simple prism + nacreous
9	<i>Patinopecten yessoensis</i>	27348	1.411	3.081	0.990	foliate
10	<i>Crossostrea gigas</i>	27349	1.713	3.041	0.994	simple prism + foliate
11	<i>Tridacna crocea</i>	27350	1.166	0.831	0.992	horizontal crossed lamellar
12	<i>Cristaria plicata</i>	27351	0.855	2.335	0.992	vertical composite prism + nacreous
13	<i>Tellina venulosus</i>	27352	0.637	0.401	0.983	horizontal composite prism + homogeneous
14	<i>Glycymeris ezoensis</i>	27353	0.864	0.415	0.996	vertical crossed lamellar
15	<i>Dosinia japonica</i>	27354	0.575	0.297	0.987	horizontal composite prism + crossed lamellar + homogeneous
16	<i>Pseudocardium sachalinense</i>	27355	0.934	0.628	0.985	vertical crossed lamellar
17	<i>Mytilus grayanus</i>	27356	0.631	0.956	0.999	fibrous prism + nacreous
18	<i>Mactra chinensis</i>	27357	0.563	0.991	0.996	vertical crossed lamellar
19	<i>Nemocardium samarangae</i>	27358	0.444	0.420	1.000	horizontal composite prism + crossed lamellar
20	<i>Solen gordonis</i>	27359	0.377	0.285	0.991	vertical crossed lamellar
21	<i>Circe scripta</i>	27360	0.615	0.800	0.983	vertical crossed lamellar + homogeneous
22	<i>Spondylus squamosa</i>	27361	1.290	1.166	0.987	foliate + crossed lamellar
23	<i>Corbicula sandai</i>	27362	0.543	0.399	0.985	vertical crossed lamellar
24	<i>Lima vulgaris</i>	27363	0.767	1.164	0.994	foliate + crossed lamellar
25	<i>Unio biwae</i>	27364	1.062	0.880	0.996	vertical composite prism + nacreous
26	<i>Lanceolaria oxyrhyncha</i>	27365	0.769	1.136	1.000	vertical composite prism + nacreous
27	<i>L. oxyrhyncha</i>	27366	0.599	1.898	1.000	vertical composite prism + nacreous
28	<i>Saxidomus purpuratus</i>	27367	0.916	0.549	0.995	horizontal composite prism + crossed lamellar
29	<i>Laevicardium mutica</i>	27368	0.980	1.515	1.000	vertical crossed lamellar
30	<i>Chlamys farreri</i>	27369	0.771	2.209	0.995	foliate
31	<i>Paphia euglypta</i>	27370	0.613	0.348	0.999	horizontal composite prism + homogeneous
32	<i>Meretrix petechialis</i>	27371	0.710	0.323	0.994	horizontal crossed lamellar + homogeneous
33	<i>Arca boucardii</i>	27372	1.075	1.064	1.000	vertical crossed lamellar
34	<i>Corbula erythrodon</i>	27373	2.193	2.374	0.999	vertical crossed lamellar
35	<i>Gari elongata</i>	27374	0.314	0.584	0.999	vertical crossed lamellar
36	<i>Isognomon perna</i>	27375	0.955	2.210	0.998	simple prism + nacreous

homogeneous structures, any elongating structural unit which intersects the internal microgrowth increment cannot be recognized.

In shells with horizontal-type crossed lamellar and composite prismatic structures, structural units are generally either inclined or almost parallel to the outer shell surface in the early stage of crystal growth. In such species as *Megacardita ferruginosa* (Adams & Reeve, 1850), *Codakia tigerina*, *Pseudocardium sachalinense*, *Anomalocardia brasiliiana* (Gmelin, 1791), *Meretrix petechialis* Lamarck, 1818, *Mercenaria stimpsoni*, *Katylsya japonica*, *Tridacna crocea*, and *Dosinia japonica* (Figure 3D), lamellae or prisms are remarkably curved during crystal growth and finally become nearly perpendicular to the outer shell surface. In

these species, the growth rate of each lamella or prism appears to decrease throughout crystal growth. In this case, the profile of internal microgrowth increments always represents a curved line in the radial and vertical section along the maximum growth axis. Thus, the curved profile of the lamellae or prisms appears to be associated with the curvature of the increments. Conversely, in the radiating-type crossed lamellar and fibrous prismatic shell structures of *Pseudocardium sachalinense*, *Mactra chinensis* Philippi, 1846, *Begonia semiorbicularata*, *Mytilus galloprovincialis*, *Patinopecten yessoensis*, *Chlamys swifti*, and *Chlamys vesiculosus*, both structural units and internal microgrowth increments are slightly curved, but they can be approximately regarded to be straight lines (Figure 3C, F).

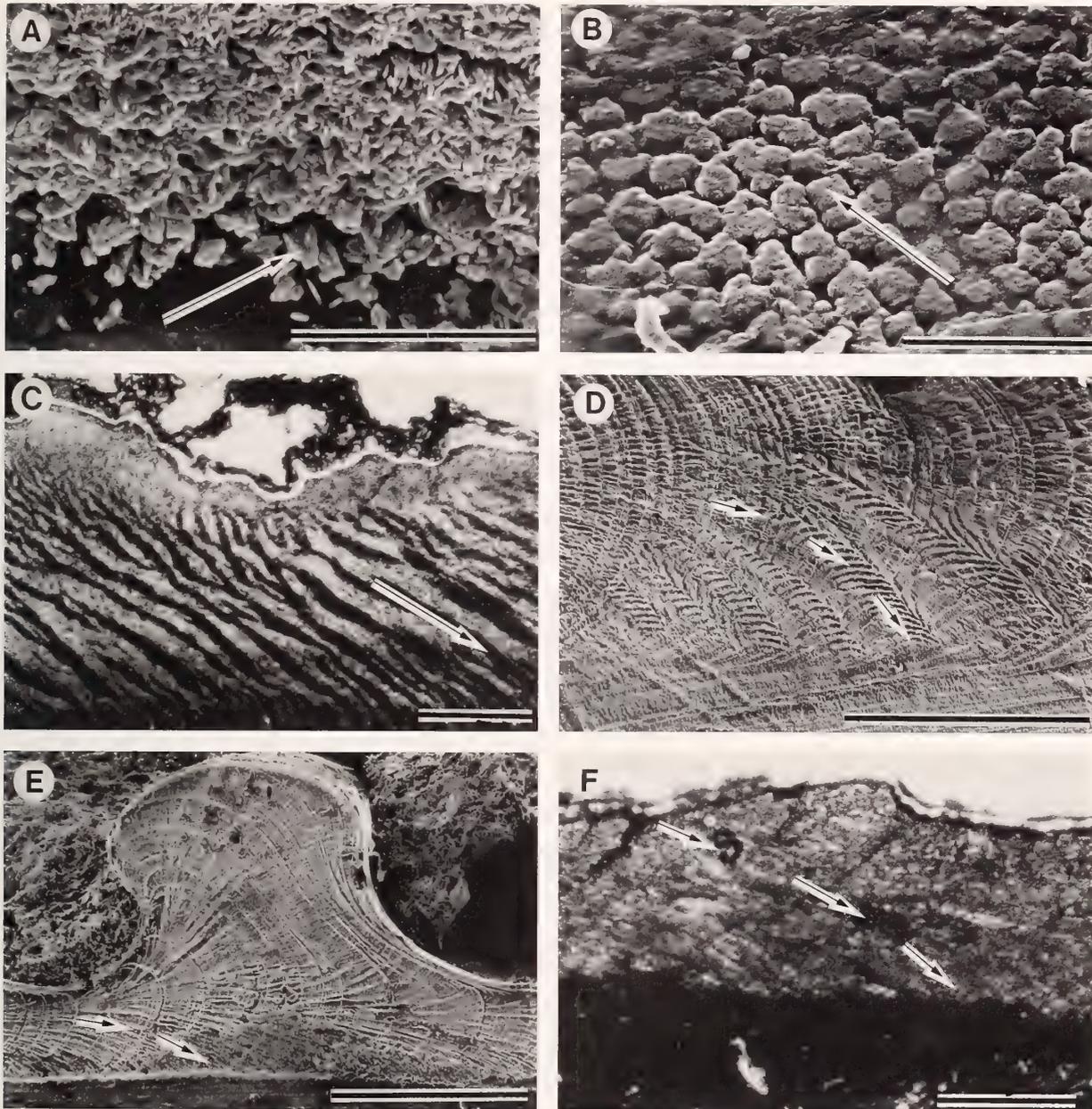


Figure 3

Scanning electron (A, B, D, E) and optical (C, F) micrographs of selected bivalve shells. A. Inner view of incipient clusters of crystals at the periostacal edge showing an example of the initial stage of crystal growth in the crossed-lamellar shell in *Geloina papua* from Iriomote Is., Okinawa, southwest Japan (UMUT RM 27334), the lower direction is the ventral side. Arrow shows a hemispherical cluster of crystallites. Scale bar: 50 μm . B. Inner-ventral view of the growing front of a first-order composite prism showing that many second-order prisms continue to grow spherically in *Tapes philippinarum* from Yokohama, Kanagawa Prefecture, Central Japan (UMUT RM 27335). Arrow shows an incipient second-order prism. Scale bar: 50 μm . C. Radial and vertical shell section on the acetate peel showing the geometric selection of the first-order lamella in *Beguina semiorbiculata* from Honda Bay, Palawan, Philippines (UMUT RM 27336). The right direction is the ventral side. Arrow shows the direction of a first-order lamella elongation. Scale bar: 500 μm . D. Radial and vertical shell section of *Dosinia japonica* from Sagami Bay, Kanagawa Prefecture, central Japan (UMUT RM 27337). The right side is ventral. Arrows show the growth direction of a curved first-order lamella. Scale bars: 500 μm . E. Radial and vertical shell section of *Paphia amabilis* from Sagami Bay, Kanagawa Prefecture, central Japan (UMUT RM 27338). The right side is ventral. Arrows show the growth direction of a second-order prism. Scale bars: 500 μm . F. Radial and vertical shell section of *Chlamys vesiculosus* from Misaki, Kanagawa Prefecture, central Japan (UMUT RM 27339). The right side is ventral. Arrows show the direction of a foliate blade elongation. Scale bars: 500 μm .

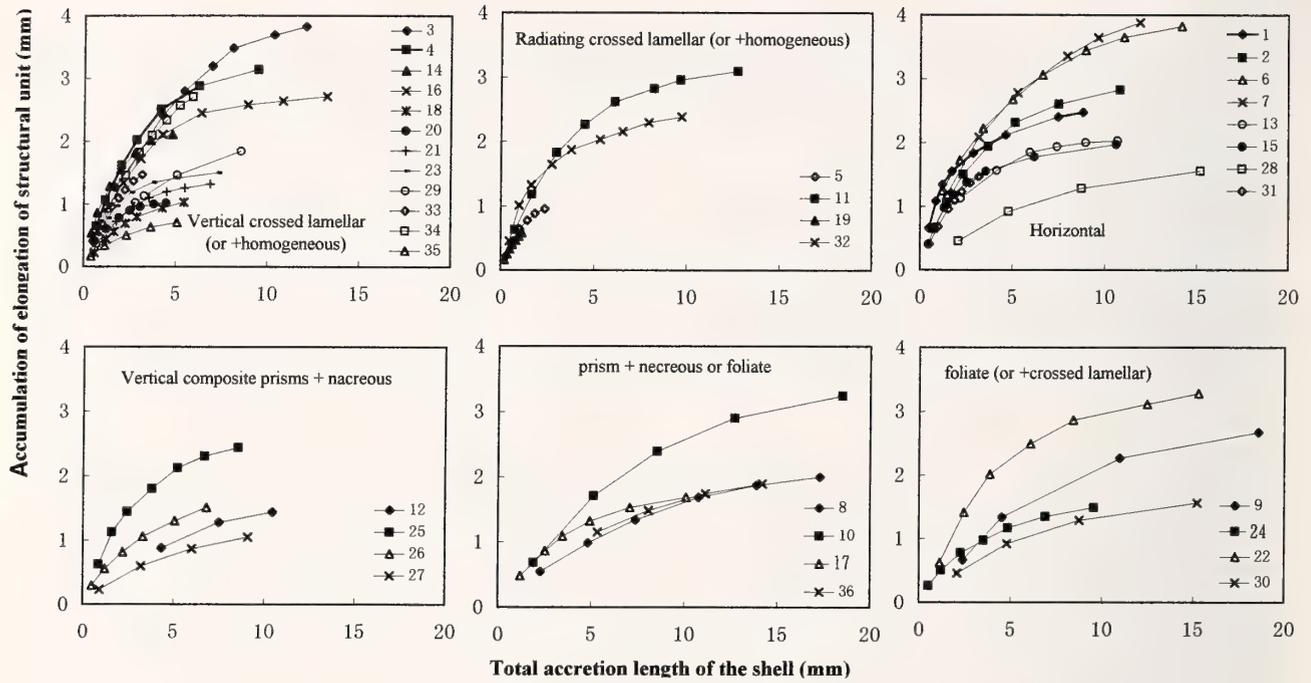


Figure 4

Relationship between the accretion rate of the shell and the elongation rate of the structural unit. In all specimens which have various types of shell microstructures in the outer shell layer, the relative speed of elongation of structural unit per shell accretion tends to decrease during elongation. The numbers in the legends correspond to the species (see Table 2 for labels).

Biometric Analysis

Speed of crystal growth, which is controlled both genetically and environmentally, may be a significant factor in determining the geometric pattern of the microstructural units because microscopic-level growth of the shell is constrained by the process of geometric selection among structural units. For estimating the geometric effects on microstructure construction, the relative rate of crystal growth to shell accretion is represented by the ratio of growth increments widths along a structural unit versus those along the outer shell surface around pallial attachment (Figure 2). Microgrowth increment width along a structural unit ($C(S)$, Figure 2) is regarded as the elongation of the structural unit which represents accretion of crystals during a given time interval, while the width along the outer shell surface ($M(S)$, Figure 2) as the amount of shell accretion. Though width of microgrowth increment itself is periodically changed by seasonal and daily fluctuation of environments (Pannella & MacClintock 1968; Jones 1985; Tanabe 1988), the ratio of growth increment along a structural unit to that along the outer shell surface seems to be independent of such fluctuation and is considered to be the primary parameter determining the geometric condition of growth of structural units. Then, the ratio of an individual is represented by a measurement of a structural unit terminated at the pallial attachment.

The relationship between the growth increment along a structural unit $C(S)$ and along the outer shell surface $M(S)$ is shown in Figure 4, where S is the growth step along a structural unit. The growth curve of the structural unit exhibits the relative growth of crystal growth to shell accretion, and appears to be approximated well by the logarithmic curve which passes through the origin of the co-ordinate (Figure 4). Therefore, accumulation of elongation of a structural unit ($\Sigma C(S)$) is empirically approximated by the following equation:

$$\Sigma C(S) = A \ln \left(\frac{\Sigma M(S)}{B} + 1 \right) \quad (1)$$

where B is a constant representing the effect of gradual decline in the crystal growth, A is a constant which is proportional to the crystal growth rate, and $\Sigma M(S)$ means the total accretion length of the shell.

The values A and B were calculated in each growth curve of the structural units from the measurements taken from actual specimens using the least squares method (Table 2). As a result, in crossed lamellar and horizontal composite composite prismatic structures, B is shown to be positively correlated with A at the level of 99% confidence (Figure 5), indicating that the faster the crystals grow, the more rapidly the speed of crystal growth tends to decrease. The shells of columnar prismatic and foliated structures gen-

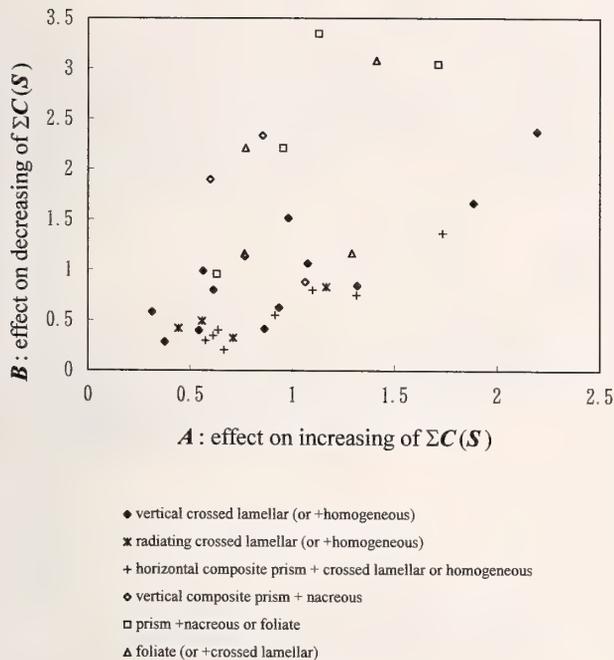


Figure 5

Relationship between two constants *A* and *B* which are given in the equation (1) representing relative growth of the structural unit with shell accretion. Positive correlation is recognized in crossed lamellar and horizontal composite prismatic structures at the confidence level of 99%.

erally occur in the high-*B* area, showing more rapid decline of crystal growth, though correlation between *A* and *B* is not so clear as that in crossed lamellar and horizontal composite prismatic structures.

COMPUTER SIMULATION

In order to clarify the nature of microscopic growth, computer simulations were performed. For simplicity, the following geometric conditions, some of which have been recognized empirically in actual specimens, were incorporated into the simulations. Namely, each microstructural unit is approximated by an enlarging ellipse initiated either on the inner surface of the periostracum (Figures 3A, 6A; see also Ubukata, 1994) or at the growing edge of the radiating axis of the shell (Figures 3B, 6B). Indeed, the shape of the incipient microstructural unit is not always hemispherical but more or less variable among shell microstructures, but essential nature of the geometric model is independent of the shape of the unit. This is formulated by the following equation in *O-xy* co-ordinate system (Figure 7):

$$\frac{(x - \Sigma M(i))^2}{a(s_i)^2} + \frac{y^2}{b(s_i)^2} = 1$$

where $\Sigma M(i)$ represents the *x* co-ordinate of the center of the ellipse given by the parameter *i* which labels each

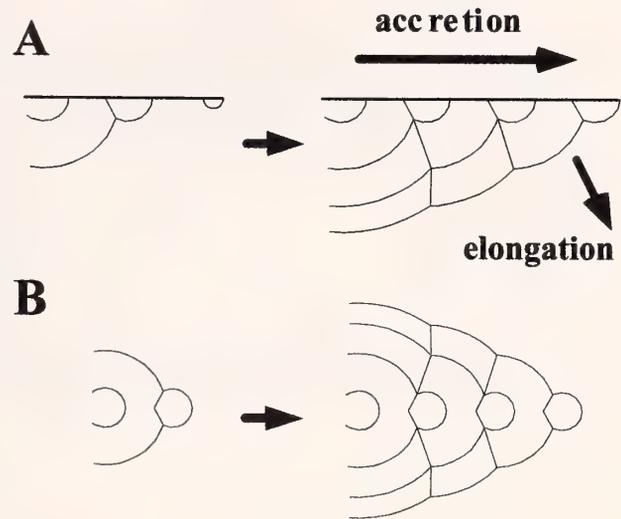


Figure 6

Schematic diagrams showing the growth process of hemispherical structural units at the shell edge. Initiation of structural units occurs on the inner surface of the periostracum (A) or at the growing edge of the radiating axis of the shell (B). Growth rate of each structural unit remains constant or decreases.

structural unit, and $a(s_i)$ and $b(s_i)$ are longer and shorter diameters of an ellipse given by the parameter s_i which means the growth stage of each structural unit labeled by *i* (Figure 7). In the present model, the value of $\Sigma M(i)$ is assumed to increase at a constant rate throughout crystal growth in each structural unit. The value of $\Sigma M(i)$ is regarded to be the total accretion length of the shell. It also represents the total length of periostracum secretion if any external sculpture is constructed.

The common function is given for $a(s_i)$ and $b(s_i)$ in all increments. The value of $a(s_i)$ is not always equal to that of $b(s_i)$ because the growth rate of each structural unit appears to decrease throughout crystal growth in the crossed lamellar and horizontal composite prismatic shell structures. The aspect ratio of an ellipse, namely $a(s_i)/b(s_i)$, means the extent of anisotropy of growth direction of each structural unit. The ellipse continues to grow until it comes into contact with a neighboring ellipse on its lateral sides.

If the speed of crystal growth is constant relative to the speed of shell accretion throughout the growth of each structural unit, and if $a(s_i)$ is maintained at a value equal to $b(s_i)$, $a(s_i)$ and $b(s_i)$ should satisfy the following equation:

$$\frac{a(s_i + \epsilon) - a(s_i)}{\epsilon} = \frac{b(s_i + \epsilon) - b(s_i)}{\epsilon} = \alpha$$

where α is an arbitrary constant, and ϵ is the magnitude of the growth step. In this case, the result of computer simulation indicates that the structural units and the internal microgrowth increments are not curved (Figure 8A). The structural units become inclined to the outer shell surface due to the retardation of the starting time of their

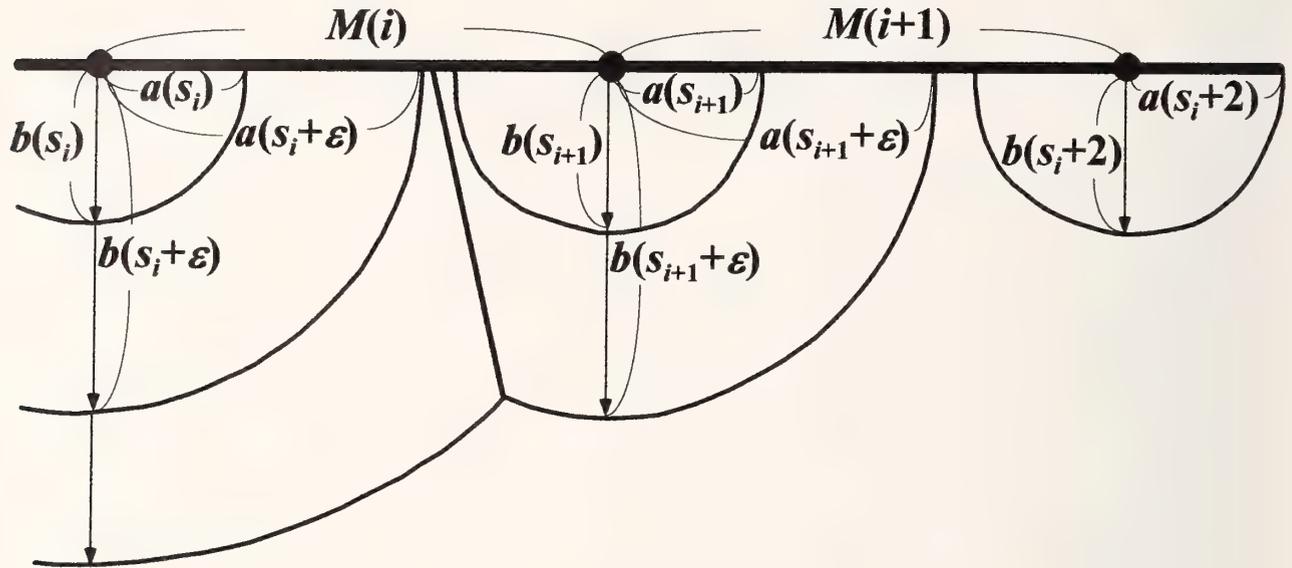


Figure 7

Schematic diagrams showing the geometric selection model in which each microstructural unit is regarded as an enlarging ellipse. Bold points show the initiation sites of the structural units. Each sphere of the structural unit continues to grow until it comes into contact with neighboring spheres on its lateral sides. Each structural unit elongates in association with inclination.

growth to the radial direction. The degree of inclination of the structural units is determined by the ratio of the crystal growth rate to the shell accretion rate. The elongation axes of the structural units and internal microgrowth increments intersect at 90°. The computer-produced figure in this case (Figure 8A) closely represents the geometric patterns of the columnar prismatic structure studied in Ubukata (1994). It is, however, different from the geometric pattern of the horizontal type composite prismatic, fibrous prismatic, foliated, and crossed-lamellar structures.

If the relative speed of crystal growth is constant and $a(s_i)$ is not equal to $b(s_i)$, $a(s_i)$ and $b(s_i)$ are expressed by the following equation:

$$\frac{a(s_i + \epsilon) - a(s_i)}{\epsilon} = \alpha_a, \quad \frac{b(s_i + \epsilon) - b(s_i)}{\epsilon} = \alpha_b \quad (2)$$

where α_a and α_b are arbitrary constants. The structural units and the internal microgrowth increments also become straight and the elongation axes of the structural units are inclined to the increments (Figure 8B). The computer output in this condition closely represents the geometric patterns of foliated shells in *Patinopecten yessoensis*, *Chlamys swifti*, and *Chlamys vesiculosus* (Figure 3F), and of fibrous prismatic shells in *Mytilus galloprovincialis*, *Mytilus grayanus*, and *Modiolus modiolus*.

In the horizontal type composite prismatic and crossed-lamellar structures, the relative speed of crystal growth tends to decrease as each structural unit elongates (Figure 3D, E). In this case, the function which represents $a(s_i)$

or $b(s_i)$ should satisfy the following conditions: (1) its differential form is expressed by decreasing function which approaches zero asymptotically; (2) it should include a constant term representing the effect of gradual decline in crystal growth, and if the value of the constant is zero, the function should be expressed by equations (2). Although the relationship between the functions of $a(s_i)$ and $b(s_i)$ and the functions of $C(s_i)$ is very complicated depending upon the nature of geometric selection among structural units (Figure 8C-F), the growth curve of the structural unit appears to be approximated well by the logarithmic curve. Consequently, if the value of ϵ is sufficiently small, decreasing rates of $a(s_i)$ and $b(s_i)$ may be tentatively represented by the following equations:

$$\frac{a(s_i + \epsilon) - a(s_i)}{\epsilon} = \frac{\alpha_a}{\beta s_i + 1},$$

$$\frac{b(s_i + \epsilon) - b(s_i)}{\epsilon} = \frac{\alpha_b}{\beta s_i + 1}$$

where β is an arbitrary constant.

Figure 8C, D shows some results of simulation when both $a(s_i)$ and $b(s_i)$ decrease as each structural unit elongates. Under this condition, structural units and internal microgrowth increments are both curved because of geometric selection. In both cases when $a(s_i)$ is equal to $b(s_i)$ (Figure 8C) and when $a(s_i)$ is not equal to $b(s_i)$ (Figure 8D), the elongation axes of structural units are initially inclined to the increments toward the ventral direction,

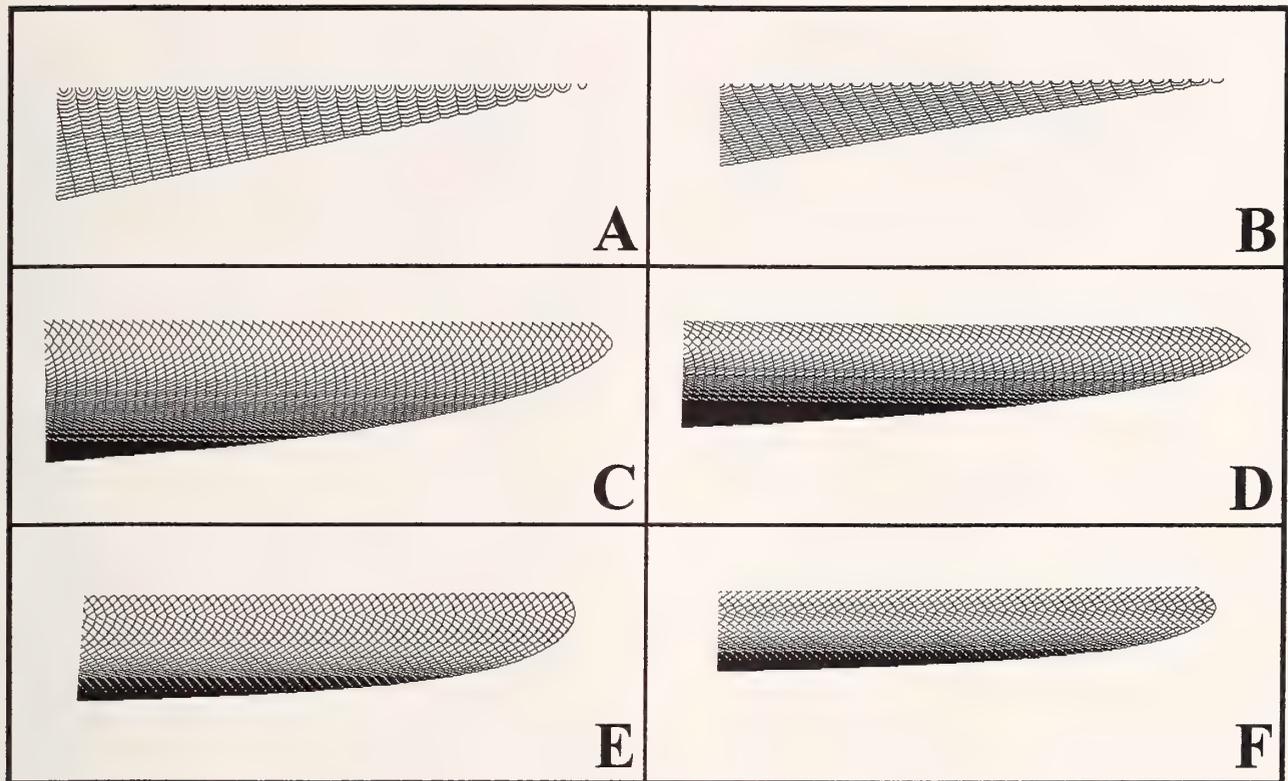


Figure 8

Selected results of computer simulations. A, B. Initiation of structural units occurs on the inner surface of the edge of periostracum. C-F. Initiation of structural unit occurs in the growing front of the shell. A. $a(s_i) = 0.2M(i)$, $b(s_i) = 0.2M(i)$; B. $a(s_i) = 0.3M(i)$, $b(s_i) = 0.15M(i)$; C. $a(s_i) = 10/(0.1M(i) + 1)$, $b(s_i) = 10/(0.1M(i) + 1)$; D. $a(s_i) = 10/(0.1M(i) + 1)$, $b(s_i) = 7/(0.1M(i) + 1)$; E. $a(s_i) = 100$, $b(s_i) = 10/(0.1M(i) + 1)$; F. $a(s_i) = 70$, $b(s_i) = 10/(0.1M(i) + 1)$.

then become perpendicular to the increments as the crystal grows, and finally they are inclined to the increments toward the dorsal direction. The geometric pattern shown in Figure 8C, D differs from that observed in any real specimen.

When $a(s_i)$ is fixed and only $b(s_i)$ decreases as crystals grow, structural units and internal microgrowth increments are also curved because of geometric selection (Figure 8E, F). When $a(0)$ is equal to $b(0)$, elongation axes of the structural units and internal microgrowth increments intersect at 90° in the initial stage of crystal growth and become slightly inclined to the increments as crystals grow (Figure 8E). The geometric pattern given in Figure 8E closely represents the microscopic features of the crossed-lamellae and horizontal prismatic structures (Figure 3E, F). If initial values of $a(0)$ and $b(0)$ are different, elongation axes of the structural units are inclined to the increments in the initial stage of crystal growth, and the inclination of structural units tends to increase during crystal growth because of geometric selection (Figure 8F). The geometric pattern shown in Figure 8F was not found in specimens examined.

DISCUSSION

When the structural units appear almost straight, the crystal growth rate does not conspicuously decrease. In this case, geometric patterns of simple and vertical-type composite prismatic structures are well represented by the computer simulation when isotropic crystal growth is assumed. On the other hand, geometric patterns of the fibrous prismatic, foliated, and radiating-type crossed lamellar structures are well exhibited by the computer simulations under the condition that the growth of the structural unit in the horizontal direction is faster than in the inner direction. This fact suggests that the primary direction of crystal growth in these structures is inclined toward the ventral direction independent of geometric selection process. The primary inclination of crystal growth is probably originated by anisotropy of crystal growth. The relationship between the directions of the structural unit elongation and internal microgrowth increment may be determined by the relationship between crystal elongation and crystal axis, though the relationship is not made clear in this study.

The faster the crystal growth decreases, the more con-

spicuously the structural units and microgrowth increments are curved. Many authors reported mechanisms of decline of crystal growth in mollusks, such as chemical controls of inorganic ions in extrapallial fluid (Crenshaw, 1972; Campbell & Boyan, 1976; Runnegar, 1990; Simkiss & Wilbur, 1989), physicochemical controls by soluble organic matrix (Crenshaw & Ristedt, 1976; Wheeler et al., 1981), or mechanical controls by insoluble organic matrix (Bevelander & Nakahara, 1969, 1980). If decline of the crystal growth rate in the shell originated only in the gradient of chemical potential of the extrapallial fluid and the secretory activity of epithelial cells along the mantle in the radial direction, the decline rate of structural units should appear as isotropic; that is, lateral growth of the structural unit should also decrease. However, the angle between the structural units and internal microgrowth increments in actual specimens is well represented by computer simulation under the conditions that only the elongation rate of a structural unit toward the inner surface decreases during crystal growth, and that the lateral growth rate of a structural unit is constant (Figure 8E, F). This fact indicates anisotropy of the decline in the rate of crystal growth, which appears to be explained only by the retardation of the secretory activity of the mantle cells. In addition, Figure 5 shows that the faster the crystals grow, the more rapidly the speed of crystal growth tends to decrease. These facts suggest that an inhibiting mechanism of crystal growth is at work, a mechanism which is dependent on the speed of crystal elongation, although its physicochemical mechanism is unclear.

During growth of many mineral aggregates, a characteristic competition for space between neighboring crystallites is common in nature (Grigor'ev, 1965). Ubukata (1994) explained geometric varieties of the prismatic structure on the basis of analyzing growth dynamics of prisms using the analogy with growth of druse minerals, and showed an important role of architectural constraint from the viewpoint of constructional morphology (Seilacher, 1970). The results of computer simulation in the present study suggest that the geometric selection model, which was originally applied to inorganic systems, generally represents growth kinematics of bivalve shell microstructure. The process of geometric selection among crystals links biological factors and morphological pattern at a microscopic level in bivalve shell, though the process itself is ultimately controlled by genetic programming and environmental factors.

The growth kinematics of the shell is exhibited by stacking microgrowth increments, and macroscopic or mesoscopic features of the shell, e.g., external shell sculpture and relative shell thickness to the size, depend upon the profile of microgrowth increments. Since the profile of the internal microgrowth increments is determined by the mode of crystal growth, anisotropy and inhibition of crystal growth may play an important role in constructing the morphological pattern of the shell.

CONCLUSION

In many bivalve species, geometric patterns of various shell microstructures in the radial and vertical sections depend upon the nature of geometric selection among structural units during growth, as in the case of the prismatic shells described by Ubukata (1994). Therefore, curved appearances of the structural unit and internal microgrowth increment in the radial and vertical section originated in the decline of the crystal growth rate during the elongation process of the structural unit. Consequently, the more rapidly the rate of crystal growth decreases, the more remarkably the microgrowth increments become curved. Elongation of the structural unit decreases more remarkably than lateral expansion does, as a result of anisotropy of the decreasing rate of crystal growth. Therefore, anisotropy of crystal growth is considered to be a control of geometric profile of growth increments.

Some problems concerning local details of the microstructure still remain. In the computer simulation, each microstructural unit initiated at the growing edge is approximated by an enlarging ellipse, whereas the shape of the real one is more or less variable among shell microstructures and may depend on the direction of the crystal-axis. I believe that the simplified method of simulations presented here is regarded as essentially valid for recognition of growth kinematics of the bivalve shell morphology at a microscopic level, but more elaborate methods in which information about crystallographic nature is incorporated should be required for synthesizing biomineralogy and constructional morphology. This study will be the first step in linking the biomineralogical nature and geometric pattern of the shell.

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A New Species of Eastern Pacific *Fissidentalium* (Mollusca: Scaphopoda) with a Symbiotic Sea Anemone

by

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Abstract. *Fissidentalium actiniophorum* sp. nov. is described morphometrically from specimens collected from deep water off California. The nearest geographical members of *Fissidentalium* are *Fissidentalium megathyris* and *Fissidentalium erosum*. *Fissidentalium actiniophorum* is distinguished from these species primarily on the basis of shell and soft-body-part proportions. Five shell and five soft-part measurements were taken. From these an additional eight shell and four soft-part factors or indices were derived for a total of 22 factors or indices. *Fissidentalium actiniophorum* differed statistically from both *F. megathyris* and *F. erosum* in all shell measurements, all derived shell factors, and most soft-part measurements. It differed from either *F. megathyris* or *F. erosum* in one of the two ratios of the gonadal length to the total visceral length. It did not differ from either species in the ratio of the gut lobe length to the total visceral length, or in some of the ratios of gonadal length to total visceral length.

INTRODUCTION

The Pulse Project of Scripps Institution has been collecting a large species of undescribed scaphopod since about 1992 off southern California from depths of about 4100 m. Most specimens of this scaphopod carried a sea anemone on the concave functionally dorsal shell surface (Figure 1). The sea anemone was also undescribed. Sea anemone and scaphopod relationships of this nature have been occasionally noted before (Shimek & Moreno 1996; Scarabino, personal communication); however, in the present case, most of the scaphopod shells from living animals carried a sea anemone. No shells from dead scaphopods had sea anemones on them, although most showed anemone scars.

The sea anemones may be the same species found on some *Fissidentalium megathyris* (Dall, 1890) shells collected offshore of central California (Shimek & Moreno, 1996). The scaphopod, distinctly different from any other *Fissidentalium*, is described here. The sea anemone is being described separately (A. Wakefield Pagels, 1996, personal communication).

MATERIALS AND METHODS

Specimens examined for both descriptive and comparative purposes came from samples collected at depths varying

from 4100 m to 4134 m in a rectangle bounded by 34.20°N in the south, 34.78°N in the north, 122.97°W in the east, and 123.23°W in the west (Table 1). This is station M of the Pulse Project conducted by Dr. Ken Smith, Scripps Institution of Oceanography. In the subsequent enumeration of specimen listing the collection data, the first digit of a three digit number or the first two digits of a four digit number represent the cruise when the specimens were collected. The last two digits of these numbers indicate the location within station M.

The new species was compared to *F. megathyris* and *F. erosum* Shimek & Moreno 1996, using the electronically stored supplemental data available by anonymous FTP (Shimek & Moreno, 1996). Those data were generated from specimens of *F. megathyris* and *F. erosum*. The *F. megathyris* were originally loaned from the California Academy of Sciences, San Francisco (CAS), and the National Museum of Natural History, Washington (USNM) (Shimek & Moreno, 1996). Specimens of *F. erosum* utilized for comparison are in the collections of the Los Angeles County Museum of Natural History (LACM); USNM; The British Natural History Museum (BMNH); and the collections of Dr. Guillermo Moreno and the author (Shimek & Moreno, 1996). Type specimens designated in this paper were deposited in the LACM, USNM, and the BMNH.

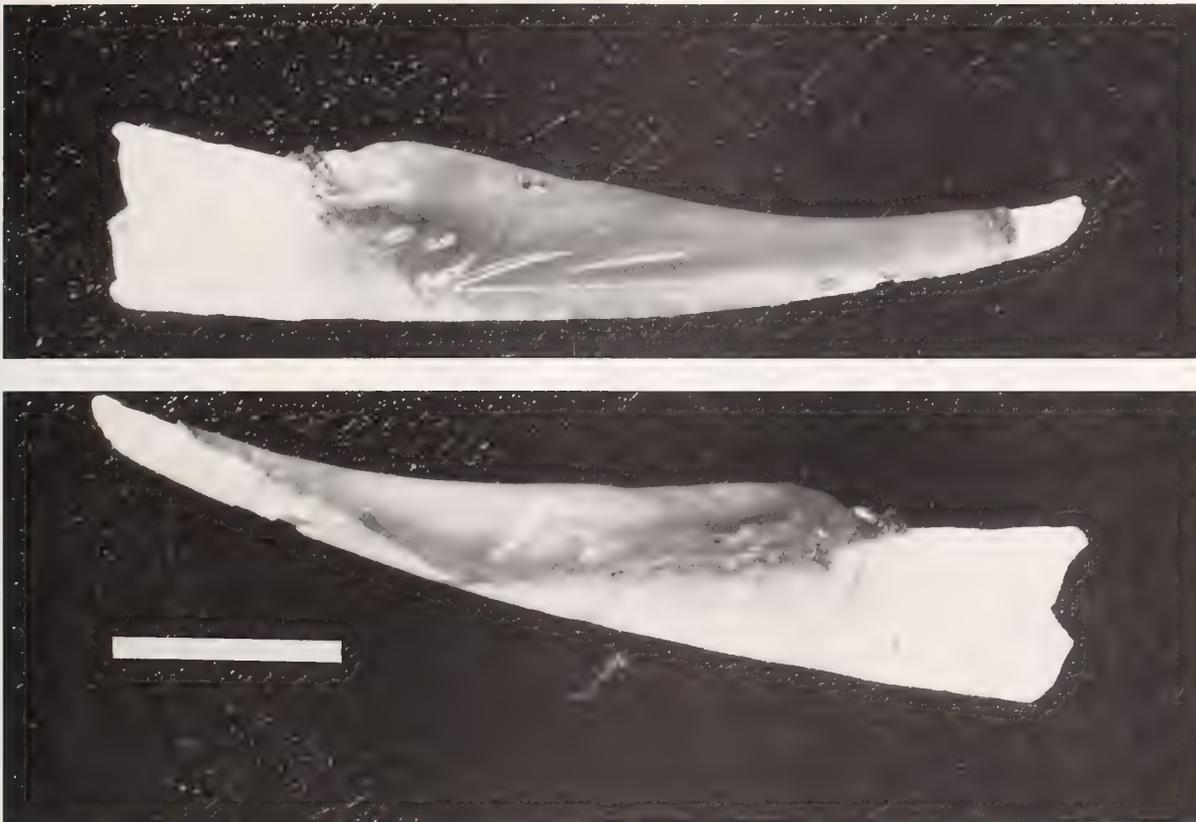


Figure 1

F. actiniophorum Shimek, sp. nov. with a sea anemone attached. Scale bar is 10 mm. This illustration was exposed to indicate the relationship between the anthozoan and the scaphopod, and resulted in loss of scaphopod shell detail. See Figures 2 and 3.

Shell Measurements and Morphometrics

For the shell description, I used an approach of quantitative shell morphometric analyses based on the mathematical properties of shell shape (Raup, 1966). Shell measurements were made following Shimek (1989), as modified by Shimek & Moreno (1996: fig. 1). The morphometric analyses ideally require "perfect" undamaged shells. Many of the adult shells from the Pulse collections were in very good condition and could be used without hesitation for this work. Nevertheless, to increase sample sizes, I occasionally found it necessary to examine and measure shells with minor fractures, apertural lip breaks, and apical fractures. In these cases, the actual shell measurements were reported and no attempt was made to estimate "perfect" conditions. Such shells were more common in the comparative specimens of *F. megathyris* and *F. erosum*. I tried to be as conservative as possible in the use of these shells, but their use undoubtedly increased variance in the analyses. For detailed derivations of the indices and measurements, see Shimek (1989).

The complete array of shell measurements was not taken

Table 1

Fissidentalium actiniophorum specimens examined.

Number of specimens	Degrees		Date collected	Station number
	North latitude	West longitude		
8	34.73	123.13	February 21, 1992	1108M
1	34.78	123.07	February 26, 1992	1121M
13	34.62	123.12	June 26, 1992	1206M
11	34.68	123.05	July 25, 1992	1219M
12	34.63	123.02	August 22, 1992	1406M
7	34.60	123.13	October 17, 1992	1506M
22	34.72	123.07	October 30, 1992	1516M
11	34.75	123.03	February 24, 1993	1625M
9	34.72	123.10	July 19, 1993	1716M
5	34.73	123.20	November 4, 1993	1809M
4	34.20	123.13	November 7, 1993	1820M
2	34.68	123.08	February 5, 1994	1906M
5	34.68	123.18	February 10, 1994	1916M
20	34.65	122.97	June 17, 1994	2017M
11	34.67	123.18	September 22, 1994	2231M
14	34.70	123.23	October 22, 1994	2304M

on some specimens because of the presence of the sea anemone in the anatomically anterior or functionally dorsal, concave, curved region of the shell. The anemone was left in place on some specimens to assist in the description of that species. Additionally, if the measurements were made from dead shells, then soft-body-part measurements were impossible to obtain.

The comparative specimens of *F. megathyris* came from numerous localities. *Fissidentalium megathyris* was described from specimens collected near the Galapagos Islands. Shimek & Moreno (1996) used a discriminant analysis classification for the factor of collection location to verify that the Californian *F. megathyris* specimens were indistinguishable from the Galapagos type specimens. Because of this, the *F. megathyris* from all of the museum collections were pooled when used as comparisons to *F. actiniophorum*. All of the *F. erosum* used for comparison were collected from the type locality, a single site off central California (Shimek & Moreno, 1996).

Soft-Body-Part Measurements

Soft-body-part proportions were measured from fixed material, which has been shown to provide reliable quantitative data (Voight, 1991; Shimek & Moreno, 1996). The methodology and measurements follow Shimek & Moreno (1996). Three basic soft-body-part components, the buccopodal or buccal region, the gut region, and the gonadal region, were measured. Some of these regions may be fixation artifacts; nevertheless, they provided consistent landmarks.

The buccal region was measured ventrally from the so-called periostracal groove on the outside of the mantle surrounding the ventral aperture to the groove separating this ventral component from the remaining soft body parts. The gut region was measured ventrally from the groove separating the gut area from the buccal region to the position of the anus. The gonadal region was measured ventrally from the anus to the mantle attachment ring on the mantle surrounding the dorsal aperture, and dorsally from the most posterior margin of the stomach to the mantle attachment ring surrounding the dorsal aperture.

Scanning Electron Microscopy

Whole radulae were cleaned of tissue residue in 5% sodium hypochlorite, dehydrated to 100% ethanol, and air dried. Shells were cleaned in alcohol and air dried. All specimens were mounted with silver paint on aluminum stubs, and gold-palladium plated. Micrographs were taken with an JEOL JSM-6100 Scanning Electron Microscope (SEM) at 15 KeV.

Statistics

The means and standard deviations of the measurements or the derived indices were computed. The whorl expan-

Table 2

Shell measurements taken of *Fissidentalium actiniophorum* (see Shimek & Moreno, 1996: fig 1 for a diagram of the measurements).

Basic Measurements	
LTot	= Total Length
Larc	= Length from the Posterior Aperture Forward to the Point of Maximum Distance to the Shell from a Chord Running Between the Dorsal Edges of Both Apertures.
ApW	= Aperture Width
ApH	= Aperture Height
arc	= Maximum Distance to the Shell from a Chord Running between the Dorsal Edges of Both Apertures.
Derived Indices	
lnLTot	= Natural Logarithm of (LTot)
lnLarc	= Natural Logarithm of (Larc)
lnApW1	= Natural Logarithm of ((ApW)+1)
lnApH1	= Natural Logarithm of ((ApH)+1)
lnWmax1	= Natural Logarithm of ((Wmax)+1)
Lindex	= Natural Logarithm of ((LWmax)+1)/Natural Logarithm of (LTot)
whratio	= (ApW)/(ApH)
Apratio	= Natural Logarithm of ((ApW)+1)/Natural Logarithm of ((ApH)+1)
Ws	= $\frac{LTot}{\sqrt{(LTot - Larc)^2 + (arc)^2}}^{1/(\tan(arc)/LTot - Larc)}$

sion rate is a logarithmic function, and calculations of this index are sensitive to small changes of shape. I used the mean of the natural logarithm of this and other logarithmically transformed or derived indices for comparative purposes. The mean of a logarithmically transformed numerical array is the median of the untransformed array. The median is a better indicator of the central tendency of these arrays than the mean as it is less sensitive to extreme values (Sokal & Rohlf, 1981). The mean of these factors are also given for comparative purposes.

The morphometric factors and indices were compared between and within populations by using standard statistical graphics software (Manugistics, 1992). The data were compared utilizing the distribution-free or non-parametric Kruskal-Wallis test to avoid having to making unwarranted assumptions about the distributions of the tested factors.

I used five basic measurements and eight calculated values to describe the shell (Table 2). Throughout this study, statistical significance was defined as $P = \alpha \leq 0.05$.

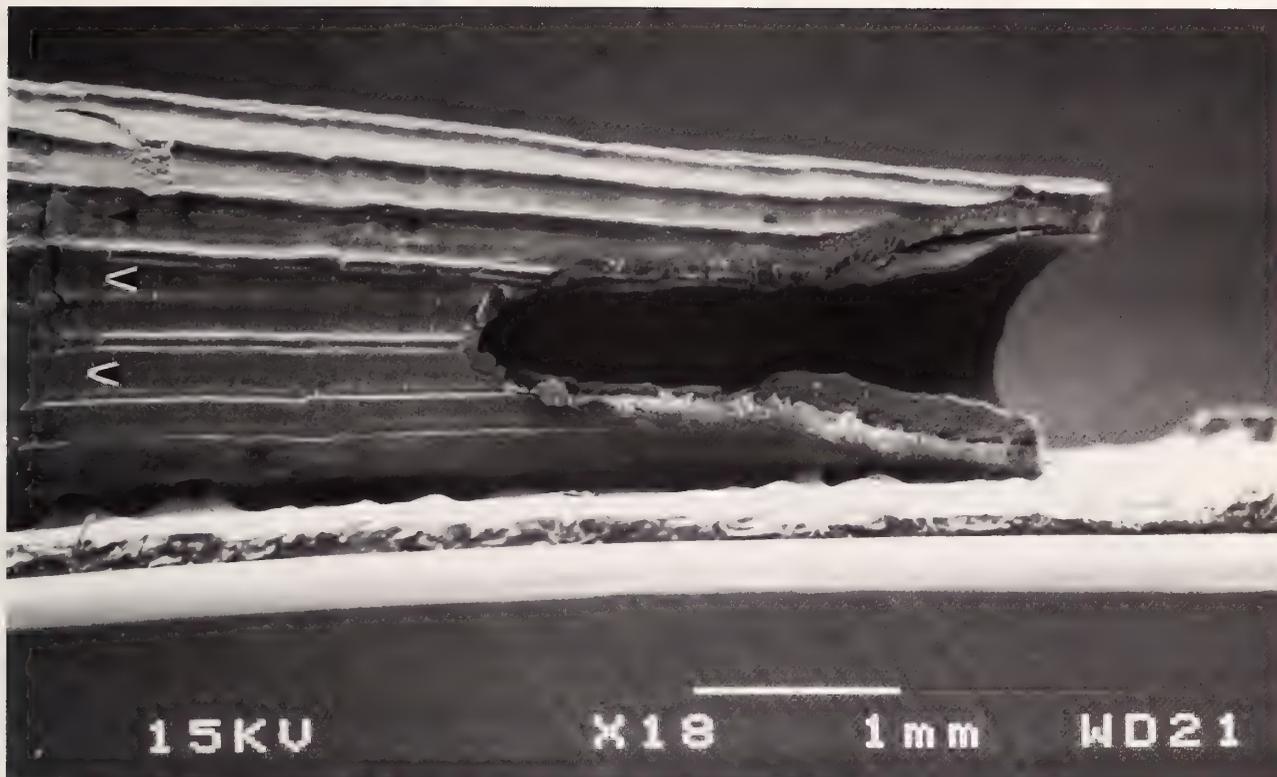


Figure 2

F. actiniophorum, Shimek, sp. nov. dorsal aperture, convex side, juvenile animal about 30 mm long. Note the slit or notch in the shell. This specimen had an anthozoan attached which has been removed. Arrowheads indicate areas of slight shell erosion at the edges of the attachment of the sea anemone.

SYSTEMATICS

Class Scaphopoda Bronn, 1862

Order Dentaliida Da Costa, 1776

Family DENTALIIDAE Gray, 1834

Fissidentalium P. Fischer, 1885

Type species: *Dentalium ergasticum* P. Fischer, 1882 (designation by monotypy).

Fissidentalium contains numerous large, generally robust, deep-water species. The shells often possess many pronounced longitudinal ribs or striae. *Fissidentalium actiniophorum* is an exception to these generalizations. It does not have a particularly robust shell, and the longitudinal striae, while present, are faint compared to most *Fissidentalium*. The generic name refers to the presence of a narrow posterior (on the convex side) slit proceeding ventrally from the dorsal aperture (Emerson, 1962; Palmer, 1974b; Steiner, 1992). This slit is found in many *Fissidentalium* species, including *F. actiniophorum* (Figure

2), but is lacking in a few, notably *F. megathyris*. *Fissidentalium* is easily recognized and widespread throughout the deep waters of the Pacific (Pilsbry & Sharp, 1897); however, most of the species have been described on the basis of limited collections and are relatively similar in gross morphology (Pilsbry & Sharp, 1897; Palmer, 1974a).

Fissidentalium actiniophorum Shimek, sp. nov.

Type material: The holotype and two paratypes are illustrated (Figure 3).

Holotype: LACM no. 2792.

Paratypes: LACM no. 2793 (Paratype A in Figure 3); USNM no. 886326 (Paratype B in Figure 3); LACM no. 2809 (6 specimens); LACM no. 2810 (4 specimens); LACM no. 2811 (2 specimens); BMNH no. 1996120 (1 specimen with sea anemone); BMNH no. 1996121 (2 specimens; collected with sea anemones, anemones subsequently removed).

Type locality: All type specimens came from samples collected at station M of the Pulse Project conducted by

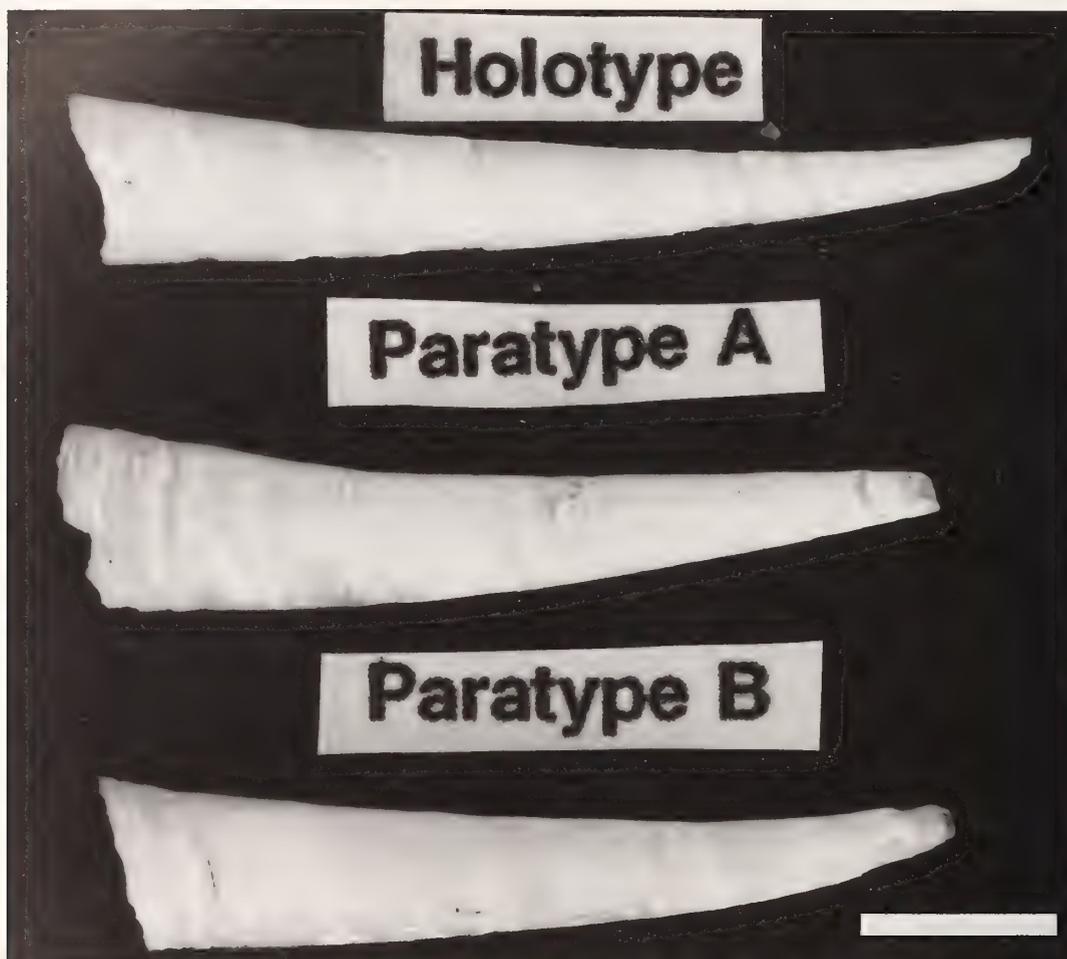


Figure 3

Type specimens; Holotype is LACM # 2792. Paratype A is LACM # 2793. Paratype B is USNM # 886326. Note faint longitudinal striae.

Dr. Ken Smith, Scripps Institution of Oceanography at depths varying from 4100 m to 4134 m.

Holotype collection data: Sta. 1809 M, Date: 4 November 1993, 34°44'N, 123°12'W.

Paratype collection data: LACM no. 2793, USNM no. 886326. Sta. 1820 M, Date: 7 November 1993, 34°42'N, 123°08'W. LACM no. 2809—Sta. 1625 M, Date: 24 February 1993, 34°45'N, 123°02'W. LACM no. 2810—Sta. 1809 M, Date: 4 November 1993, 34°44'N, 123°12'W. LACM no. 2811—Sta. 1906 M, Date: 5 February 1993, 34°41'N, 123°05'W. BMNE no 1996120—Sta. 2017 M, Date: 17 June 1994, 34°39'N, 122°58'W, BMNH no. 1996121—Sta. 1916 M, Date: 10 February 1994, 34°41'N, 123°11'W.

All other *F. actiniophorum* specimens also came from this station. The holotype had no anthozoan attached, but

had the residue of attachment present. Some of the paratypes initially had anthozoans attached. Many anthozoans were not removed to facilitate the description of the anemone. If the anthozoans were not removed, then measurements of arc could not be taken and the derived indices utilizing that factor could not be calculated. The shells were cleaned in a solution of 2.5% sodium hypochlorite prior to measurement and photography.

Material examined: I examined 133 live-collected and 22 dead shell specimens of *F. actiniophorum*. Shells from dead specimens were measured only if they appeared to be intact without any damage. No dead shells carried an anthozoan. Ninety of the live-collected specimens carried an anemone; forty-three did not. Additional collections of *F. megathyris* and *F. erosum* specimens, including the type material, were examined for the comparative purposes (Tables 3, 4).

Table 3

Summary statistics of each of the meristic factors for *Fissidentalium megathyris*, *F. erosum*, and *F. actiniophorum*. The number of specimens measured varied due to the condition of the shell or soft part, and the presence of anemones.

	<i>Fissidentalium</i>		
	<i>megathyris</i>	<i>erosum</i>	<i>actiniophorum</i>
LTot			
Sample size	76	14	153
Average \pm 1 SD	78.06 \pm 12.64	69.20 \pm 5.24	47.78 \pm 8.30
Median	80.58	69.08	48.05
Minimum	16.27	62.19	19.19
Maximum	102.19	77.77	91.72
Range	85.92	15.58	72.53
Larc			
Sample size	76	14	94
Average \pm 1 SD	30.87 \pm 5.78	31.67 \pm 4.36	21.30 \pm 5.17
Median	31.00	31.50	21.38
Minimum	7.95	25.09	10.10
Maximum	42.26	39.09	31.76
Range	34.31	14.00	21.66
ApW			
Sample size	76	14	155
Average \pm 1 SD	13.54 \pm 2.71	11.89 \pm 0.56	8.06 \pm 1.09
Median	13.84	11.82	8.20
Minimum	2.29	11.16	4.34
Maximum	18.04	13.12	10.84
Range	15.75	1.96	6.50
ApH			
Sample size	76	14	155
Average \pm 1 SD	12.68 \pm 2.41	11.74 \pm 0.55	7.80 \pm 1.06
Median	12.76	11.67	7.94
Minimum	2.00	11.04	4.32
Maximum	16.56	12.70	10.00
Range	14.56	1.66	5.68
arc			
Sample size	76	14	94
Average \pm 1 SD	5.34 \pm 2.25	4.43 \pm 1.22	2.18 \pm 0.75
Median	5.06	4.32	2.15
Minimum	1.49	2.46	0.72
Maximum	13.81	6.40	3.93
Range	12.32	3.94	3.21
lnLTot			
Sample size	76	14	153
Average \pm 1 SD	4.34 \pm 0.24	4.23 \pm 0.08	3.85 \pm 0.188
Median	4.39	4.24	3.87
Minimum	2.79	4.13	2.95
Maximum	4.63	4.35	4.52
Range	1.84	0.22	1.56
lnLarc			
Sample size	76	14	94
Average \pm 1 SD	3.41 \pm 0.24	3.45 \pm 0.14	3.03 \pm 0.26
Median	3.43	3.45	3.06
Minimum	2.07	3.22	2.31
Maximum	3.74	3.67	3.46
Range	1.67	0.44	1.15
lnApW1			
Sample size	76	14	155
Average \pm 1 SD	2.65 \pm 0.25	2.56 \pm 0.04	2.20 \pm 0.13
Median	2.70	2.55	2.22
Minimum	1.19	2.50	1.68

Table 3
Continued.

	<i>Fissidentalium</i>		
	<i>megathyris</i>	<i>erosum</i>	<i>actiniophorum</i>
Maximum	2.95	2.65	2.47
Range	1.76	0.15	0.80
lnApH1			
Sample size	76	14	155
Average \pm 1 SD	2.59 \pm 0.25	2.54 \pm 0.04	2.17 \pm 0.13
Median	2.62	2.54	2.19
Minimum	1.10	2.49	1.67
Maximum	2.87	2.62	2.40
Range	1.77	0.13	0.73
lnWmax1			
Sample size	76	14	155
Average \pm 1 SD	2.59 \pm 0.25	2.54 \pm 0.04	2.17 \pm 0.13
Median	2.62	2.54	2.19
Minimum	1.10	2.49	1.67
Maximum	2.87	2.62	2.40
Range	1.77	0.13	0.73
lnApH1			
Sample size	76	14	155
Average \pm 1 SD	2.59 \pm 0.25	2.54 \pm 0.04	2.17 \pm 0.13
Median	2.62	2.54	2.19
Minimum	1.10	2.49	1.67
Maximum	2.87	2.62	2.40
Range	1.77	0.13	0.73
Apratio			
Sample size	76	14	155
Average \pm 1 SD	1.02 \pm 0.02	1.00 \pm 0.01	1.01 \pm 0.02
Median	1.02	1.00	1.01
Minimum	0.99	0.99	0.97
Maximum	1.08	1.02	1.08
Range	0.09	0.03	0.11
Ws			
Sample size	76	14	94
Average \pm 1 SD	2543 \pm 17,915	615 \pm 1064	2.4 \times 10 ¹¹ \pm 1.7 \times 10 ¹¹
Median	99.89	233.40	961.06
Minimum	5.33	40.47	34.24
Maximum	156,440.00	3726.50	1.47 \times 10 ¹¹
Range	156,434.67	3686.03	1.47 \pm 10 ¹¹
lnWs			
Sample size	76	14	94
Average \pm 1 SD	4.93 \pm 1.77	5.43 \pm 1.38	8.04 \pm 4.10
Median	4.60	5.45	6.87
Minimum	1.67	3.70	3.53
Maximum	11.96	8.22	25.72
Range	10.29	4.52	22.18
Total viscera			
Sample size	22	19	126
Average \pm 1 SD	37.59 \pm 3.68	31.42 \pm 4.79	25.44 \pm 6.06
Median	36.55	31.70	24.81
Minimum	31.80	19.80	0.00
Maximum	49.10	38.90	40.92
Range	17.30	19.10	40.92
Buccal lobe			
Sample size	22	19	124
Average \pm 1 SD	14.87 \pm 1.77	14.32 \pm 2.49	8.17 \pm 2.09

Table 3
Continued.

	<i>Fissidentalium</i>		
	<i>megathyris</i>	<i>erosum</i>	<i>actiniophorum</i>
Median	15.30	14.70	8.36
Minimum	10.40	8.40	2.76
Maximum	17.40	18.30	14.11
Range	7.00	9.90	11.35
Gut lobe			
Sample size	22	19	124
Average \pm 1 SD	8.13 \pm 2.08	6.96 \pm 1.71	5.70 \pm 1.38
Median	8.45	7.30	5.68
Minimum	4.40	4.30	2.80
Maximum	12.20	9.80	10.92
Range	7.80	5.50	8.12
Gonad lobe—ventral			
Sample size	22	19	124
Average \pm 1 SD	14.58 \pm 3.10	10.14 \pm 2.66	9.78 \pm 3.36
Median	14.90	10.30	9.33
Minimum	9.20	6.30	3.74
Maximum	21.30	17.20	23.75
Range	12.10	10.90	20.01
Gonad lobe—dorsal			
Sample size	22	19	104
Average \pm 1 SD	15.52 \pm 2.40	12.23 \pm 2.13	8.86 \pm 2.44
Median	15.10	12.10	8.92
Minimum	10.40	8.80	2.81
Maximum	22.10	16.70	15.40
Range	11.70	7.90	12.59

Etymology: The epithet *actiniophorum* (from Greek: *aktinos* = "a ray or beam"; referring to the sea anemone or actinarian, and *phoreus* = "a bearer") refers to the association between the scaphopod and sea anemone that is borne on the functionally dorsal surface of most specimens. The name was suggested by Dr. Eugene Kozloff.

Diagnosis: A white *Fissidentalium* with numerous faint external longitudinal striae; shell surface dull with irregular annulations parallel to the ventral aperture; most live specimens have a sea anemone attached to the concave surface of the shell. Ventral aperture slightly wider than high. Young specimens with a posterior slit extending down the convex side of the shell from dorsal aperture (Figure 2). Gonadal length longer than either of the other two soft-body-part regions.

Detailed description: Specific measurements of the holotype and paratypes are given in Table 5. Unless otherwise noted, all measurements in the description are means \pm one standard deviation of all *F. actiniophorum* specimens and were taken from Table 3.

Shell large, mean total shell length 47.8 ± 8 mm, evenly curved; shell length from dorsal aperture to point of max-

imum curvature 21.3 ± 5.2 mm; point of maximum arc posterior to, but near, the shell middle (Figure 3).

Ventral aperture slightly oblique to dorso-ventral axis; approximately circular, slightly wider than high; aperture width 8.1 ± 1.1 mm; aperture height 7.8 ± 1.1 mm.

Shell curvature slight; maximum curvature 2.2 ± 0.75 mm; whorl expansion rate $2.4 \times 10^{10} \pm 1.7 \times 10^{10}$.

Length of preserved, unrelaxed, soft-body-part mass 25.9 ± 5.2 mm; length of buccal region 8.2 ± 2.1 mm; gut region 5.7 ± 1.4 mm. Ventral gonadal region length 9.8 ± 3.4 mm; dorsal gonadal region length 8.9 ± 2.4 mm.

Radula (Figure 4) of "*Antalis* type" (Chistikov 1975), similar to *F. megathyris* and *F. erosum*; lateral teeth convex anteriorly, concave posteriorly bearing pointed forward projections where bent; marginal teeth with wavy contours and three curvatures; rachidian teeth concave dorsally, with transverse ridges, cross-section "S"-shaped allowing teeth to fit tightly together. Rachidian and lateral teeth movable on radular ribbon; marginal teeth immobile, imbedded in ribbon.

Shell, thin compared to *F. megathyris* and *F. erosum*, about $150 \mu\text{m}$ thick, with three layers; a thin outer aprismatic layer, $2\text{--}4 \mu\text{m}$ thick; a middle layer of vertically

Table 4

Results of pairwise tests between *F. actiniophorum* and each of *F. megathyris*, and *F. erosum* for the meristic factors. The test was the non-parametric Mann-Whitney U test of unpaired data. Tested taxon = Taxon tested against *F. actiniophorum*; Z = Large sample test statistic; and P = probability that the tested taxon data and *F. actiniophorum* data could be drawn randomly from the same population. n = total number of values.

Variable	Tested taxon	Z	P	n
A. Shell measurements				
LTot	<i>megathyris</i>	-11.209	< 0.001	229
	<i>erosum</i>	-6.087	< 0.001	167
Larc	<i>megathyris</i>	-9.050	< 0.001	170
	<i>erosum</i>	-5.287	< 0.001	108
ApW	<i>megathyris</i>	-11.300	< 0.001	231
	<i>erosum</i>	-6.186	< 0.001	169
ApH	<i>megathyris</i>	-11.250	< 0.001	231
	<i>erosum</i>	-6.186	< 0.001	169
Arc	<i>megathyris</i>	-10.022	< 0.001	170
	<i>erosum</i>	-5.442	< 0.001	108
B. Derived shell measurements				
lnLTot	<i>megathyris</i>	-11.209	< 0.001	229
	<i>erosum</i>	-6.084	< 0.001	167
lnLarc	<i>megathyris</i>	-9.050	< 0.001	170
	<i>erosum</i>	-5.287	< 0.001	108
lnApW1	<i>megathyris</i>	-11.300	< 0.001	231
	<i>erosum</i>	-6.186	< 0.001	169
lnApH1	<i>megathyris</i>	-11.250	< 0.001	231
	<i>erosum</i>	-6.186	< 0.001	169
lnHmax1	<i>megathyris</i>	-11.250	< 0.001	231
	<i>erosum</i>	-6.186	< 0.001	169
Apratio	<i>megathyris</i>	-3.350	< 0.001	231
	<i>erosum</i>	2.690	0.007	169
whratio	<i>megathyris</i>	-4.160	< 0.001	231
	<i>erosum</i>	2.415	0.015	169
Ws	<i>megathyris</i>	6.969	< 0.001	170
	<i>erosum</i>	2.986	0.002	108
Total viscera	<i>megathyris</i>	-6.909	< 0.001	146
	<i>erosum</i>	-4.059	< 0.001	143
Buccal lobe	<i>megathyris</i>	-7.303	< 0.001	146
	<i>erosum</i>	-6.405	< 0.001	143
Gut lobe	<i>megathyris</i>	-4.669	< 0.001	146
	<i>erosum</i>	-3.018	0.002	143
Gonadal lobe (ventral)	<i>megathyris</i>	-5.388	< 0.001	146
	<i>erosum</i>	-0.723	0.470	143
Gonadal lobe (dorsal)	<i>megathyris</i>	-7.027	< 0.001	126
	<i>erosum</i>	-4.787	< 0.001	123
D. Derived soft part measurements				
Buccal lobe/total viscera	<i>megathyris</i>	-4.368	< 0.001	146
	<i>erosum</i>	-6.111	< 0.001	143
Gut lobe/total viscera	<i>megathyris</i>	0.528	0.598	146
	<i>erosum</i>	0.116	0.908	143
Gonadal lobe (ventral)/total viscera	<i>megathyris</i>	-0.555	0.579	146
	<i>erosum</i>	2.263	0.024	143
Gonadal lobe (dorsal)/total viscera	<i>megathyris</i>	-3.910	< 0.001	126
	<i>erosum</i>	-2.712	0.007	123

oriented prisms, about 30 μm thick; and an inner crossed-lamellar layer, about 120 μm thick (Figure 5).

Shell white, dull, not polished; numerous irregular annulations present; patchy eroded areas common. Shell api-

cal end often missing, due to decollation (Reynolds, 1992), or predation (Shimek, 1990). A secondary shell extends from the dorsal aperture on many specimens (See Paratype B, Figure 3). Longitudinal striae visible with magnification

Table 5

Type specimen measurements. All measurements are in millimeters. Measurements and derivations are described in Shimek & Moreno, 1996. H = Holotype; P = Paratypes; NM = Not measured; ND = Not derived. LACM = Los Angeles County Natural History Museum, USNM = Natural History Museum of the United States, BMNH = British Museum of Natural History.

Category	H	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Museum	LACM	LACM	USNM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM	LACM
Lot number	2792	2793	886326	2809	2809	2809	2809	2809	2809	2809	2809	2809	2809	2809	2809	2809	2809	2809	2809
Anthozoan present	NO	YES	YES	NO	YES	NO	YES	NO	YES	NO	YES	NO	YES	NO	YES	NO	YES	NO	YES
A. Shell measurements																			
Total length	50.55	46.10	48.05	47.34	48.68	51.4	51.8	55.81	56.31	31.71	56.51	58.97	61.21	38.71	43.06	40.46	51.01	44.00	
Aperture height	8.61	8.46	8.16	8.66	7.50	8.16	7.88	7.82	9.05	5.58	8.97	8.34	9.81	6.74	7.00	5.82	8.37	7.96	
Aperture width	8.48	9.06	8.54	8.86	7.64	7.82	7.90	8.12	9.46	5.59	8.87	8.57	9.65	7.06	7.59	6.94	8.76	7.54	
arc	2.00	2.86	1.56	2.06	NM	NM	2.74	NM	3.74	NM									
Length to Max. arc	28.35	28.00	25.33	21.26	NM	NM	20.14	NM	26.10	NM									
B. Derived shell measurements																			
lnL/Tot	3.92	3.83	3.87	3.86	3.88	3.94	3.95	4.02	4.03	3.46	4.03	4.10	4.11	3.66	3.76	3.70	3.93	3.78	
lnL/arc	3.34	3.33	3.23	3.06	ND	ND	3.00	ND	3.26	ND									
lnAp/W1	2.25	2.31	2.26	2.29	2.16	2.18	2.19	2.21	2.35	1.88	2.29	2.26	2.37	2.09	2.15	2.07	2.28	2.14	
lnAp/H1	2.26	2.25	2.21	2.27	2.14	2.21	2.18	2.18	2.31	1.89	2.30	2.23	2.38	2.05	2.08	1.92	2.24	2.19	
Hindex	0.99	1.03	1.02	1.01	1.01	0.98	1.00	1.02	1.02	1.00	1.00	1.01	0.99	1.02	1.03	1.08	1.02	0.98	
hindex	0.98	1.07	1.05	1.02	1.02	0.96	1.00	1.02	1.02	1.00	1.00	1.01	0.99	1.02	1.03	1.08	1.02	0.98	
Ws	9077	332	40676	1852	ND	ND	287	ND	147	x	ND								
lnWs	9.11	5.80	10.61	7.52	ND	ND	5.66	ND	4.99	x	ND								
C. Soft body part length measurements																			
Total visceral length	34.38	26.97	24.76	24.16	23.85	NM	NM	25.76	26.14	23.49	40.92	39.22	35.5	NM	23.12	24.60	31.96	32.52	
Buccal lobe	10.66	8.70	6.86	9.07	6.86	NM	NM	6.06	11.41	6.52	6.42	7.77	8.74	NM	5.19	4.48	9.52	7.56	
Gut lobe	4.86	4.84	6.06	6.68	5.71	NM	NM	5.97	5.02	4.44	8.36	5.46	4.56	NM	4.36	4.94	5.99	6.34	
Gonad lobe—vent.	8.86	6.50	6.38	8.41	11.28	NM	NM	13.73	9.71	6.21	15.59	13.45	10.74	NM	7.21	7.54	8.49	9.28	
Gonad lobe—dor.	10.00	6.93	5.46	9.62	11.1	NM	NM	12.78	10.64	6.32	10.55	12.54	11.46	NM	6.36	7.64	7.96	9.34	
Gender	M	F	M	F	M	M	M	M	F	I	F	F	M	M	?	M	M	M	F

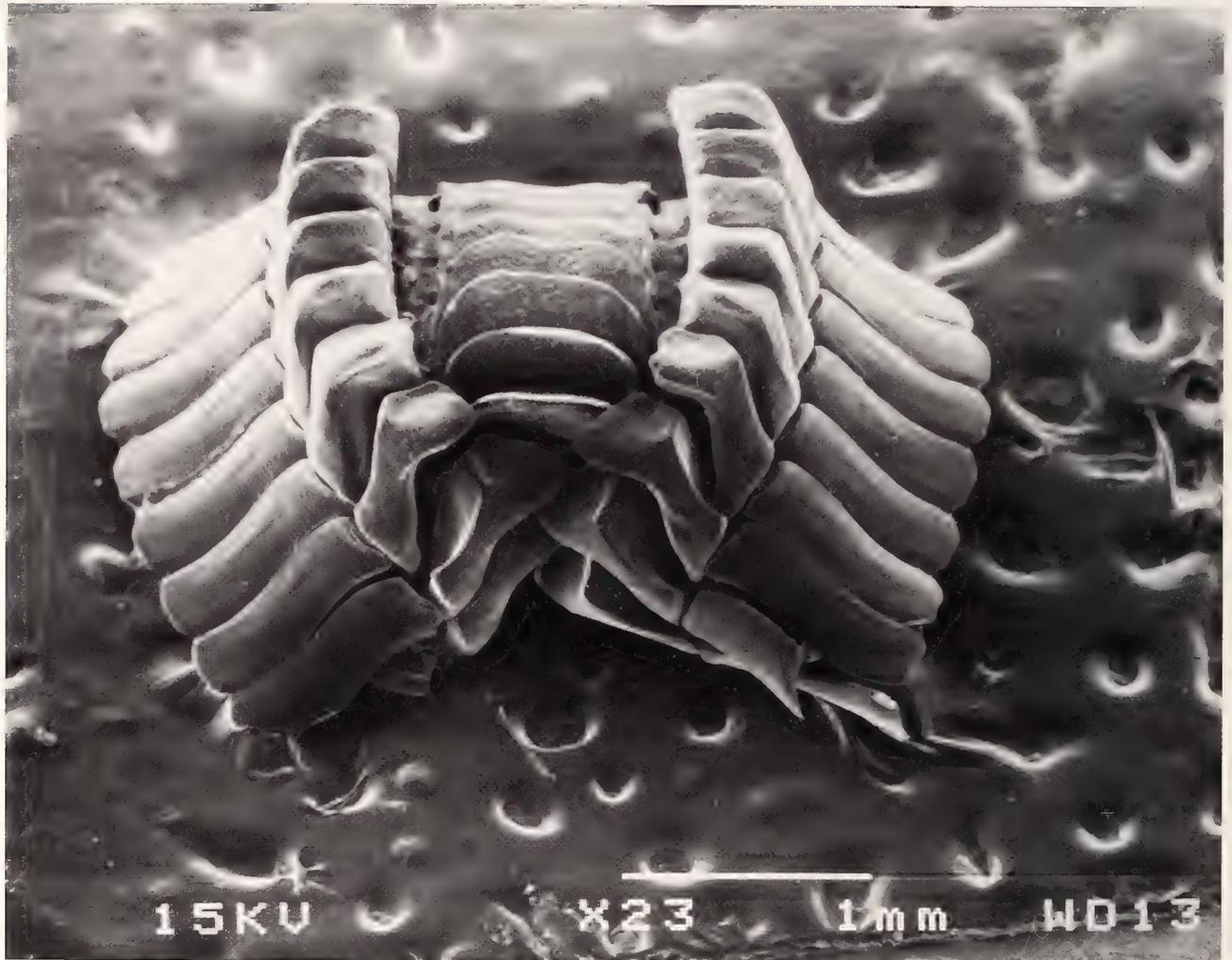


Figure 4

Radula of *F. actiniophorum*; Shimek, sp. nov. whole mount of the radula is shown from the posterior, the action plane to the top.

found near the dorsal aperture. Longitudinal striae on the rest of the uneroded shell faint, but generally visible without magnification and clearly visible with magnification. Faint surface marks at edges of the sea anemone attachment zone observed on some animals (Figure 2).

Remarks: The gender of 90 specimens was determined when the animals were measured. Based on gonadal examination, most of the *F. actiniophorum* examined were adults, containing either masses of sperm or ova. Only 10 *F. actiniophorum* juveniles or small animals of indeterminate sex were collected, probably due to the sampling method. Where gender was determined, the sex ratio was approximately 1:1; thirty-eight females and 42 males were collected. There were slight, non-significant differences in gender with regard to the presence of the anemones on the shell. Of the 90 animals whose gender was determined, 56

had anemones on the shell (31 ♂, 25 ♀), 24 were without anemones (11 ♂, 13 ♀).

There may be a general correlation between scaphopod gonadal length and season (G. Steiner, personal communication). Preliminary statistical analysis indicated that such a correlation may occur with these samples; however, given the small individual sample sizes, variations in the size of the individuals and gonads, and the pooling necessary for adequate analysis, the variance in the data was too extreme to confirm this (Shimek, unpublished data).

Whether the symbiosis of anthozoan and scaphopod is mutually beneficial is unclear. Obviously the anthozoan gains a substrate to attach to in an area that may be bereft of suitable attachment sites. Any costs or benefits to the scaphopod of this association are not immediately apparent; however, there does appear to be some slight superficial shell erosion due to attachment of the anemone on

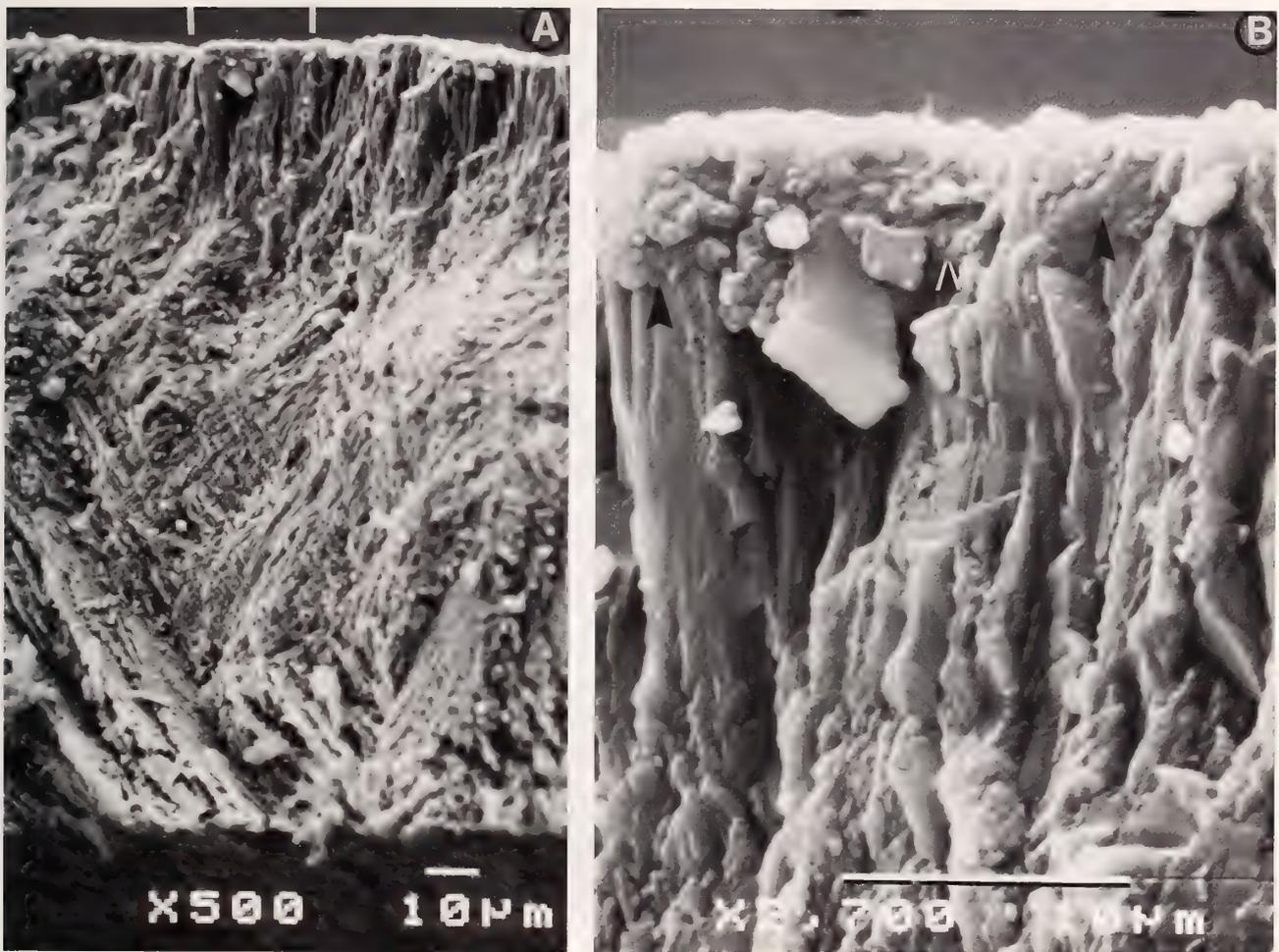


Figure 5

Cross section of a fractured *F. actiniophorum* Shimek, sp. nov. shell showing microstructure. The outer surface of the shell is at the top. A. The entire thickness of the shell is visible. B. Higher magnification of the area below the vertical white bars above the shell in Figure 5A. Note the thin amorphous outer layer (indicated above the arrowheads in Figure 5B) on top of the layer of vertical prisms, and the thicker inner crossed-lamellar structure (Figure 5A).

some specimens (Figure 2). Additionally, it seems unlikely that the scaphopod could move through sediments as easily with the anthozoan attached as it might be able to without the anemone. Rapid movement through sediments, however, is more a feature a gadilid scaphopods rather than dentaliids (Shimek, 1990) and may be relatively unimportant to this species.

The only other large scaphopods found geographically near *F. actiniophorum* are *F. erosum* and *F. megathyris*, which are found in shallower water, generally from 1000 m to 2500 m for *F. megathyris*, and around 3300 m for *F. erosum* (Nybakken et al., 1992; Shimek & Moreno, 1996). The latter two species are almost indistinguishable from each other in most regards as to shell shape, but are significantly larger and decidedly more robust than *F. actiniophorum* (Figure 6). *Fissidentalium actiniophorum* was

visually distinct when compared to either *F. erosum* or *F. megathyris*. It is smaller than either, and lacks the pronounced ribbing of *F. megathyris* and the extensive surface erosion of *F. erosum*. The basic color differs as well; *F. actiniophorum* is a milky white, while the other two species are more of an ivory color.

On the basis of shell and gross soft-body-part morphology, *F. actiniophorum* was clearly distinct and statistically significantly different from *F. erosum* and *F. megathyris* (Table 4). The significant differences between *F. actiniophorum* and these two morphologies were related to both relative and proportional differences in size, and were reflected in both external and some internal meristic factors (Table 3, 4). Because of all of these differences, I concluded that *Fissidentalium actiniophorum* was a distinct species.



Figure 6

Left lateral views of the shells of *F. actiniophorum* Shimek, sp. nov. (top) and *F. megathyris* (bottom). Scale bar = 5 mm.

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BOOKS, PERIODICALS & PAMPHLETS

The Eastern Oyster: *Crassostrea virginica*

edited by VICTOR S. KENNEDY, ROGER I. E. NEWELL and ALBERT F. EBLE. 1996. Maryland Sea Grant College. 734 pp. Hardcover \$95.00. Available from Maryland Sea Grant College, University of Maryland System, 0112 Skinner Hall, College Park, Maryland 20742 USA. Web site: <http://www.mdsg.umd.edu>.

There has been a long tradition of scientific research on the eastern oyster, *Crassostrea virginica* (Gmelin, 1791), a prominent member of the nearshore fauna of eastern North America. The stated aim of this rather large book is to provide an updated text that complements Paul Galtsoff's classic 1964 *The American Oyster*. A total of 26 authors have contributed to 21 peer-reviewed chapters focusing on diverse aspects of this oyster's biology. The result is a remarkably comprehensive and well-referenced review of our current knowledge of this important species. The book's scope gives it relevance not only to malacologists but also to a broad cross-section of marine biologists.

The first chapter differs qualitatively from the others and consists of a catalogue of selected species of living oysters. It is a useful summary of recent systematic nomenclature in this notoriously difficult taxon; however, it prominently reiterates a major error by Harry (1985). He proposed that *Ostrea puelchana* has a worldwide distribution in the southern hemisphere but was apparently unaware that he was synonymizing taxa with highly distinct reproductive and developmental modes (Chanley & Dinamani, 1980; Castro & Lucas, 1987).

Much of the first half of the book concerns the morphology of *C. virginica* and the text is liberally punctuated with useful diagrams and micrographs. The amount of detail in many of these chapters is impressive, particularly Chapter 3, which deals with the shell and ligament. These early chapters constitute a valuable reference source for anyone interested in bivalve morphology. However, the casual reader may find them heavy going.

Additional chapters concentrate on a variety of topics such as feeding and digestive physiology, reproduction and larval biology, population genetics, ecology, diseases, and defense mechanisms. These chapters have relevance to a greater audience than the book's title might suggest. In particular, anyone interested in estuarine ecology and marine parasitology would profit from perusing the contents. The authors faced a dilemma common to everyone reviewing the oyster literature: how to summarize the vast amount of pertinent, but qualitatively heterogeneous, publications

available. In my opinion, the authors of Chapters 9 and 11 (reproduction and population genetics, respectively) did an especially good job of critically reviewing the literature, pointing out problem areas to the reader and clearly articulating future research priorities.

The concluding chapters (19–21) deal respectively with culture, historical relocations and management issues of *C. virginica*. Of these, Chapter 20, dealing with transfers within the natural range and introductions to new areas, is the most compelling. It summarizes the probable role of oyster transfers in spreading pathogens and the striking inability (relative to the Asian *C. gigas*) of this species to establish significant new populations outside of its natural range.

Given the unusual length of this book, it may seem churlish to point out a few surprising omissions. Despite the impressive amount of morphological data presented, there is no substantial account given of the dramatic soft-part rearrangements that occur during metamorphosis. The intriguing and well-documented distinct spawning pathways used for sperm and for eggs in this species are barely mentioned. Most conspicuous by its absence is a concluding chapter containing a critical discussion of the projected long-term future of this species as the sole commercial oyster species and as a prominent, but significantly reduced, member of eastern North American estuarine fauna. Issues such as the steps necessary to restore water quality, the relative absence of significant culture of this species, and the potential cost and benefits of introducing exotic cupped oysters for culture are controversial. However, they are pertinent issues and it would be informative to learn the views of many of the most prominent eastern oyster biologists on these topics.

Diarmaid Ó Foighil

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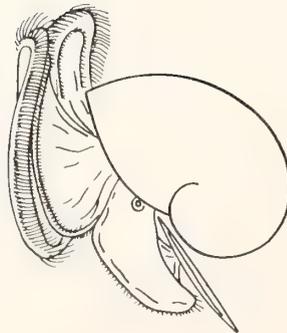
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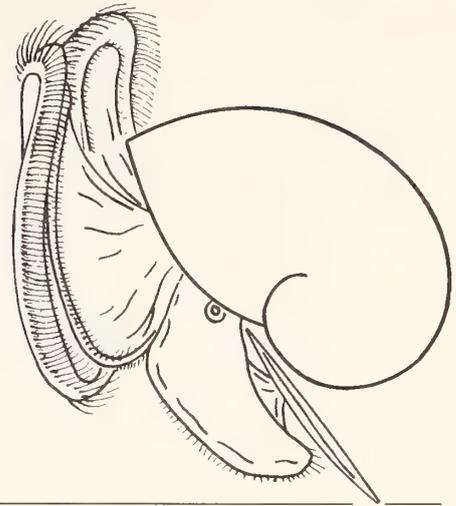
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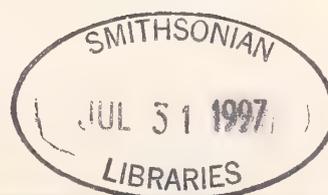
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THE VELIGER

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Late Cretaceous Occurrences on the Pacific Slope of North America of the Melanopsid Gastropod Genus *Boggsia* Olsson, 1929

by

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Abstract. The shallow-marine gastropod *Potamides tenuis* Gabb, 1864, from Upper Cretaceous (Campanian Stage) rocks in northern California, western Washington, and southwestern Canada, belongs to the gastropod genus *Boggsia* Olsson, 1929, formerly known only as two species from lower Eocene strata of northwestern Peru. The northern California specimens of *Boggsia tenuis*, are early Campanian in age, plentiful, and were deposited on an inner shelf in storm-lag accumulations composed of nearshore-marine and shelf-dwelling mollusks. The Washington specimens are middle Campanian in age and are rare. The Canadian specimens are middle to late Campanian in age and are also rare.

Boggsia tenuis has an anterior canal that is turned sideways and a very low, smooth protoconch poorly demarcated from the teleoconch. These features were previously unknown for the genus, hence its familial placement was uncertain. It can now be placed in family Melanopsidae, which ranges from Early Cretaceous (Albian) to Recent. New World melanopsids range from Early Cretaceous (Albian) to early Eocene and were shallow-marine dwellers. *Boggsia tenuis* is the first report of a melanopsid from the Pacific slope of North America. Old World melanopsids range from Late Cretaceous to Recent and are restricted to brackish or freshwater deposits.

INTRODUCTION

This paper concerns a shallow-marine gastropod species that is mostly found in Upper Cretaceous (lower Campanian Stage) rocks near Chico and Pentz, northern California (Figure 1). Rare specimens are found about 135 km northwest of Seattle on Sucia Island, San Juan County, Washington, and about 120 km northwest of Vancouver on Hornby Island, eastern British Columbia. The species has long been known as *Potamides tenuis* Gabb, 1864, but it is not a potamidid and is herein assigned to genus *Boggsia* Olsson, 1929. This particular genus was previously known only as two species from lower Eocene

shallow-marine rocks of northern Peru, but the familial position of the genus was uncertain due to lack of information regarding the protoconch and the anterior end of the aperture. These features are preserved in *Boggsia tenuis*, and the genus can now be placed in family Melanopsidae.

As will be discussed below, the classification of family Melanopsidae has been inconsistent, with some workers regarding it as a subfamily of Thiaridae and other workers regarding it as a family of its own. The geologic history of family Melanopsidae is poorly known because most members lived in brackish or freshwater habitats, which have a low potential for preservation. The fossil record

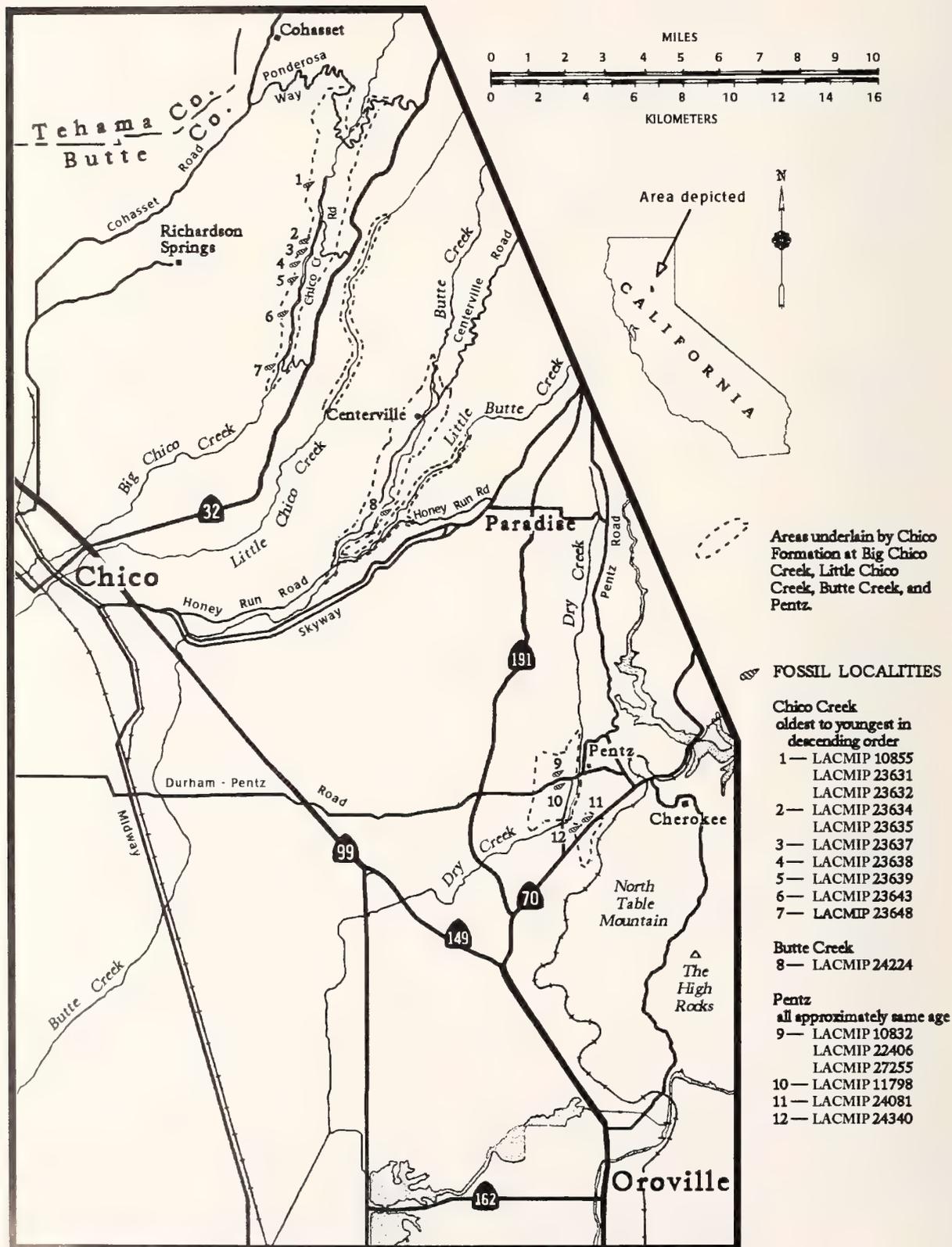


Figure 1

Index map for northern California localities of *Boggsia tenuis* (Gabb, 1864).

of melanopsids in the New World is very sketchy, and the recognition of *Boggsia* as a melanopsid from Upper Cretaceous rocks in California, Washington, and British Columbia, as well as from Eocene rocks in Peru, helps greatly in understanding the evolutionary history of this family. The shallow-marine habitat of *Boggsia* allowed the genus to achieve more widespread distribution than it could have if it lived in brackish or freshwater environments.

Abbreviations used are: CIT, California Institute of Technology (collections now stored at LACMIP); GSC, Geological Survey of Canada, Ottawa; LACMIP, Natural History Museum of Los Angeles County, Section of Invertebrate Paleontology, Los Angeles; UCLA, University of California, Los Angeles (collections now stored at LACMIP).

SYSTEMATIC PALEONTOLOGY

Superorder CAENOGASTROPODA Cox, 1959

Order NEOTAENIOGLOSSA Haller, 1882

Superfamily CERITHIOIDEA Ferrussac, 1819

Family MELANOPSIDAE H. & A. Adams, 1854

Discussion: The family Melanopsidae usually has been regarded as a subfamily of Thiaridae Troschel, 1857. In a cladistic analysis, Houbrick (1988) showed melanopsids to be distinct from thiarids and deserving of full familial status. In his analysis, the Melanopsidae is in a separate branch but relatively close to the branch supporting the Thiaridae.

Family Melanopsidae is characterized by members having an operculate oval aperture with an anterior channel, a simple protoconch not clearly demarcated from the teleoconch, and a usually calloused columellar lip bent anteriorly (Davies & Eames, 1971; Bandel & Riedel, 1994).

Genus *Boggsia* Olsson, 1929

Original description: "Shell melanoid to sub-turriteloid, subulate, with numerous convex to subangulated whorls; sutures distinct, strongly oblique or descending; early whorls smooth or finely sculptured with revolving spirals; later whorls smooth; growth lines oblique but not sinuous; aperture subovate, *Littorina*-like in shape and with a thin outer lip" (Olsson, 1929:78).

Type species: *Turritella anceps* Woods, 1922, by original designation; early Eocene of northwestern Peru.

Discussion: Olsson was mistaken in reporting that *Boggsia* has a round aperture because he based his description on incomplete specimens. Although he did not figure *Turritella anceps*, the type species of *Boggsia*, illustrations of this species by Woods (1922:pl. 8, figs. 12, 13; pl. 9,



Figures 2–3

Reprints of Woods (1922:pl. 8, figs. 12, 13) illustrations of *Turritella anceps* Woods, 1922, the type species of *Boggsia*; apertural views, $\times 1.6$. Specimens stored at Sedgwick Museum, Cambridge, England. Figure 2. Same as Woods figure 12. Figure 3. Same as Woods figure 13.

figs. 1, 2) show that the anterior ends of the type specimens are broken, even though Woods mentioned that the aperture is rounded in front. The same is true for *T. annectens* Woods (1922:pl. 9, figs. 3, 4), the only other species assigned by Olsson to genus *Boggsia*.

Wenz (1938:fig. 887) reprinted two of the original illustrations of *T. anceps*, but the reprint of Woods' (1922) figure 12 is poor, and it is not obvious that the larger specimen has a broken anterior end of the aperture. Woods' (1922:pl. 8, figs. 12, 13) illustrations of *Turritella anceps* are included herein (Figures 2, 3). The extreme anterior parts of the apertures of these specimens look exactly like those of incomplete specimens of "*Potamides*" *tenuis* Gabb whose extreme anterior parts of the apertures are missing (e.g., Figure 13). These specimens of "*Potamides*" *tenuis* have all of the diagnostic characters of genus *Boggsia*, especially in terms of the shape of the elongate teleoconch with anteriorly subangulated whorls that show sculpture on the spire. Well-preserved specimens of "*P.*" *tenuis* show the following additional characters not available from the type species: a short anterior canal that is not twisted but is turned sideways; a very low, smooth protoconch that is difficult to distinguish from the teleoconch; and a thin to moderately thick columellar callus. The western North American Cretaceous "*Potamides*" *tenuis*, which is herein unequivocally assigned to genus *Boggsia*, thus adds valuable new morphologic information about the genus and establishes that *Boggsia*'s so-called round aperture is only an appar-

ent feature associated with specimens whose anterior end is broken.

Because Olsson (1929) mistakenly believed that *Boggsia* had a rounded aperture without an anterior channel, he assigned *Boggsia* to the family Pseudomelaniidae Fischer, 1885. Wenz (1938) later questionably used this familial assignment. Family Pseudomelaniidae is characterized by an oval-rounded aperture without an anterior channel, a smooth and slightly elevated protoconch, and a smooth to weakly ornamented teleoconch. Olsson did not have available specimens of *Boggsia* whose extreme anterior end of the aperture was intact, nor did he have any information regarding the protoconch morphology of *Boggsia*. The morphologic features of *B. tenuis*, however, dictate that genus *Boggsia* cannot belong to family Pseudomelaniidae. Instead, the genus belongs in family Melanopsidae, whose characters were listed earlier under "Family Melanopsidae."

Genus *Nudivagus* Wade, 1917, also resembles *Boggsia*, in terms of the turruculate shell with a slightly curved, short anterior canal. *Nudivagus*, which is smoothish, is known primarily from Upper Cretaceous strata of the southeastern United States. Abbass (1973) also reported it from Lower Cretaceous (Aptian Stage) strata of the Isle of Wight, southern England. The familial status of *Nudivagus* has been somewhat problematical, and the most recent workers that addressed this problem were Sohl (1960) and Abbass (1973). Both believed it to be a member of family Procerithiidae.

With future taxonomic revisions, we consider it likely that turruculate gastropods distinguished by a short and slightly curved anterior canal, like that seen on *Boggsia*, on *Nudivagus*, and on certain fossil forms of "*Faunus*" (discussed below) will be grouped together either as a subgroup of melanopsids or as a new family, closely related to the melanopsids.

Boggsia tenuis (Gabb, 1864)

(Figures 4 to 17)

Potamides tenuis Gabb, 1864:130-131, 227, pl. 20, fig. 86; 1869, p. 227. Stanton in Turner, 1894:460. Stewart, 1927:356, pl. 23, figs. 8, 9. Anderson, 1958:164. Russell et al., 1986:191:1-2.

Potamides tenuis Gabb. Whiteaves, 1879:121 (in part), pl. 15, figs. 8a-8c; 1903:363. Not *Potamides tenuis*, variety *nanaimoensis* Whiteaves, 1879:12-122, pl. 15, figs. 9, 9a [= *Anchura nanaimoensis* (Whiteaves) fide Elder & Saul, 1996].

Original description: "Shell elongated, slender; spire high; whorls increasing gradually in size, seven to seven and a half. Upper two-thirds sloping almost perpendicularly; lower third sloping rapidly inwards towards the suture, which is narrowly channelled. Angle of whorls marked by pretty distinct, elongated tubercules, which, on the body whorl, sometimes take the form of elongated

sinuous ribs; at other times the surface of this whorls is smooth. Aperture elongated, acute behind, widest in the middle, contracted in advance. Outer lip acute, sinuous; inner lip thinly incrustated. Canal gently curved. Length, 0.75 inch [19 mm]; width of body whorl, 0.25 inch [6.3 mm]" (Gabb, 1864:130-131).

Supplementary description: Moderately small in size (up to 25 mm high, estimated), elongate-turritid to fusiform, approximately eight whorls (including protoconch); high-spined, spire approximately one-half of shell height. Sutures oblique, impressed. Protoconch approximately one whorl, very low, smooth, and poorly differentiated from teleoconch. Teleoconch approximately six whorls; sculpture changes from early whorls to later whorls. Upper spire whorls with flattish posterior portion, a strong angulation on anterior one-third of whorl, and 10 to 11 broad opisthocline axial ribs. Strength of axial ribs variable; either broadly swollen from suture to suture or only as knobby swellings on the angulation. Upper spire whorls with minute (usually same strength as the growth lines) spiral threads, producing, on some specimens, a reticulate pattern where intersecting the opisthocline growth lines, especially in the high-sloping area between the angulation and anterior suture. Spiral ribs rarely moderately strong over entire whorl; on some specimens, a single moderately prominent spiral rib present in area between angulation and anterior suture. On middle spire whorls, axial ribs either better developed than on preceding whorls, or none at all; knobby swellings on angulation weak to obsolete; spiral ribs minute to obsolete.

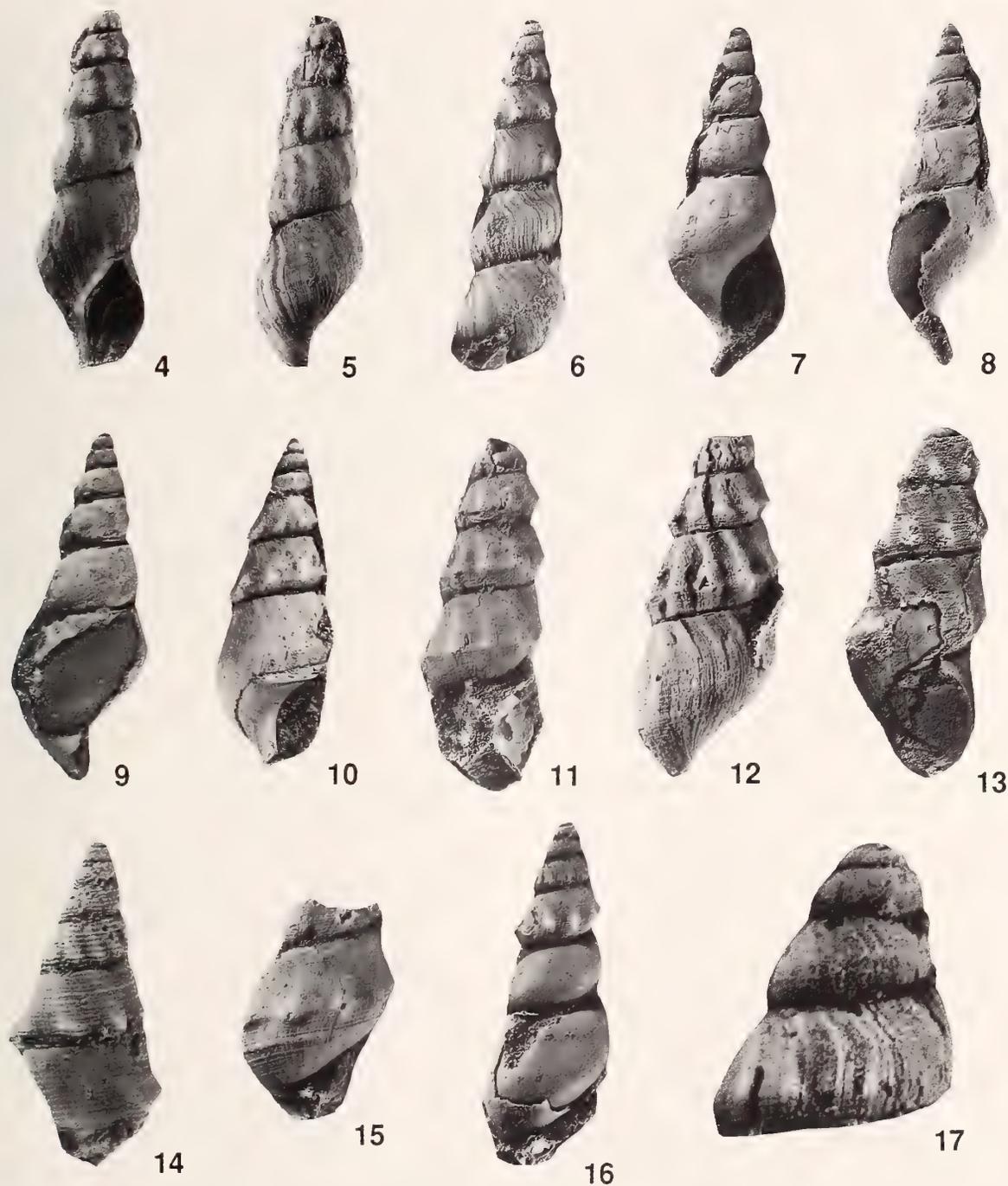
Adult body whorl smooth; opisthocline growth lines usually moderately strong, especially near outer lip. Aperture small, elliptical, tapered anteriorly. Anterior canal spoutlike, very shallow, short, projecting, and bent sideways. Columella smooth, not twisted, with a thin to moderately thick callus; rarely a groove present between columellar callus and base of body whorl. Outer lip thin, not carrying a varix.

Lectotype: ANSP 4288 (designated by Stewart, 1927).

Type locality: Near Pentz, Butte County, northern California.

Hypotypes: ANSP 27858 and LACMIP 7898 to 7907.

Distribution: NORTHERN CALIFORNIA: Chico Creek, Butte County, Chico Formation, lowermost part of Ten Mile Member (LACMIP locs. 10855, 23631, 23632, 23634, 23635, 23637, 23638, 23639, 23643, 23648); Butte Creek, Butte County, Chico Formation, lowermost part of Ten Mile Member (LACMIP loc. 24224); Pentz area, Butte County, Chico Formation, informal Pentz Road member (LACMIP locs. 10832, 11798, 22406, 24081, 24340, 27255). WESTERN WASHINGTON: Sucia Island, San Juan County, Cedar District Formation (LACMIP loc. 10442). BRITISH COLUMBIA: Hornby Island, probably the Spray Formation.



Explanation of Figures 4 to 17

Specimens coated with ammonium chloride.

Figures 4 to 17. *Boggsia tenuis* (Gabb, 1864). Figures 4-5. Hypotype LACMIP 7898, LACMIP loc. 24340, height 22.7 mm, $\times 2.4$. Figure 4. Apertural view. Figure 5. Abapertural view. Figure 6. Hypotype LACMIP 7899, LACMIP loc. 24081, abapertural view, height 19.7 mm, $\times 2.7$. Figures 7-9. Hypotype LACMIP 7900, LACMIP loc. 24340, shell material partially decorticated, height 15.2 mm, $\times 3.5$. Figure 7. Apertural view. Figure 8. Left-lateral view. Figure 9. Abapertural view. Figure 10. Hypotype LACMIP 7901, LACMIP loc. 24081, apertural view, height 13.5 mm, $\times 3.7$. Figure 11. Hypotype LACMIP 7902, LACMIP loc. 24340, apertural view, height 18.7 mm, $\times 2.9$. Figure 12. Hypotype LACMIP 7903, LACMIP loc. 22406, abapertural view, height 13.4 mm, $\times 3.9$. Figure 13. Hypotype LACMIP 7904, LACMIP loc. 23637, apertural view, height 16.6 mm, $\times 3.2$. Figure 14. Hypotype LACMIP 7905, LACMIP loc. 23637, right-lateral view, height 8.3 mm, $\times 6$. Figure 15. Hypotype LACMIP 7906, LACMIP loc. 24081, left-lateral view, height 7.4 mm, $\times 4.7$. Figures 16-17. Hypotype LACMIP 7907, LACMIP loc. 10832. Figure 16. Abapertural view, height 13.5 mm, $\times 3.9$. Figure 17. Abapertural view of protoconch and uppermost spire, height 2.5 mm, $\times 17$.

Geologic age: Early Campanian in California, middle Campanian in Washington, and middle to late Campanian in British Columbia.

Discussion: A total of 683 specimens were studied. Preservation is poor to excellent, and there is no obvious evidence of abrasion. Specimens that have retained their protoconchs, however, are very rare. Nearly all the specimens are juveniles (less than about 15 mm high).

Specimens of *B. tenuis* in northern California are known from 17 localities: 10 from the Chico Creek area, one from the Butte Creek area, and six from the Pentz area (Figure 1). Specimens from Chico Creek range from the lowermost part of the Ten Mile Member of the Chico Formation to near the top, but are more common in the lowermost part. Their range extends throughout Chron 33R and into Chron 33N (= early Campanian). A single specimen from Butte Creek was collected from the lowermost part of the Ten Mile Member and is also early Campanian in age, utilizing the detailed molluscan biostratigraphic work by Saul (1959). Russell et al. (1986) and Baum et al. (1987) inferred that this member at Chico Creek consists of inner shelf sediments deposited by storm-surge events and that the fossils accumulated in lensoidal shell lags. Russell et al. (1986) inferred that the basal part of the Ten Mile Member at Butte Creek represents a shoreface environment.

Specimens from the Pentz area were collected from the lower Chico Formation in the informal Pentz Road member of Russell et al. (1986), who reported the member to be early Campanian in age, based on the ammonites *Submortonicerias chicoense* (Trask) and *Baculites chicoensis* (Trask). The presence of the gastropod *Anchura callosa* Whiteaves, 1903, in these rocks suggests, utilizing the work of Elder & Saul (1996), that the Pentz Road member is similar in age to the lower Ten Mile Member of Chico Creek. The depositional environment of these particular rocks will be discussed below.

Specimens are present in great numbers in the Pentz area at LACMIP locs. 10832 and 24340, where 370 and 118 specimens were found, respectively. Fifty specimens were found at LACMIP loc. 24081. The few adult specimens that have been found are from LACMIP locs. 24081 and 24340. The best preserved and largest specimens are from LACMIP loc. 24340. Specimens of *B. tenuis* that have retained their anterior canal are rare and are also from this locality. One of these specimens (hypotype LACMIP 7900) that best shows the anterior canal is illustrated in Figures 7 to 9. The smooth-looking shell of this specimen is only an apparent feature because much of the shell material has been removed by weathering. The second best locality for preservation is LACMIP loc. 24081.

Whiteaves (1879) reported two specimens of "*Potamides*" *tenuis* from Upper Cretaceous strata on the northwest side of Denman Island, British Columbia, and other

specimens from Upper Cretaceous strata on Sucia Island, Washington. In 1903, he corrected himself and reported that the Denman Island specimens were actually from the northwest side of nearby Hornby Island and that the Sucia Island specimens are not "*P.*" *tenuis*. We obtained Whiteaves' (1879:pl. 15, fig. 8a-c) hypotype GSC 5762 of "*P.*" *tenuis* that was collected from the northwest side of Hornby Island (latitude 49°35", longitude 124°43"), which is just offshore of the east-central part of Vancouver Island, British Columbia. The specimen belongs to *B. tenuis*. The exact locality where it was collected is indefinite but is most likely from within the Spray Formation, to which Elder & Saul (1996) assigned a middle to late Campanian age. The Hornby Island occurrence is the youngest, as well as the northernmost, record of *B. tenuis*.

A few specimens of *B. tenuis* from Sucia Island (LACMIP loc. 10442) were detected in the LACMIP collection. They are from the Cedar District Formation, which Muller & Jeletzky (1970) assigned a Campanian age. Elder & Saul (1996) refined the age of this formation as middle Campanian.

Whiteaves (1879) also named and described *Potamides tenuis*, variety *nanaimoensis* Whiteaves (1879:121-122, pl. 15, figs. 9, 9a) from the northwest side of Hornby Island in strata that Elder & Saul (1996) tentatively assigned to the Spray Formation of late middle to late Campanian age. Elder & Saul (1996) reported also that Whiteaves (1879) based his description of this "variety" on juvenile specimens belonging to the aporhaid *Anchura nanaimoensis* (Whiteaves).

The specimens of *Boggsia* from the United States and Canada extend the geologic range of this genus into the Late Cretaceous (Campanian) and extend the geographic range into western North America. Previously, the genus was only known as two Eocene species from the extreme northwestern part of Peru, South America. Woods (1922) originally assigned these two species to genus *Turritella*, although he was somewhat reluctant to do so. They are *Turritella anceps* Woods (1922:81, text fig. 8, pl. 8, figs. 12, 13; pl. 9, figs. 1, 2) and *Turritella annexens* Woods (1922:81-82, pl. 9, figs. 3, 4). The former is from nearshore sandy deposits containing beach pebbles in the Negritos Formation, and the latter is mainly from the Parinas Sandstone. Marsaglia & Carozzi (1991) correlated these formations to the lower Eocene. Both species are represented by plentiful specimens. Olsson (1929:12-13, unfigured) assigned these two species to his genus *Boggsia*. He noted that the genus had a marine rather than a freshwater habit.

Russell et al. (1986:191-192, fig. 12) reported that the Upper Cretaceous strata in the Pentz area comprise the estuarine facies of their Pentz Road member (informal). They described this member as containing faunal assemblages that represent shallow-marine to brackish conditions. They referred to the faunal assemblage containing the specimens of *Potamides tenuis* as the "*Potamides ten-*

uis assemblage" and reported it to contain a mixture of soft-bottom bivalves and transported rocky shoreline gastropods that were deposited under estuarine conditions. Our findings dispute this paleoenvironmental interpretation. *Boggsia tenuis* (Gabb) was not a rocky shoreline dweller. Rather, it was a soft-bottom dweller and probably a shallow burrower, as indicated by its short anterior canal. In the Pentz area, specimens of *B. tenuis* are associated with a moderately diverse assemblage of subtidal, shelf-dwelling mollusks, such as ammonites. We see no indication that the specimens of *B. tenuis* were deposited under estuarine conditions.

Most melanopsids have a body whorl with a robust cylindrical shape and an aperture with an anterior notch, but lacking an anterior canal. Some melanopsids, however, have a short but distinct anterior canal. Those that are similar to *Boggsia* in that they have a turriculate shape, as well as a distinct anterior canal, are certain fossil forms of "*Faunus*." The aperture of *Boggsia tenuis* is very similar to "*Faunus*" *cerithiformis* (Watelet, 1851: 121, pl. 1, figs. 1, 2) from uppermost Paleocene (Sparnacian) strata in the Paris Basin, France. A well-preserved LACMIP collection specimen of this species from Pourcy, France, has a curved, spoutlike anterior canal just like *Boggsia*. *Boggsia tenuis* differs from "*F.*" *cerithiformis* by being smaller, narrower, and having axial ribbing.

The spoutlike anterior canal of *Boggsia tenuis* is also very similar to that of "*Faunus*" *dufresnei* (Deshayes, 1825:120, pl. 12, figs. 3, 4; Cossmann & Pissarro, 1910–1913:pl. 19, fig. 117–7; Farchard, 1936:pl. 23, fig. 11) from upper Paleocene (Thanetian Stage) and lower Eocene (Ypresian Stage) strata in Paris Basin, France. *Boggsia tenuis* differs from "*F.*" *dufresnei* in the following features: smaller, narrower, and angulate whorls with axial ribs becoming obsolete on adult whorls rather than more pronounced. Unlike *Boggsia tenuis*, as "*F.*" *dufresnei* becomes more mature, the outer lip thickens considerably, the sculpture on the body whorl becomes very prominent, and the anterior canal becomes much less apparent. "*Faunus*" *dufresnei* is now assigned to genus *Pseudobellardia* Cox, 1931. Wenz (1939:fig. 2003 a–d) figured the growth stages of a species of *Pseudobellardia*, and he placed *Pseudobellardia* in the melanopsids.

In 1991, Houbbrick discussed *Faunus sensu stricto* and put the single living species, *Faunus ater* (Linnaeus, 1758) in subfamily Melanopsinae of family Thiaridae. It is important to mention, however, that on *Faunus ater* the anterior canal has been replaced by a wide, deep sinus. *Faunus ater* does not have an anterior canal, and in this respect is unlike "*F.*" *cerithiformis* and "*F.*" *dufresnei*.

Tracey et al. (1993) reported the geologic range of melanopsids to be Late Cretaceous (Turonian) to Recent, but this range can be emended based on a report by Kollman (1984) of a melanopsid species from Baja California, Mexico. Allison (1955) used the name *Microschiza* (*Cloughtonia*) *scalaris* (Conrad, 1852) for this earliest

species and assigned it to family Pseudomelaniidae. Kollman (1984) placed the species in the melanopsid genus *Megalonoda* Kollmann, 1984. *Megalonoda scalaris* is the earliest member of the family and is of Early Cretaceous (Albian) age. It is from the Alisitos Formation, Baja California, Mexico (Allison, 1955). Kollman (1984) reported that this genus is also known from Upper Cretaceous strata in Austria, Greece, and North Africa. Although Kollman (1984) reported that *Megalonoda* is restricted to deposits of brackish water, the deposits in the Alisitos Formation, Baja California, are tropical shallow-marine in origin and are associated with reef corals, nerineid gastropods, caprinid rudistid bivalves, and numerous other shallow-marine invertebrates.

The Cretaceous New and Old World genus *Megalonoda* has a distinctive robust cylindrical shape that closely resembles the late Miocene *Melanopsis handmanniana* Fischer, 1996 [= *Melanopsis fossilis* Wenz, 1929, *vide* Fischer, 1996] from Austria and the Recent *Melanopsis* (*Canthidomus*) *costata* Férussac, 1828, from Syria and Jordan. It could be that during the Late Cretaceous, the marine *Megalonoda* migrated from Baja California, Mexico, to Europe, where the genus adapted to brackish and freshwater environments and has endured in those environments ever since.

Melanopsids live today in a variety of freshwater to brackish-water habitats, including saline lakes, freshwater lakes, rivers, streams, and springs in the areas surrounding the Mediterranean Sea, the Black and Caspian seas, and in New Zealand and New Caledonia (Tchernov, 1975; Geary, 1990). Transition of marine forms to freshwater forms might have occurred in Late Cretaceous times, according to Bandel (1993). Bandel & Riedel (1994) reported several smooth-shelled genera of melanopsids from Upper Cretaceous (upper Santonian–?lower Campanian) freshwater deposits in the Ajka region, Bakony Mountains, Hungary. From Paleocene to late Eocene time, many Paris Basin species (Cossmann & Pissarro, 1910–1913) seem to have inhabited brackish and shallow-marine environments (Tracey et al., 1993). At least one late Oligocene subspecies is known from Hungary (Báldi, 1973), and several late Miocene and Recent species are known from central and eastern Europe (Geary, 1990; Fischer, 1996).

None of the ancient or Recent Old World melanopsids resembles the shape of *Boggsia*, possibly because the shell of *Boggsia* was adapted for living in a shallow-marine environment. This habitat also allowed for a much wider paleogeographic distribution than if *Boggsia* had been restricted to brackish or freshwater habitats.

A review of the scant literature revealed that fossil melanopsids are not likely to be part of an admixed molluscan fauna consisting of freshwater species and shallow-marine species. For example, Bandel & Riedel (1994) reported that although the melanopsid-bearing Upper Cretaceous (upper Santonian–?lower Campanian) freshwater

deposits in the Bakony Mountains of Hungary were part of a river-mouth coastal swamp near a sea, the molluscan fauna consists only of typical freshwater forms containing fully grown unionid bivalve shells. Similarly, Geary (1990) reported that late Miocene melanopsids in scattered freshwater deposits from the margins of the Pannonian basin of eastern and central Europe never co-occur with marine organisms.

Boggsia tenuis closely resembles *Brotiopsis wakinoensis* (Kobayashi & Suzuki, 1936) from Lower Cretaceous (Barremian) brackish-water deposits of Japan and Lower Cretaceous freshwater deposits of South Korea. Kase (1984:127–128, pl. 20, figs. 1–6) illustrated this species, and the specimen in his figure 4 especially resembles *B. tenuis* in terms of the slender turriculate shell with opisthocline and spinose axial ribs. *Brotiopsis wakinoensis*, which shows considerable variability, is imperfectly known and is represented by incomplete external molds of juvenile to early adult? specimens. The anterior part of the aperture and the protoconch are unknown. It is possible that with better preserved material, *Brotiopsis wakinoensis* might prove to be a melanopsid. If so, it would be the earliest one.

ACKNOWLEDGMENTS

Klaus Bandel (Universität Hamburg, Germany) shared his knowledge of caenogastropods. Lindsey T. Groves (LACMIP) provided access to collections and obtained some literature. Jean Dougherty (GSC) arranged for the loan of a specimen. The manuscript benefited from comments by two anonymous reviewers.

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APPENDIX LOCALITIES CITED NORTHERN CALIFORNIA

The northern California localities are listed in groups corresponding to the following (arranged north to south) geographic areas: Chico Creek, Butte Creek, and Pentz areas:

CHICO CREEK

- U. S. Geological Survey, 15-minute, Paradise Quadrangle, 1953, Butte County, northern California. Chico Formation, unless otherwise noted = lowermost part of Ten Mile Member. Age: Late Cretaceous (early Campanian). Unless otherwise noted, collectors = L. R. Saul and R. B. Saul, August, 1952.
- LACMIP 10855 [= CIT 1309]. 30.5 m (100 ft.) S and 114 m (375 ft.) E of NW corner of section 12, T. 23 N, R. 2 E. Collectors: W. P. Popenoe & Clark, October 24, 1935.
- LACMIP 23631. West side of Chico Creek Canyon about 0.5 km (0.3 mi.) up "deep" ravine and 1.1 km (0.66 mi.) S of Mickey's Place. On line between sections 11 and 12, 533 m (1750 ft.) S of NW corner of section 12, T. 23 N, R. 2 E.
- LACMIP 23632. 7.6 m (25 ft.) farther up "deep" ravine than LACMIP loc. 23631.
- LACMIP 23634. On E bank of Chico Creek about 104 m (300 ft.) S of twin meadows and W from the H_B House, 518 m (1700 ft.) S and 160 m (525 ft.) E of NW corner of section 13, T. 23 N, R. 2 E.
- LACMIP 23635. On E bank of Chico Creek W from H_B House and approximately 122 m (400 ft.) S of twin meadows, 543 m (1800 ft.) S and 122 m (400 ft.) E of NW corner of section 13, T. 23 N, R. 2 E.
- LACMIP 23637. On E bank of Chico Creek approximately 0.8 km (0.5 mi.) S of southern H_B gate and W of sharp bends in Chico Creek county road; locality is just barely inside E line of SE corner of section 14 at 381 m (1250 ft.) N of SE corner of section 14, T. 23 N, R. 2 E.
- LACMIP 23638. On E bank of Chico Creek in concretions weathering out of 4.5-m (15-ft.) bank about 0.5 km (0.3 mi.) S of LACMIP loc. 23637; there is a large westward bend in the creek to the north of the loc. 23638, and the creek then runs straight in a southerly direction; 168 m (550 ft.) S and 260 m (850 ft.) W of NE corner of section 23, T. 23 N, R. 2 E.
- LACMIP 23639. In concretions in massive, greenish-gray sandstone, approximately 213 m (700 ft.) downstream from LACMIP loc. 23638; southern edge of NE 1/4 of the NE 1/4 of section 23, T. 23 N, R. 2 E.
- LACMIP 23643. West side of Chico Creek in concretions weathering out of sandstone cropping out at stream edge, 671 m (2200 ft.) S and 762 m (2500 ft.) W of NE corner of section 26, T. 3 N, R. 2 E.
- LACMIP 23648. Sandstone bluff on W side of Chico Creek about 0.4 km (0.25 mi.) above Salt Springs and approximately 61 m (200 ft.) above Chico Creek, 533 m (1750 ft.) S and 549 m (1800 ft.) E of NW corner of section 35, T. 23 N, R. 2 E.

BUTTE CREEK

- LACMIP 24224. From nodules in mine tunnel on E bank of Butte Creek, about 3 m (10 ft.) above water's edge,

4.5 km (2.8 mi.) by road NW of Honey Run Road covered bridge, approximately 610 m (2000 ft.) S and 76 m (250 ft.) E of NW corner of section 17, T. 22 N, R. 3 E, U.S. Geological Survey, 15-minute, Paradise Quadrangle, 1953, Butte County, northern California. Chico Formation, lowermost part of Ten Mile Member. Age: Early Campanian. Collector: W. P. Popenoe, August 29, 1952.

PENTZ AREA

U. S. Geological Survey, 7.5-minute, Cherokee Quadrangle, 1949, Butte County, northern California. Chico Formation, Pentz Road member (informal) of Russell et al. (1986). Age: Early Campanian.

LACMIP 10832 [= CIT 1012]. Fossiliferous layers cropping out in the beds of small gullies in the field on both sides of the E-W highway connecting Pentz and Chico, about 1.3 km (0.8 mi.) N86°W of Pentz, NW $\frac{1}{4}$ of the NW $\frac{1}{4}$ of section 25, T. 21 N, R. 3 E. Collectors: W. P. Popenoe and D. W. Scharf, August 15, 1931.

LACMIP 11798. Across the road and S from LACMIP loc. 10832. Collector: W. P. Popenoe.

LACMIP 22406. Gullies W of Pentz, 260 m (850 ft.) S and 107 m (350 ft.) E of NW corner of section 25, T. 21 N, R. 3 E. Collector: W. P. Popenoe, 1946.

LACMIP 24081. Fossiliferous conglomerate approximately 2.4 km (1.5 mi.) S of Pentz along Wicks-Pentz-

Magalia Road and approximately 0.8 km (0.5 mi.) E of road in W-flowing tributary gully to Dry Creek, near middle of section 36, T. 21 N, R. 3 E. Collector: A. Clark, 1935.

LACMIP 24340. Conglomerate beds cropping out just below a drainage canal, SE side of Oroville Highway, about 1.2 km (0.75 mi.) NE of intersection of the highway and Pentz-Magalia-Oroville Road, and 427 m (1400 ft.) S and 183 m (600 ft.) W of the NE corner of section 36, T. 21 N, R. 3 E. Collector: W. P. Popenoe, May 13, 1960.

LACMIP 27255. In concretionary lenses in gray sandstone (stained red when weathered) next to culvert under Durham-Pentz Road, about 0.8 km (0.5 mi.) W of junction with Oro-Pentz Magalia Road and 3.3 km (2 mi.) E of junction of Clark and Durham-Pentz Road; culvert is westernmost of two which are approximately 100 ft. apart; 244 m (800 ft.) S and 46 m (150 ft.) E of NW corner of section 25, T. 21 N, R. 3 E. Collector: L. R. Saul, August 23, 1954.

WASHINGTON SUCIA CREEK

LACMIP 10422. Float on beach, south side of Fossil Bay near its mouth, section 25, T. 38 N, R. 2 W, Sucia Island, San Juan County, Washington. Cedar District Formation. Age: Middle Campanian. Collectors: R. Durbi, H. L. Popenoe, & W. P. Popenoe, July 24, 1935.

Development of the Embryonic Shell Structure in *Nautilus*

by

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Abstract. Microstructural features of embryonic shells of *Nautilus macromphalus* and *N. pompilius* at different stages of development were observed by optical and scanning electron microscopy on the basis of specimens recovered from the Kasai and Toba Aquaria, Japan. The results of our observations reveal that the early embryonic shell development of *Nautilus* can be divided into two major stages with different shell structure and ornamentation. In the first stage, a low cap-shaped shell with a distinct median depression (= cicatrix) is secreted by the shell gland in the sequence of outer conchiolin and inner spherulitic prismatic layers. In the second stage, a new shell consisting of outermost conchiolin, outer prismatic, middle nacreous, and inner prismatic layers appears at the outer margin of the cicatrix, marked by a discontinuity in the shell structure (constriction) at the boundary. It is ornamented with longitudinal growth lines and radial undulations, indicating shell secretion at the mantle margin. During the second stage, a protoseptum, which comprises outer prismatic, middle nacreous, and inner prismatic layers, is also added on the adoral side of the cicatrix by the rear mantle. These early embryonic shell features of *Nautilus* are similar to those of Carboniferous orthocerids, but are clearly distinguished from those of coleoids and ammonoids, both starting with a spherical initial chamber.

INTRODUCTION

Since the late 19th century, a number of workers have attempted to follow reproduction and development of *Nautilus* in the field (e.g., Willey, 1902; Haven, 1977) and aquaria (e.g., Willey, 1897a, b; Mikami et al., 1980). Despite these efforts, the embryonic development of *Nautilus* had long been unknown until Arnold & Carlson (1986) described several embryos of *N. belauensis* recovered from the Waikiki Aquarium. Subsequent descriptions on gross morphology and microstructure of embryonic tissue (Arnold, 1987; Tanabe et al., 1991) and shells (Arnold, 1987; Arnold et al., 1987; Landman et al., 1989; Arnold & Landman, 1993) have given new data on the developmental biology of this interesting living fossil. Nevertheless, our understanding about the morphogenesis of *Nautilus* is still insufficient for exact comparison with other cephalopods.

In this paper, the early embryonic shell development of *Nautilus macromphalus* and *N. pompilius* is described

on the basis of specimens recovered from the Toba and Kasai Aquaria, Japan, and its phylogenetic implications are discussed.

MATERIALS AND METHODS

Adult animals of *Nautilus macromphalus* captured from off Nouméa, New Caledonia, and of *N. pompilius* from off Taar area, southern Luzon Island, the Philippines, were transported by air to the Toba and Kasai Aquaria, respectively. They were kept in large tanks with a semi-open circulatory system of natural seawater. The material utilized was recovered from eggs in the two aquaria during 1992-1995, and consists of one embryo of *N. pompilius* from the Kasai Aquarium and five embryonic shells of *N. macromphalus* from the Toba Aquarium. The embryo examined comes from an egg laid on October 12, 1993. It was taken from the egg capsule on January 10, 1994 after incubating 102 days at a mean water temperature of 23°C. The living embryo was fixed with 2% glu-

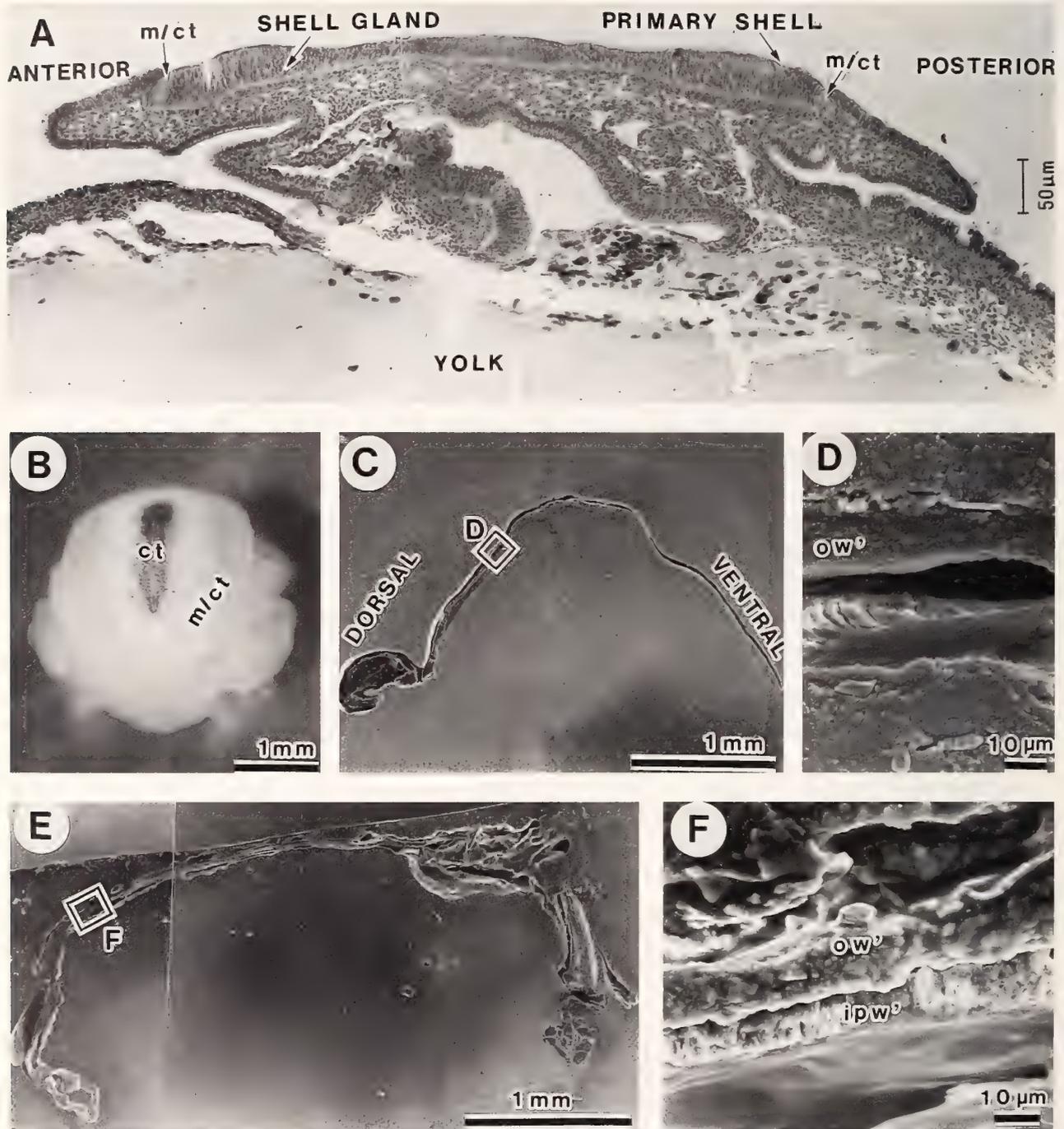


Figure 1

Embryo and embryonic shells in the pre-chambered stage without a prosepium. A-B. The 102-day-old embryo of *Nautilus pompilius*. UMUT RM 19958. Median dorso-ventral section of the apical portion (A) and frontal view of the embryo (B), showing the spherical shaped, dark organic primary shell with a median depression (cicatrix). Undifferentiated eyes and tentacles that are connected with a large external yolk sac are visible from the outside. ct: cicatrix, m/ct: mantle primordium-cicatrix boundary. C-D. Median dorsoventral section (C) and close-up (D) of the cicatrix of *Nautilus macromphalus*, that consists only of the outer organic (conchiolin) layer (ow'). UMUT RM 19959. E-F. Sagittal cross section (E) and close-up (F) of the cicatrix of *N. macromphalus*. The cicatrix is double-walled, consisting of the outer conchiolin (ow') and inner spherulitic prismatic (ipw') layers. UMUT RM 19960.

taraldehyde for 48 hours, and dehydrated through a graded series of ethanols, n-butylalcohols, and benzol, and then embedded in paraffin (melting point 58°C) without decalcification. Serial sections along the dorsoventral and sagittal axes were prepared for both specimens at intervals of 5–10 μm , and were stained with hematoxylin-eosin. They were observed and photographed by an Olympus model AHBS 515 optical microscope.

The five embryonic shells were removed from live embryos or from animals that were already dead when the egg capsules were opened. They were cleaned with distilled water, and freeze-dried with t-butylalcohol. Four of them were embedded in epoxy-resin and cut along the median dorsoventral or sagittal planes using a low-speed saw. The sectioned surface of each shell was etched with 5% acetic acid for 30 seconds, washed with distilled water, coated with platinum after drying, and then observed by scanning electron microscopy (Hitachi Model S-2300). One remaining shell was coated with platinum without etching, and the outer and inner shell surfaces were observed by SEM. All specimens utilized are housed in the University Museum, University of Tokyo (UMUT).

For comparison, SEM observations were also made on well-preserved specimens of two orthocerids, *Kionoceras* sp. and "*Orthoceras*" sp. retaining aragonitic shell material from the Middle Pennsylvanian (Desmoinesian) Buckhorn Asphalt, Arbuckle Mountains, Oklahoma.

These specimens were already described by Ristedt (1968, 1971) and are now kept in the Institut für Paläontologie, Universität Bonn (GPIBo).

OBSERVATIONS

Pre-Chambered Primary Shell (= Cicatrix)

This stage of development is represented by the 102-day-old embryo of *N. pompilius* and two embryonic shells of *N. macromphalus*. The embryo measures about 2.2 mm in basal diameter and attains an early organogenetic stage (Figure 1A, B). It is connected to a large external yolk sac. Primordia of arms, gills, and eyes are partly visible from outside in the embryo (Figure 1B). The main embryonic body is covered with the mantle primordium. In the apical end of the embryo, the mantle primordium is made of a row of tall (approx. 30–40 μm) columnar epithelial cells (shell gland) (Figure 1A). The shell gland secretes a primary shell. The epithelial cells on the outside of the shell secretion site are much shorter (approx. 20 μm thick) than those of the shell gland. The primary shell is elliptical in outline and consists of a dark-colored, thin (approx. 10 μm thick) conchiolin layer. It is currently called the cicatrix (Stenzel, 1964; Erben & Flajs, 1975; Arnold et al., 1987; Arnold, 1988). The outer surface of the cicatrix lacks apparent growth lines and, instead, is sculptured by a distinct median groove (about

Figure 2

Embryonic shell of *N. macromphalus* in the pre-chambered stage, with a proseptum. UMUT RM 19961. A, C–F. Median dorsoventral section of the entire shell (A) and close-up views at different shell portions (C–F) (see A for their positions). B. Close-up of the apical shell portion showing the boundary between the cicatrix (ct) and post-cicatrix (pct) stages marked by the constriction (C_1). Concentric growth lines appear in the post-cicatrix shell stage. The lower side of the photograph represents the dorsal side. C–D. Shell structure in the adapical portion (C) and its close-up in the apex area (D), showing the cicatrix and the underlying protoseptum. The cicatrix consists of outer conchiolin (ow') and inner spherulitic prismatic (ipw') layers, whereas the protoseptum is composed of outer prismatic (opp), middle nacreous (mnp), and inner prismatic (ipp) layers. E. Microstructure of the shell wall in the post-cicatrix stage. Near the aperture, the shell consists of outermost periostracal (ow), outer prismatic (opw), and middle nacreous (mnw) layers. F. Changes of the shell structure near the boundary between the cicatrix and the post-cicatrix shell. The inner spherulitic prismatic layer of the cicatrix (ipw) forms a thick swelling (varix) just before the boundary and then rapidly thins out and disappears adorally (left side). On the dorsal side of the cicatrix (= the lower side of the photograph), a new shell consisting of outermost periostracal (ow), outer prismatic (opw), middle nacreous (mnw) and inner prismatic (ipw) layers appear, marked by a clear constriction at the boundary with the cicatrix (C_1). mnp & ipp: middle nacreous and inner prismatic layers of the protoseptum, respectively.

Figure 3

Embryonic shell of *N. macromphalus* in the pre-chambered stage, with a protoseptum in formation. UMUT RM 19962. A. Frontal view of the apical shell portion, showing the cicatrix with a distinct median depression. The outer conchiolin layer (ow') is partly detached, where the inner spherulitic prismatic layer is exposed. The lower side of the photograph represents the ventral side. B. Close-up of the exposed surface of the inner spherulitic prismatic layer (B portion in A), showing irregularly oriented spherulites. C. Free-hand fractured shell at the apical portion, showing the inner spherulitic prismatic layer of the cicatrix (ipw'), and outer prismatic (opp) and middle nacreous (mnp) layers of the protoseptum. D. Close-up of the inner surface of the middle nacreous layer of the protoseptum. E. Crater-shaped shallow depression on the inner surface of the shell in the mid-apical portion, which represents an attachment scar of the initial portion of the siphuncular cord. F. Close-up of E, showing the inner organic membrane (iom) within the attachment scar of the siphuncular cord. Middle nacreous (mnp) and outer prismatic (opp) layers of the protoseptum are absent in this portion.

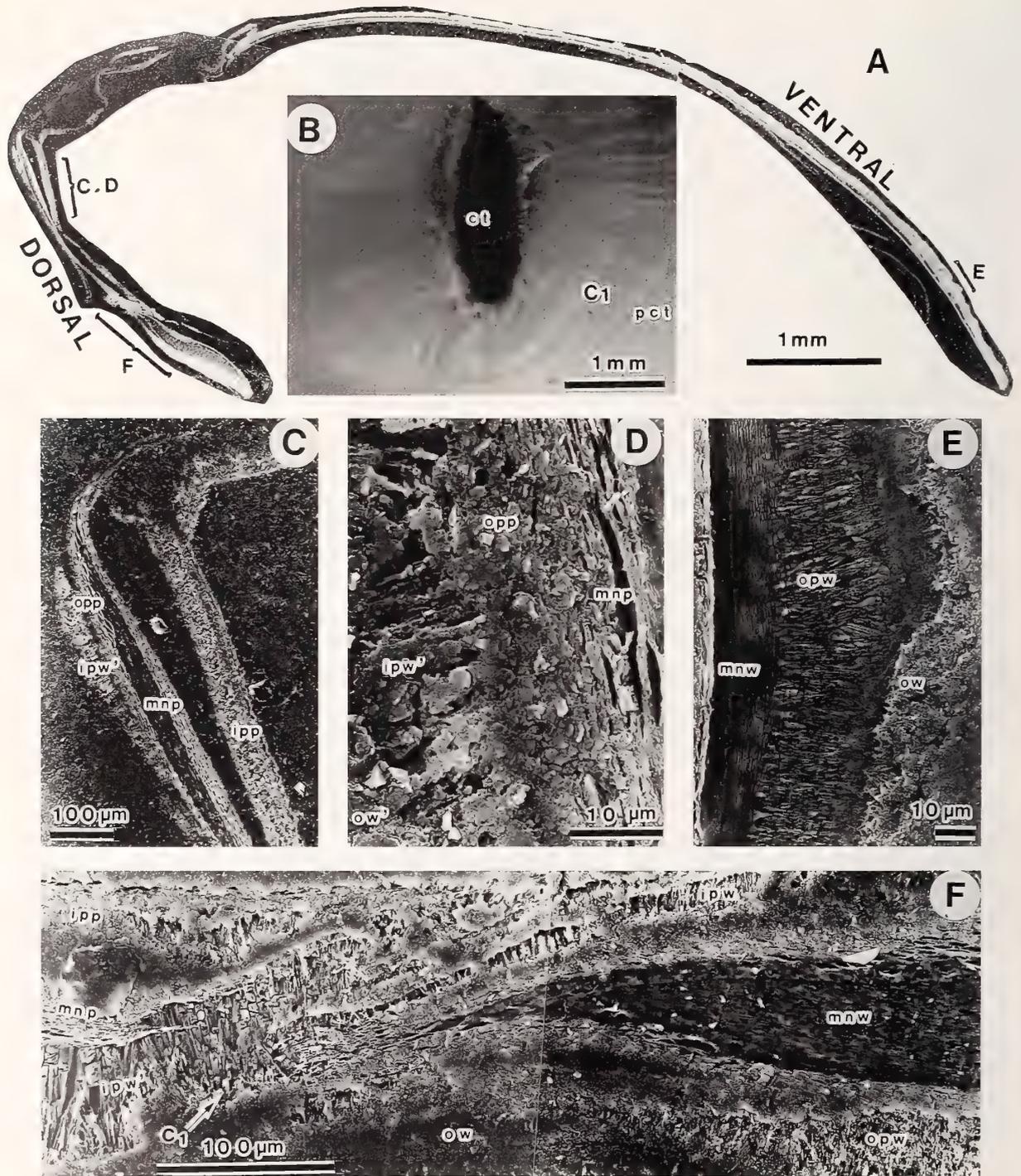


Figure 2

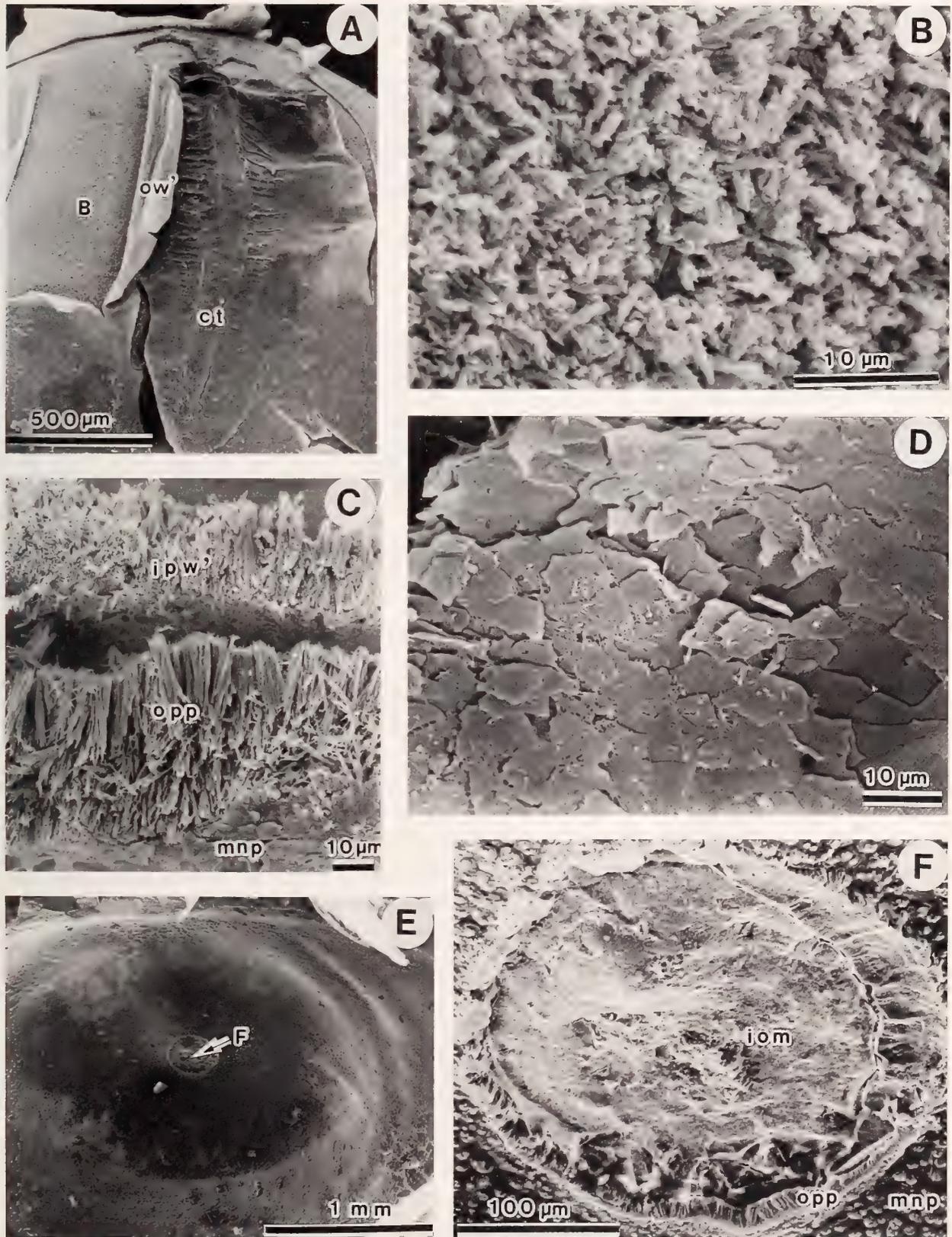


Figure 3



Figure 4

Median dorsoventral section of the embryonic shell of *N. macromphalus* in one-chambered shell stage, showing the positions of Figures 5–7. s1: first septum. UMUT RM 19963.

100 μm wide), and evenly spaced, transverse undulations that are arranged perpendicular to the median groove (Figure 1B; see also Figures 2B and 3A, showing the same portion in more developed embryonic shells).

One of the two embryonic shells (Figure 1C, D) is correlated in the degree of development to the shell of the 102-day-old embryo, because the shell comprises a black conchiolin layer only (ow' in Figure 1D). The other embryonic shell (Figure 1E, F) may represent a later stage of development, since it is double-layered, consisting of outer conchiolin and inner spherulitic prismatic layers (ow' and ipw' in Figure 1F).

Pre-Chambered Shell with a Protoseptum

This stage of development is represented by two specimens of *N. macromphalus* (Figures 2, 3). Both shells are cyrtoconic with a high apical angle and a large whorl expansion rate, measuring about 6 mm in apertural (= basal) diameter and 3 mm in height (Figure 2A). The apex is moved to the posterodorsal side as the shell grows so that the ventral shell wall is 3 times longer than the dorsal one, reflecting a logarithmic spiral growth. The shell is secreted on two different sites, namely, at the adoral shell margin and on the inner side of the cicatrix.

Shell secretion at the mantle margin starts with the appearance of a new shell on the cicatrix margin. The new shell gradually thickens adorally, marking a clear discontinuity in the shell structure (constriction) at the boundary with the cicatrix (C_1 in Figure 2B, F). It is made up of four layers; namely, outermost periostracum, outer prismatic, middle nacreous, and inner prismatic layers. The

first three layers are deposited at the shell margin (Figure 2E), whereas the inner prismatic layer is accreted on the posterior side (Figure 2F). At this stage of development, a reticulate ornamentation consisting of longitudinal "growth lines" and prominent radial lines appears on the new shell (Figure 2B). On the adoral side of the cicatrix, a thick layer, called the protoseptum, is secreted underneath the cicatrix wall by a rear mantle. It consists of outer prismatic, middle nacreous, and inner prismatic layers (Figure 2C, D).

In the specimen observed without sectioning, a clear craterlike shallow depression, about 300 μm diameter, is present at the mid-portion on the inner surface of the cicatrix (Figure 3E, F). The inner surface within the depression is covered with an organic membrane (iom in Figure 3F). A thin prismatic layer, about 20 μm thick, is locally distributed around the depression edge, making a steep slope toward the inner side. This prismatic layer is interpreted as the outer prismatic layer of the protoseptum, because it covers the middle nacreous layer of the protoseptum at the margin. The peculiar depression is similar in position to and possibly identical to the structure called the dorsal circular terminus of the cicatrix (Arnold et al., 1987) or the dorsal septal depression (Landman et al., 1989). It apparently represents an attachment scar of the initial portion of the siphonal cord (see Mutvei et al., 1993: fig. 3A, B).

One-Chambered Shell

A single embryonic shell of *N. macromphalus* shown in Figures 4–7 attains this stage of development. It roughly corresponds to the shell of the 145 day-old embryo of

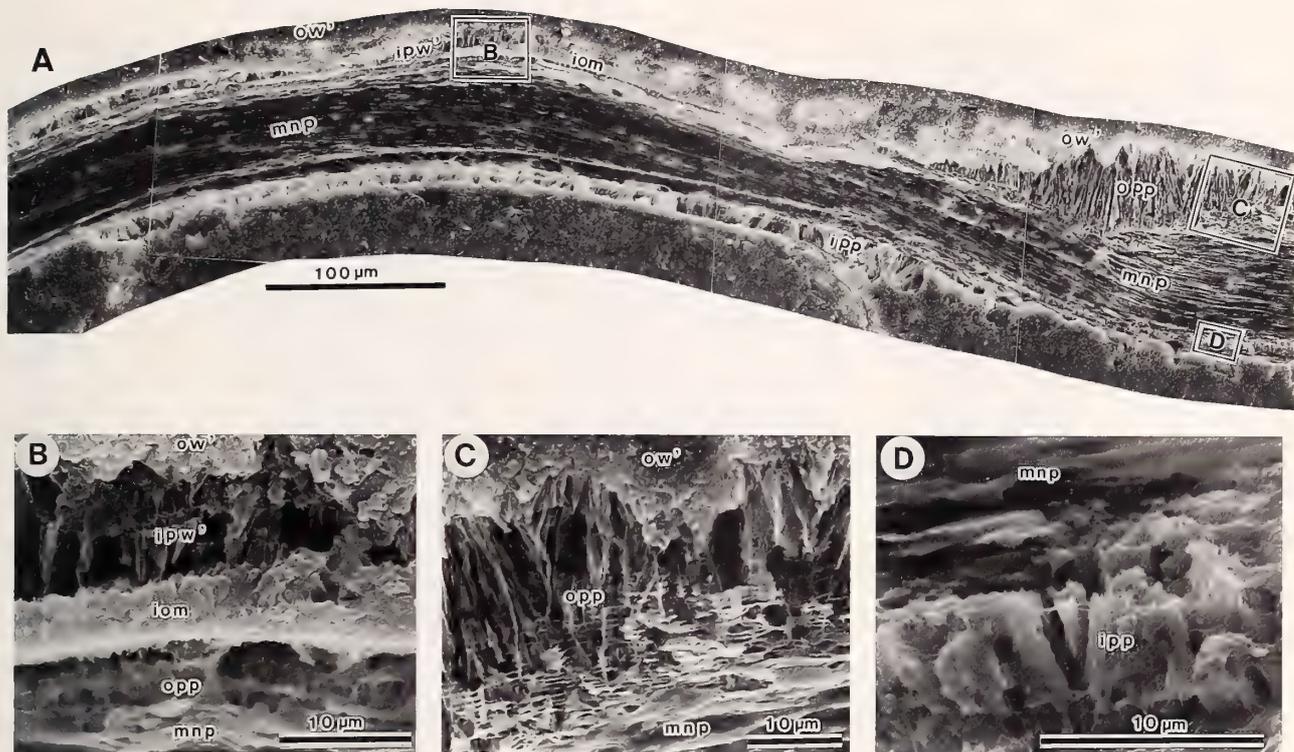


Figure 5

Microstructural details of the apical shell portion in the specimen shown in Figure 4. A. Distribution of the cicatrix and underlying protoseptum. ow' & ipw': outer conchiolin and inner spherulitic prismatic layers of the cicatrix, respectively. opp, mnp, & ipp: outer prismatic, middle nacreous, and inner prismatic layers of the protoseptum, respectively. The top of the photograph represents the adapical end. B. Close-up of the adapical end of the shell, showing the thin inner organic layer between the cicatrix and protoseptum. C. Close-up of the marginal apical portion, showing the thickly developed outer prismatic layer of the protoseptum underneath the conchiolin layer of the cicatrix. D. Inner side of the apical shell portion, showing the irregularly developed inner prismatic layer of the protoseptum.

N. belauensis described by Tanabe et al. (1991). At this stage of development, the mantle margin is made up of typical adult cephalopod-type three folds with a distinct median depression between the ventral and middle ones, where the periostracum gland secretes an accretionary growing shell (Tanabe et al., 1991: fig. 5B). The shell is cyrtconic with a posteriorly shifted apex and measures 6.8 mm in apertural diameter and 4.8 mm in height. The shell microstructure in this stage is essentially identical to that in the pre-chambered shell stage, except for the presence of a first septum. At the apical end, the shell wall consists of outer conchiolin, inner spherulitic prismatic, and innermost conchiolin layers of the cicatrix proper (ow', ipw', and iom in Figure 5B, C), and outer prismatic, middle nacreous, and inner prismatic layers of the protoseptum (opp, mnp, and ipp in Figure 5C, D). The middle nacreous layer of the protoseptum is thickest (approx. 100 µm thick) on the dorsal side of the cicatrix area (Figure 5A), then rapidly decreases its thickness adorally, and finally terminates just at the attachment of

the first septum to the shell wall (Figure 6A, B). The inner prismatic layer of the protoseptum varies in thickness from area to area, forming irregular clusters at the contact with the caecum (Figure 5A). It forms a conspicuous swelling at the mural part of the first septum (Figure 6A). Both the cicatrix shell wall and protoseptum terminate near the junction with the first septum, from which the dorsal shell wall begins to appear, retaining a clear constriction at the boundary with the cicatrix (c_1 in Figure 6A, B). The shell wall in the post-cicatrix stage is four-layered on both ventral and dorsal sides and consists of outermost periostracum, outer prismatic, middle nacreous, and inner prismatic layers. The middle nacreous layer of the dorsal shell abruptly thickens on the adoral side of the attachment of the first septum. The inner prismatic layer does not appear near the shell margin (Figure 7A, D). A clear constriction occurs near the shell margin (c_2 in Figure 7A, B). The first septum consisting of a thin (approx. 20 µm thick) nacreous layer is probably in the process of formation.

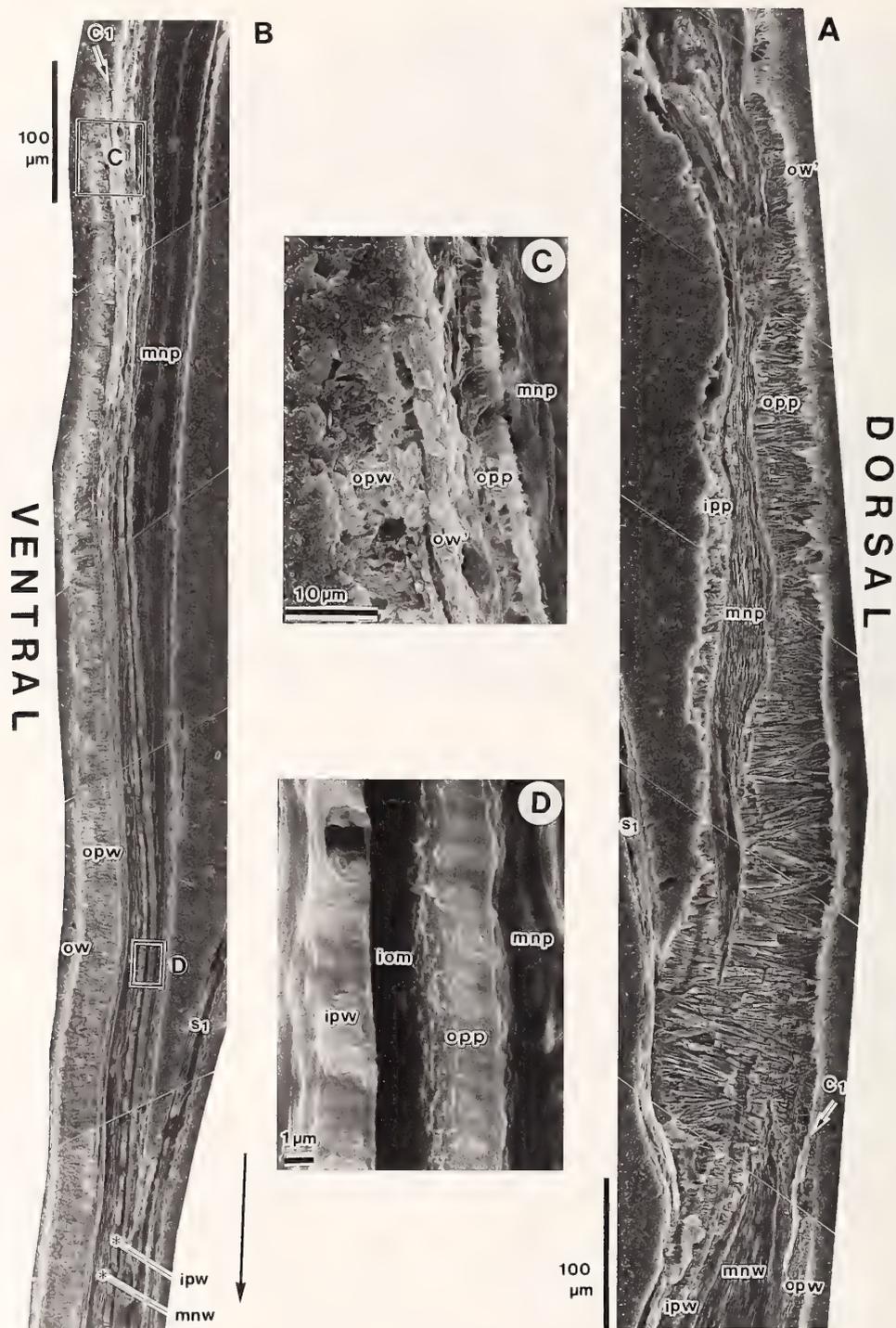


Figure 6

Microstructural details of the shell wall at the boundary between the cicatrix and post-cicatrix stages in the specimen shown in Figure 4. *s*₁: first septum; *ow*, *opw*, *mnw* & *ipw*: outermost conchiolin, outer prismatic, middle nacreous, and inner prismatic layers of the shell in the post-cicatrix stage, respectively. For other abbreviations see explanation in Figure 5. The arrow indicates the adoral direction. A, B. On both dorsal (A) and ventral (B) sides, a clear constriction (C1) is present at the cicatrix margin, from which a four-layered new shell wall of the post-cicatrix

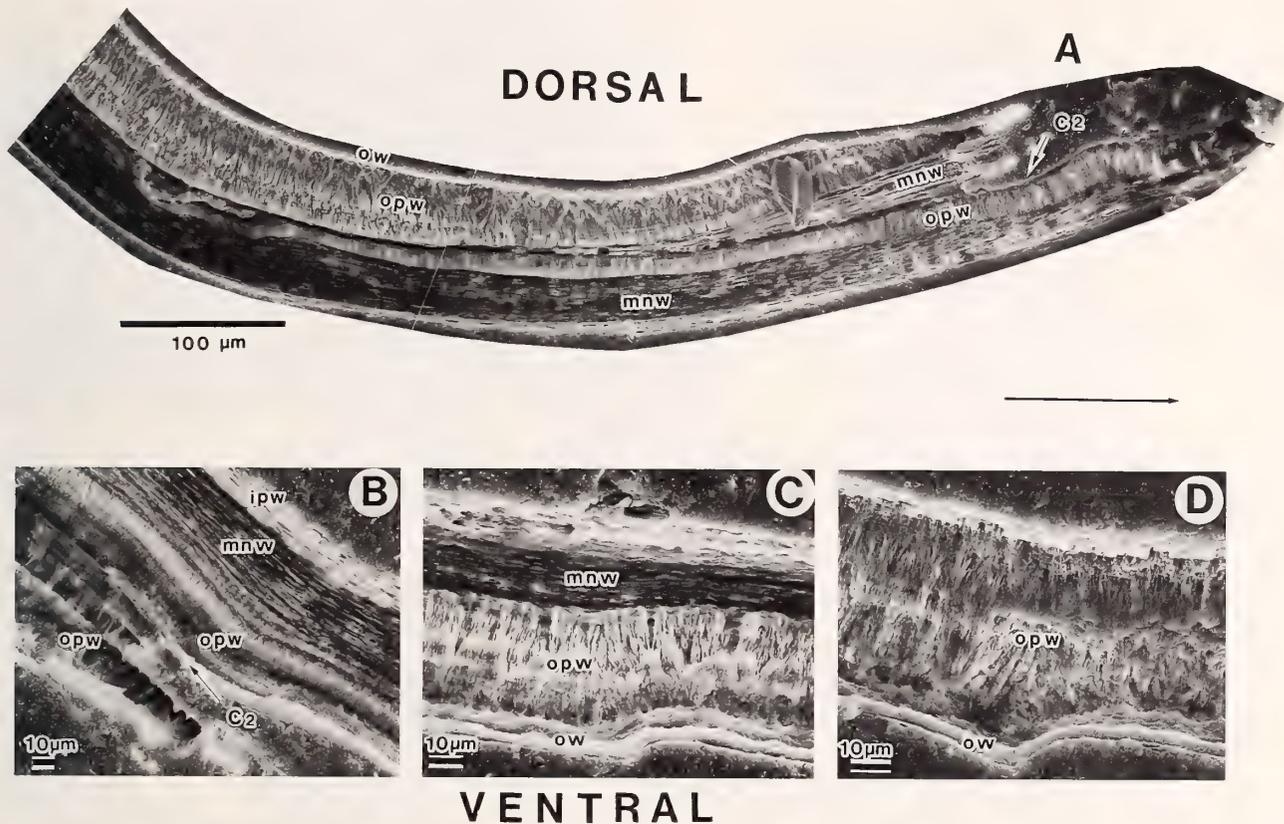


Figure 7

Shell microstructure at the post-cicatrix stage in the specimen shown in Figure 4. Note that the inner prismatic layer (ipw) is already secreted in the posterior portion (B), but does not develop near the shell margin (A, C-D). The second constriction (C_2) appears near the aperture. For other abbreviations see explanations of Figures 5 and 6. The arrow indicates the adoral direction.

Early Development of the Embryonic Shell Structure

To sum up SEM observations of embryonic shells of *Nautilus macromphalus* and *N. pompilius*, a succession of early shell development in *Nautilus* can be reconstructed (Figure 8). It is clearly divided into two major stages; **stage 1** characterized by secretion of a low cap-shaped shell (= cicatrix) by the shell gland, and **stage 2** indicated by secretion of a new shell wall at the mantle margin. The boundary between the two stages is marked by a constriction (C_1 in Figure 8C). In stage 1, a low, cap-shaped, black organic (conchiolineous) shell is first formed, followed by deposition of a spherulitic prismatic layer underneath the organic shell.

In stage 2, a four-layered shell that consists of outermost organic (conchiolin), outer prismatic, middle nacreous, and inner prismatic layers, begins to appear on the cicatrix margin (Figure 8C). This microstructural combination of the shell persisted into the post-embryonic stage. Simultaneously with the secretion of the four-layered shell, an inner prismatic layer of the prosepium is added on the inner surface of the cicatrix (opp in Figure 8C). Subsequently, the prosepium becomes thickened by secretion of the middle nacreous and outer prismatic layers (mnp and ipp in Figure 8D).

Based upon optical microscopy of adult shells, Blind (1987, 1988) observed that the inner prismatic layer in the cicatrix region continued to grow in later embryogen-

stage begins to appear. C. Close-up of the constricted portion on the ventral side, showing the outer prismatic layer of the shell in the post-cicatrix stage which covers the outer conchiolin layer of the cicatrix. D. Close-up of the ventral shell wall near the first septum, showing the thin inner organic membrane intercalated between the inner prismatic layer of the ventral shell and the outer prismatic layer of the prosepium.

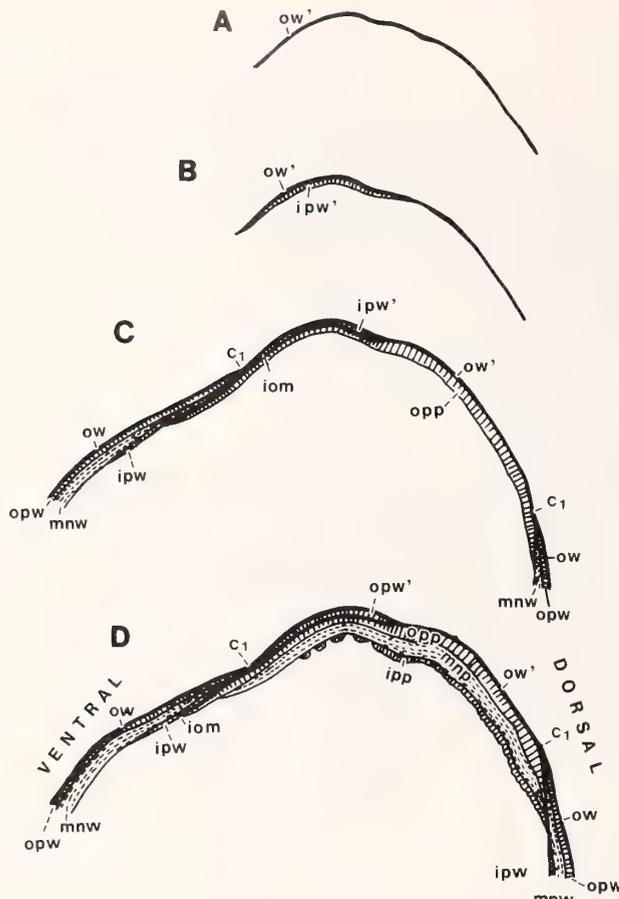


Figure 8

Diagrams showing the successive development of the early embryonic shell structure of *Nautilus*. See text for details. For abbreviations see explanations of Figures 2–7. The lower side of the figure indicates the adoral side.



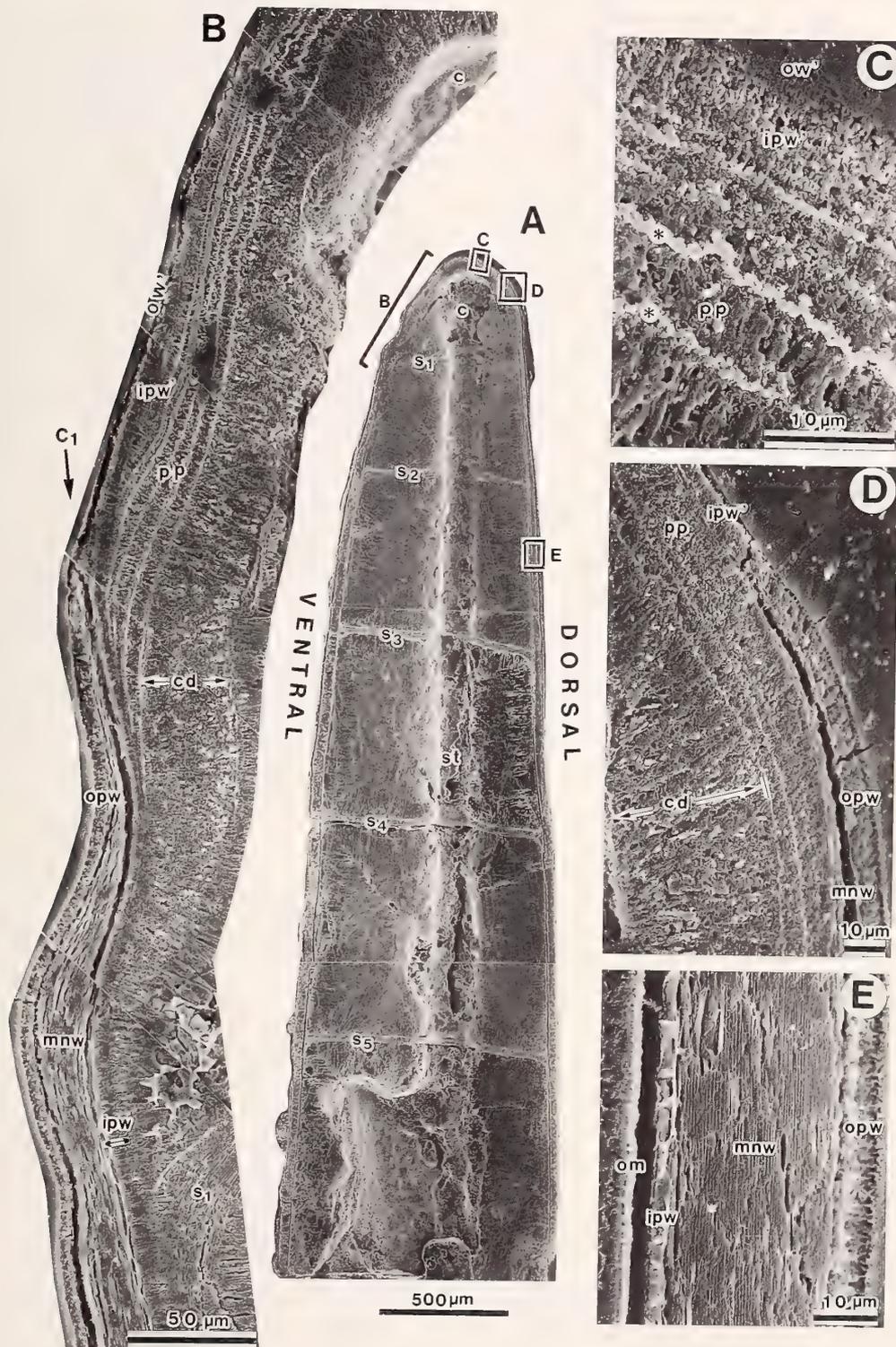
Figure 9

Apical shell portion of “*Orthoceras*” sp. (Orthocerida). GPIBo-Ri 75 (same specimen as that figured by Ristedt, 1971: pl. 29, fig. 1). From the Middle Pennsylvanian Buckhorn Asphalt, Arbuckle Mountains, Oklahoma. The elliptically shaped cicatrix (ct) is ornamented with a conspicuous median depression and evenly spaced undulations arranged perpendicular to the median depression. The boundary with the shell in the post-cicatrix stage (pct) is marked by the constriction (C1). The left and right sides of the photograph represent the dorsal and ventral sides, respectively.

esis with changing microscopic features. A similar view was presented by Arnold et al. (1987: fig. 8) in which the inner prismatic layer of the cicatrix (their outer prismatic layer of the outer wall) continuously occurs in the post-cicatrix stage without a constriction. Later, Arnold & Landman (1993) partly revised the above interpretation and emphasized the occurrence of two modes of embryonic shell development in *Nautilus*; i.e., the earlier cicatrix mode of shell formation (C-mode) and the adult mode of shell formation at the mantle edge (M-mode), without documentation of a constriction at the boundary between them. Our stages 1 and 2 undoubtedly correspond to the C- and M-modes of Arnold & Landman (1993). As stressed by these authors, the presence of the two modes

Figure 10

Shell microstructure of *Kionoceras* sp. (Orthocerida) (median dorsoventral section). GPIBo-Ri 63 (same specimen as that figured by Ristedt, 1971: pl. 28, fig. 5; pl. 30, figs. 1–5). From the Middle Pennsylvanian Buckhorn Asphalt, Arbuckle Mountains, Oklahoma. A. Overall view of the specimen, showing the portions of B–E. $s_1 \sim s_5$; septa 1–5. B. Microstructural details of the shell wall at the boundary between the cicatrix and post-cicatrix shell stages. The cicatrix is made of outer periostracal (ow') and inner spherulitic prismatic (ipw') layers. The shell wall in the post-cicatrix stage consists of outer prismatic (opw), middle nacreous (mnw), and inner prismatic (ipw) layers, whose inner surface is covered with an organic membrane (om). A clear constriction (pointed by C₁) occurs at the boundary between the two stages. C. Close-up of the apical portion, showing the thick prismatic protoseptum (pp) with intercalations of organic membranes (shown by asterisks) which cover the inner surface of the cicatrix. D. Close-up of the constricted portion on the dorsal side. A thick cameral deposit (cd) covers the inner surface of the protoseptum. E. Shell structure in the post-cicatrix stage, consisting of outer prismatic, middle nacreous, and inner prismatic layers.



of embryonic shell development reflects the difference in the degree of differentiation of the mantle during early embryogenesis.

COMPARISON WITH OTHER CEPHALOPODS

Embryonic shell features of the Orthocerida have been investigated based on exceptionally well-preserved material from the Middle Pennsylvanian (Desmoinesian) Buckhorn Asphalt, Arbuckle Mountains, Oklahoma (Ristedt, 1968, 1971; Blind, 1987). Our SEM observations of specimens of *Kionoceras* sp. and "*Orthoceras*" sp. are correlated well with the previously published data, and confirm that, as in *Nautilus*, the embryonic shells of orthocerids possess a low, cap-shaped cicatrix with a distinct median depression on their apical portion (Figure 9). In median dorsoventral section, the apical shell wall of *Kionoceras* sp. consists of outer organic and inner spherulitic prismatic layers of the cicatrix proper and of an inner prismatic layer of the protoseptum (Figure 10B, C). Middle nacreous and inner prismatic layers observed in the protoseptum of extant *Nautilus* are therefore absent in orthocerids. The shell wall of the cicatrix disappears adorally and is replaced by a new shell wall of the post-cicatrix stage. A conspicuous constriction occurs at the boundary between the cicatrix and post-cicatrix stages (pointed by an arrow in Figure 10B). It is also distinguishable from the outside of the shell (C_1 in Figure 9A). The shell wall at the post-cicatrix stage is four-layered, comprising outermost conchiolin, outer prismatic, middle nacreous, and inner prismatic layers. A thick (approx 30–40 μm) calcified layer that covers the inner surface of the apical shell region (cd in Figure 10B, D) was probably deposited inorganically as a cameral deposit. Except for the absence of a nacreous element of the protoseptum, the embryonic shell features of Carboniferous orthocerids are essentially identical with those in *Nautilus*. At least in the one-chambered shell stage, the total density of a living *Nautilus* embryo is apparently larger than that of seawater in view of the smaller volume ratio of phragmocone versus body chamber (Uchiyama & Tanabe, in press). This condition is also postulated in orthocerids (K. Tanabe's unpublished observations on the embryonic orthocerids housed in the Universität Bonn). In *Nautilus* and orthocerids, a neutral buoyant condition appears to be achieved in the middle to late embryogenesis.

The embryonic shell features of *Nautilus* and orthocerids are clearly distinguished from those of ammonoids and shelled coleoids (e.g., extant *Spirula*, Belemnitida, and Aulacocerida) by having a larger embryonic shell size and the absence of a spindle-shaped or spherical initial chamber and a prosiphon (Landman, 1987; Tanabe & Landman, in preparation). Also, in ammonoids, the appearance of a nacreous layer is prolonged in late embryogenesis, and marked changes in shell microstructure and ornamentation occur at the time of hatching (Kulicki,

1979, 1996; Landman, 1987; Landman et al., 1996, among others). Neutral buoyancy has been suggested in many ammonoids at the hatching stage, relying upon density calculations of actual specimens (Tanabe et al., 1995) and a linear relationship between diameters of initial chamber (air-chamber) and ammonitella (= embryonic shell) (Tanabe & Ohtsuka, 1985; Landman, 1987). This evidence implies that in ammonoids and possibly many fossil coleoids, the initial chamber played an important role for buoyancy regulation of the growing embryo.

ACKNOWLEDGMENTS

We thank the members of the international research project in the Philippines in 1983 (leader Prof. S. Hayasaka) who collected and transported live *Nautilus* to Japan, and the staff of the Kasai Aquarium in Tokyo for giving us an opportunity to conduct incubation experiments of *Nautilus* eggs. We are also grateful to Drs. Neil H. Landman (American Museum of Natural History, New York), John M. Arnold (University of Hawaii), and C. Kulicki (Polish Academy of Science) for stimulating discussions during the course of this study; and Dr. Heinrich Ristedt (Universität Bonn) for arranging loans of the type and figured specimens in his care. Dr. Landman also kindly read & critiqued the first draft of this paper. This work was supported by grants from the Japanese Ministry of Education, Science, and Culture (nos. 06452097 & 07304042 for 1994–1995) and the Japan Society for Promotion of Science.

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Comparative Anatomy of Three Species of *Epiphragmophora* Doering, 1874 (Pulmonata: Xanthonychidae) from Argentina

by

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Abstract. A comparative anatomical study of three species of the Neotropical genus *Epiphragmophora* Doering, 1874, is carried out. The external morphology of the animals, pallial, reproductive, digestive, and central nervous systems are described. New characters (penial muscular band, penial internal structure esophageal crop internal structure, structure of central nervous system) that could lead to a better definition of the group are described for the first time. The genital system, however, seems to offer more characters with phylogenetic potential than any other system. Based on this study, it was found that: (a) among the three species considered, *E. argentina* and *E. tucumanensis* are morphologically closer, *E. hieronymi* being different in characters of the central nervous system, esophageal crop, and terminal genitalia; (b) a previously undescribed structure, termed here "penial muscular band" is present in the three species considered and also present in *E. variegata*, *E. trenquelleonis*, and *E. escoipensis*. This character could represent the first synapomorphy described for the genus. Comparisons of the anatomical data on the three species studied with literature revealed that published information is scarce or misleading and that the genus is poorly defined.

INTRODUCTION

Epiphragmophora Doering, 1874, is a diverse genus of land snails belonging to the American family Xanthonychidae. Although almost 60 described species are recognized in this genus, most of them are based only on shell descriptions. In those species, the anatomy of the different systems is unknown. In any case, the soft parts of the body have traditionally received little attention.

This genus was established by A. Doering (1874), with *E. hieronymi* originally designated as the type species. Pilsbry (1894) applied the name *Epiphragmophora* to a number of North American taxa belonging to the "Belogona Euadenia" defined by having "mucus glands sacculated, club-shaped, bulbous or flattened, glandular, inserted on dart sack or at its base, never on vagina above dart sack (except in *Lysinoe*) pag. xxxvi." The genus, according to Pilsbry (1894), had a distribution from British Columbia southward to Argentina. However, in 1939 he recognized this as a mistake and considered *Epiphragmophora* as an "aberrant genus" restricted only to the southern species. Consequently, *Epiphragmophora* was considered a South American subfamily of Helminthog-

lyptidae, isolated both geographically and structurally from the other genera (Pilsbry, 1939).

In Nordsieck's (1987) revision of the Helicoidea, *Epiphragmophora* continued to be treated as the subfamily Epiphragmophorinae within the Xanthonychidae (of which Helminthoglyptidae is a synonym, according to Baker, 1959). Nevertheless, he stated that the short length of the bursal duct, which was viewed by Pilsbry (1939) as an important character of the subfamily, was not characteristic of all the species and that the subfamily was inadequately defined.

Schileyko (1989) raised the group to the familial rank, although in his short description, there were no precise, consistent characters that could be used to separate it from the other Xanthonychidae.

Information on the anatomy of certain Argentinean species has been provided in several papers (Hesse, 1930; Hylton Scott, 1951, 1962; Fernandez & Rumi, 1984). In general, the anatomical descriptions are brief and restricted to shell, radula, jaw, and genital systems. Some misinterpretation of anatomical characters has also been made. The ultrastructure of the mature spermatozoa in

Epiphragmophora has been described by Giusti et al. (1991) and Cuezco (1994).

The purpose of this work is to redescribe the anatomy of three of the most abundant species of *Epiphragmophora* in northwestern Argentina and to provide new information that could lead toward an adequate understanding and definition of the genus.

MATERIALS AND METHODS

Adult specimens of *Epiphragmophora argentina* (Holmberg, 1909), *E. hieronymi* Doering, 1874, and *E. tucumanensis* (Doering, 1874), were collected from their type localities. Additional material was also collected from other localities for comparative purposes. The type locality of each species is marked with an asterisk. All the material used in this study was collected during summer, the reproductive season of this group of land snails.

Abbreviations: FML, Fundación Miguel Lillo, Tucumán, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Buenos Aires, Argentina

Material examined:

E. hieronymi: FML A100, Argentina, Catamarca, *Quebrada del Tala. Dominguez coll.

E. argentina: FML A114, Argentina, Tucumán, *San Javier, Cuezco coll.; FML A115, Tucumán, El Cadillal, Reserva Aguas Chiquitas, Cuezco coll.; FML A125, San Javier, Tucumán, Cuezco coll.; MACN 577, Puesto Viejo, 70 km S. Jujuy, Castellanos coll.

E. tucumanensis: FML A101; FML A102; FML A112; FML A116; FML A124; Argentina, Tucumán, *Tafi del Valle, "El Indio" 953m up level, Cuezco coll.; FML A123: Tucumán, Concepción, Cochuna, Cuezco coll.

The specimens were drowned in water and fixed in 95% ethanol or in Baker's solution (Humanson, 1979) and later transferred into ethanol 70%. Dissections were carried out under a Wild M3C dissecting microscope and illustrations were made with the aid of a camera lucida.

Following Hoagland & Davis (1987), a primary illustration, in a standard orientation (dorso-lateral position), is presented for each of the character systems as observed within the body. These illustrations are intended to show the natural position of the systems in the body as well as the positional relationship among the organ systems. Subsequent illustrations in each case consist of different organs or portions of each system, illustrated in detail separately to clarify connections among organs and facilitate comparisons of organs among species. The procedure was as follows:

The first drawing (Figure 1) consisted of the animal without the shell. In the following drawing (Figure 2), the lung roof was removed and drawn from a ventral perspective showing the heart, pulmonary veins, and excretory system. The lap of the mantle collar overlapping the

pneumostome was partially cut in order to expose the openings of the rectum and ureters. After cutting its rectal and visceral borders, the internal surface of the kidney was drawn in detail (Figure 3). The diaphragm was then removed and the anterior region of the foot (anterior to the mantle collar) was opened. The animal was drawn again in the standard position (Figure 4) to show the reproductive system and its relationship with the digestive and nervous system. After removing the reproductive system, different portions of it were also drawn in detail (Figures 5–14). Finally, the animal was placed again in the initial position, and the digestive and central nervous systems were drawn (Figure 15). Subsequent drawings were made to show the position of the ventral ganglia of the central nervous system and portions of the digestive system (Figures 15–20). The conjunctive neural sheath was removed to see the degree of association of the ganglia before drawing them. Unless otherwise stated, the following observations apply equally to all three species. No measurements of organs were included due to the modification in size that the soft parts of the body normally suffer when the animal is drawn and fixed. The terminology used in all the anatomical descriptions follows the one proposed by Tompa (1984).

RESULTS

External Features

The external appearance of the body is similar in the three species. *Epiphragmophora tucumanensis* is one of the largest species of the genus. No pedal groove was observed and the foot sole is divided into three longitudinal regions in the three species. In some specimens these divisions are marked only by different coloration of each band, but in other specimens of the same species, two longitudinal grooves are evident. The tail is simple, showing a well-developed mid-dorsal groove without dorsal keels.

In the cephalic region, there is a conspicuous mid-dorsal row of pustules running from the mantle collar to the head. The facial grooves are well marked, especially in *E. tucumanensis* and *E. argentina* (Figure 1).

The coloration of the body is variable in both *E. argentina* and *E. tucumanensis*, ranging from light brown to dark brown. Dark shells seem to be associated with darker bodies, particularly evident in these two species. On the other hand, in *E. hieronymi*, the pale yellow body coloration seems to be constant.

Natural Position of the Systems

For convenience in descriptions, following Tillier (1989), within the general body cavity, the pedal cavity, and visceral cavity will be distinguished and the pulmonary cavity will be dealt with separately.

In fully extended animals the pulmonary system or pal-

lial system (Figure 1) is completely located under the shell in the visceral mass. Its basal portion or lung floor (also called diaphragm) separates the pulmonary cavity from the other systems of the visceral mass. The top of the lung is well marked by the periaortic intestinal loop. The whole system occupies 1.2 to 1.5 whorls.

The reproductive system (Figure 4) extends between the pedal and the visceral cavity, below the lung cavity. The proximal and medial portions of the reproductive system are located in the visceral mass, protected by the shell, while the distal part runs parallel to the longitudinal axis of the head. The entire system is fixed to the body wall through the common genital orifice on the right side of the head (Figure 4) and by the penial retractor muscle to the lung floor. The ovotestis is located in the second whorl of the shell, embedded in the upper lobe of the digestive gland. The terminal genitalia are located above the digestive and central nervous systems. The penis complex spreads on the esophagus toward the parietal side of the esophageal crop (Figure 4), while the spermoviduct runs parallel to the columnar side of the visceral mass. Movements of the penial complex from this characteristic position (parietal side of visceral mass) were observed. In those cases, the flagellum and epiphallus were close to the genital orifice overlapping the penis and vagina. In other cases, the flagellum was observed close to the level of the albumen gland in upper whorls. The lung cavity is located above the spermoviduct being separated by the diaphragm. The albumen gland spreads from the top and above the lung toward the digestive gland. It is appressed along the gastric crop. The duct of the bursa copulatrix runs parallel to the spermoviduct in *E. argentina* and *E. tucumanensis*, the bursal sac being close to the proximal part of the spermoviduct. In *E. hieronymi*, the bursal duct is shorter, running from the vagina to the base of the spermoviduct (Figures 7, 8).

The digestive tract (Figure 15) is partially overlapped by the reproductive tract. The esophagus opens dorsally in the middle of the buccal mass. In these three species of *Epiphragmophora*, the esophagus is posteriorly differentiated into an esophageal crop onto which the salivary glands are appressed. The esophageal crop runs along the parietal side of the body whorl and is continued as the gastric crop. The stomach is located above the top of the lung. The intestine runs ventrally from the gastric pouch, embedded in the digestive gland. After forming the "periaortic bend" and the "perirectal bend" (Tillier, 1989), the intestine continues by the rectum along the suture, parallel to the lung until reaching the mantle collar.

The central nervous system is entirely contained within the pedal cavity, and as in other Stylommatophoran snails, forms a ring generally located around the esophagus.

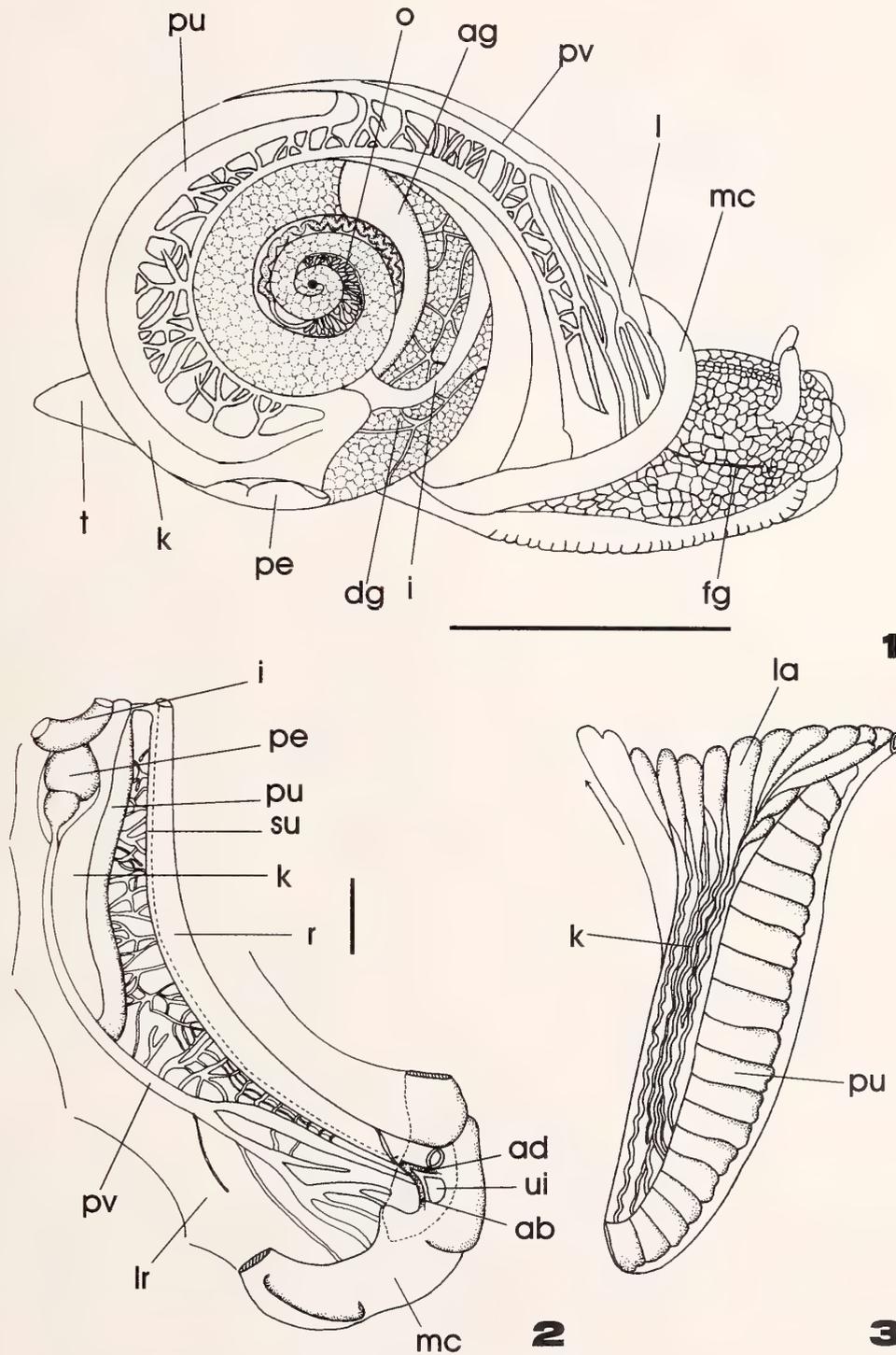
Pallial Complex

A general illustration of the pallial system of *E. argentina* is included (Figure 1). The pallial complex is com-

posed of the lung, kidney, and heart (Figure 1). The lung is long (1–1.5 whorl). In *E. tucumanensis* and *E. argentina*, the lung is mottled with black spots between the pulmonary vein and the secondary ureter. In *E. hieronymi* this pigmentation is absent. The kidney is located in the proximal left side of the lung roof (Figure 2). It is approximately triangular in shape and half the length of the lung in the three species studied. Internally, the kidney presents longitudinal, undulating lamellae that contact one with the other. In the upper zone of the kidney, the lamellae are thicker and deeper (Figure 3). However, there is no differentiation into regions so that the whole internal morphology is homogeneous. The primary ureter runs along the right side of the kidney to the top of the lung cavity and turns down along the rectum, ending in the dorsal part of the pneumostome. This last portion is called the secondary ureter. The inner walls of the primary ureter form thick folds which are mainly of a transverse disposition. Toward the mantle collar, the secondary ureter opens and splits into two grooves, the adrectal and abrectal branches (Figure 2). The adrectal branch continues straight to the mantle collar opening dorsally to the pneumostome. The abrectal branch turns obliquely and exits in a small pore on the mantle collar. The two branches delimit a triangular zone called ureteric interramus that in these three species is deeply and broadly excavated. The pericardium is located in the upper left side of the kidney and is extended toward the pallial ring by the pulmonary venous system. The main pulmonary vein runs parallel to the rectum dividing the lung roof into two portions. The pallial one is bifurcated by a number of minor transverse veins, while the columnar portion of the lung roof is smooth and transparent with few ramifications of the main pulmonary vein (Figure 2). In all three species, the main pulmonary vein splits into two main branches before reaching the mantle collar. Several minor branches separate from the two main ones, each also reaching the mantle collar. No pallial gland is differentiated. The lung floor or diaphragm in *Epiphragmophora* shows conspicuous variations in thickness; in *E. hieronymi* and *E. argentina*, the diaphragm is thin, translucent and membranous; in *E. tucumanensis* it is thick, muscular, and opaque. In this last species there is also a characteristic pattern of the muscular fibers; there is a wide central rib of longitudinal muscular fibers from which transversal fibers extend toward the edges of the lung floor.

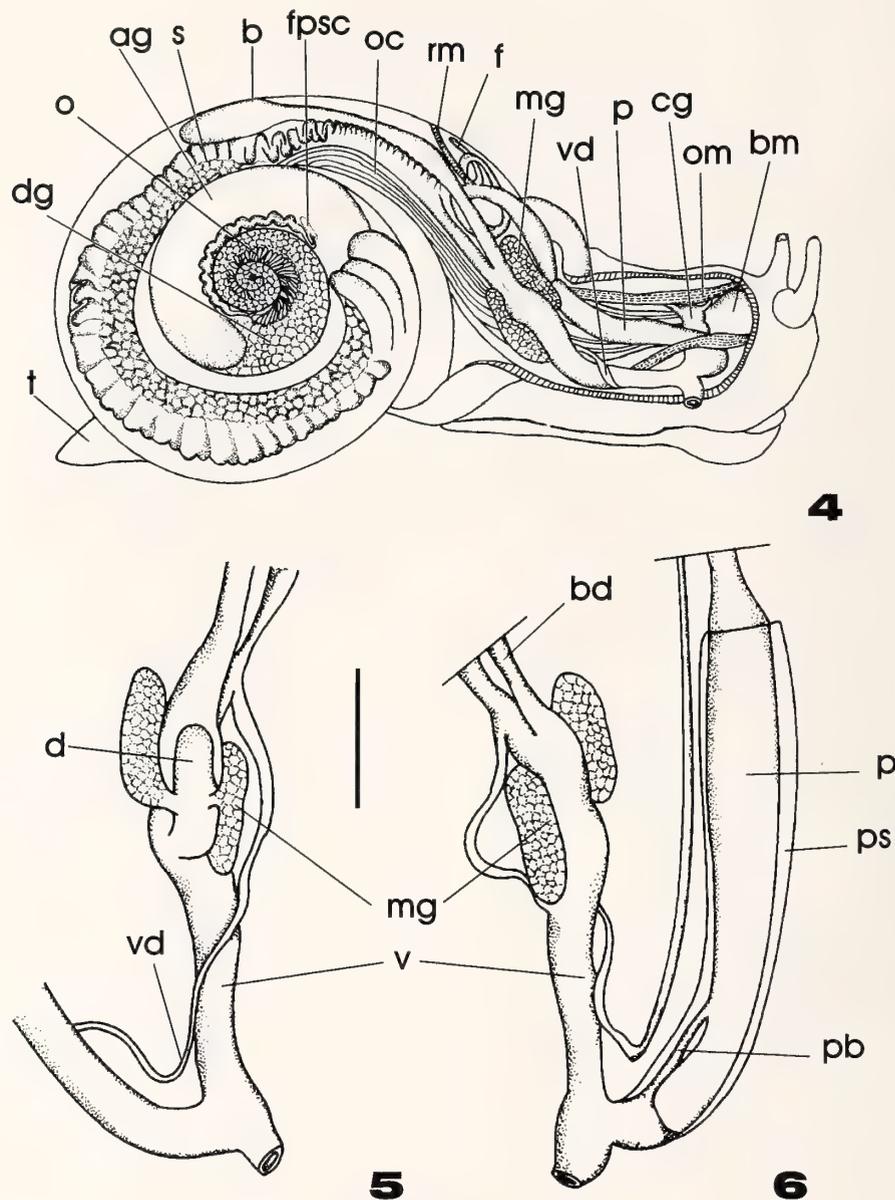
Reproductive System

Proximal genitalia: (Figure 4): The ovotestis is composed of multiple acini bearing dark points of pigmentation on the blind extreme. The hermaphroditic duct runs along the columellar side, being overlapped by the columellar retractor, the central portion of which is swollen, forming the vesicula seminalis. The fertilization pouch-spermathecal complex (FPSC) is a thin blind sac com-



Explanation of Figures 1, 2, 3

Epiphragmophora argentina. Figure 1. Natural position of the pallial system. Shell removed; scale bar = 12 mm. Figure 2. Ventral view of the lung roof to show position of the pericardium in relation to kidney and rectum; scale bar = 5 mm. 3. Detail of internal structure of kidney and primary ureter. Abbreviations: ab, abrectal branch of the ureter; ad, adrectal branch of the ureter; ag, albumen gland; dg, digestive gland; I, intestine; fg, fascial groove; k, kidney; l, lung; la, lamellae; lr, lung roof; mc, mantle collar; o, ovotestis; pe, pericardium; pu, primary ureter; pv, pulmonary vein; r, rectum; su, secondary ureter; t, tail; ui, ureteric interramus.



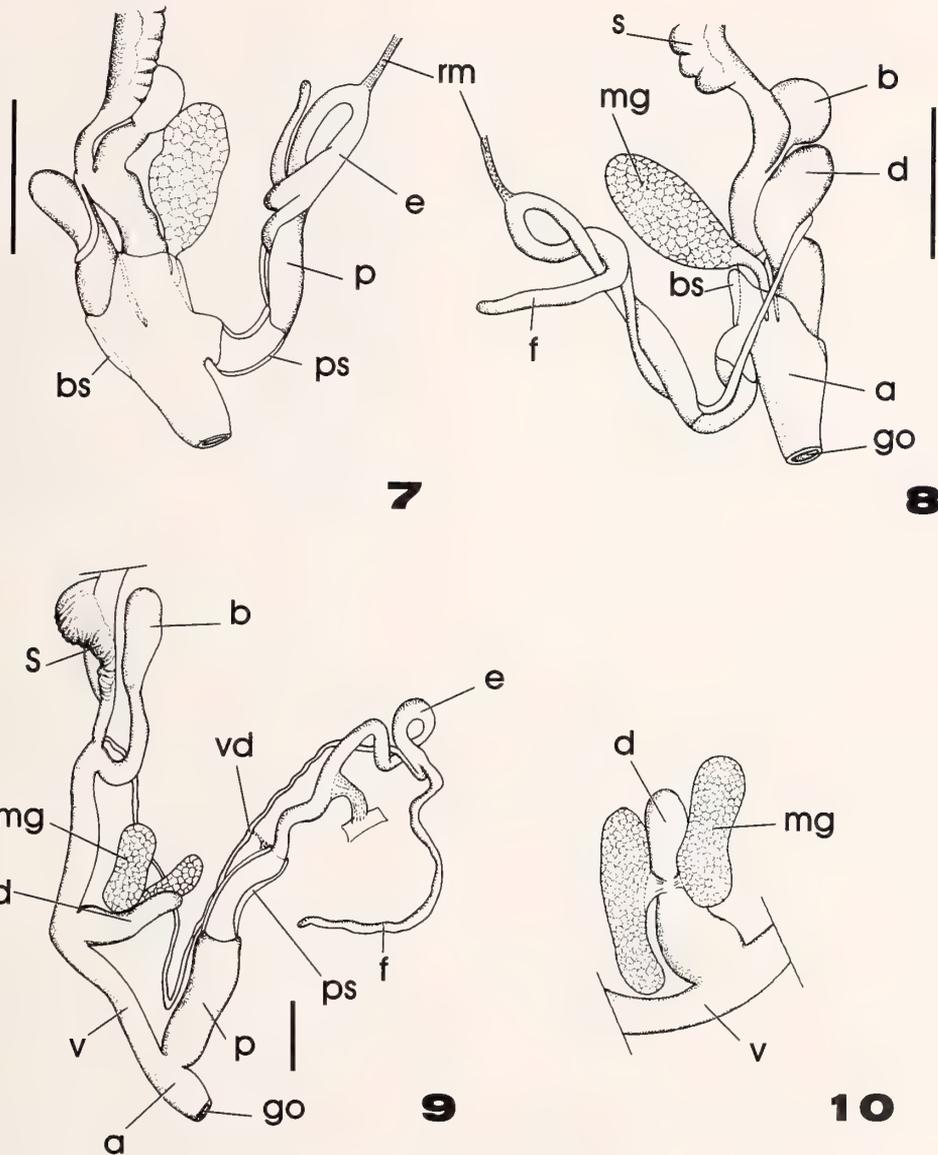
Explanation of Figures 4, 5, 6

Epiphragmophora argentina. Figure 4. Natural position of reproductive system in the pedal and visceral cavity. Figure 5. Ventral view of terminal genitalia. Note the position of the dart sac; scale bar = 5 mm. Figure 6. Dorsal view of terminal genitalia; scale bar = 5 mm. Abbreviations: ag, albumen gland; b, bursa copulatrix; bd, bursa copulatrix duct; bm, buccal mass; cg, cerebral ganglia; d, dart sac; dg, digestive gland; f, flagellum; fp, fertilization pouch-spermathecal complex; mg, mucous glands; o, ovotestis; oc, esophageal crop; om, ocular retractor muscle; p, penis; pb, penial band; ps, penis sheath; rm, penial retractor muscle; s, spermoviduct; t, tail; v, vagina; vd, vas deferens.

pletely included in the albumen gland so that it appears to be absent. The interior of this blind sac will probably reveal more than one tubule, but without the aid of histological techniques, more details were not observed. The spermoviduct is a long and convoluted tubular organ that

shows great size changes between summer and winter. Distally, the spermoviduct splits into a vas deferens and a free oviduct.

Terminal genitalia: The terminal genitalia comprise the



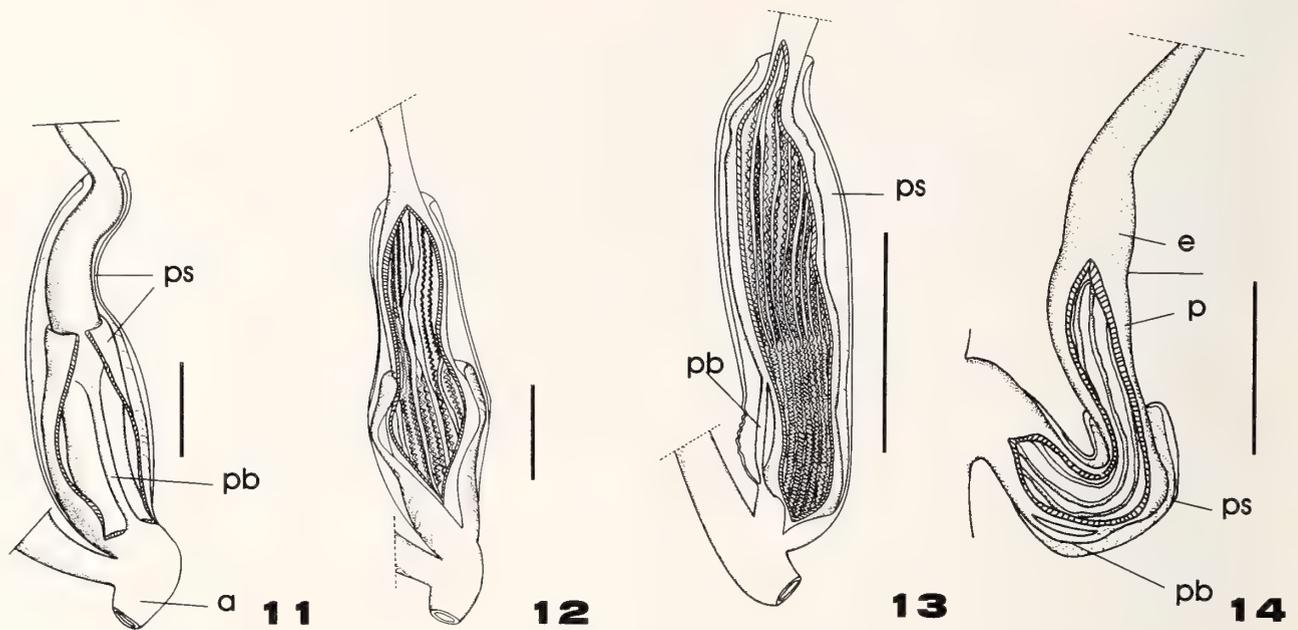
Explanation of Figures 7 to 10

Figures 7, 8: *Epiphragmophora hieronymi*. Figures 9, 10: *Epiphragmophora tucumanensis*. Figure 7. Dorsal view of terminal genitalia; scale bar = 4 mm. Figure 8. Ventral view of terminal genitalia. Note the point of insertion of the mucous gland's duct; scale bar = 4 mm. Figure 9. Dorsal view of terminal genitalia; scale bar = 5 mm. Figure 10. Detail of the mucous glands and dart complex. Note the position of the ducts inserting into the dart sac. Abbreviations: a, atrium; b, bursa copulatrix; bs, basal genitalia sheath; d, dart sac; e, epiphallus; f, flagellum; go, genital orifice; mg, mucous glands; p, penis; ps, penial sheath; rm, retractor muscle; s, spermooviduct; v, vagina; vd, vas deferens.

vagina, bursa copulatrix, vas deferens, penial complex, and atrium, as illustrated in Figure 4.

In *E. hieronymi* (Figures 7, 8), the vagina is $\frac{2}{3}$ of the penis length and is basally enveloped by a muscular sheath. The bursa copulatrix has a round sac and a short wide duct without diverticulum. It is longer than the mucous gland, reaching the terminal portion of the sper-

moviduct. The vas deferens is a straight tube that after looping around the middle part of the dart sac, adheres to the terminal genitalia by connective tissue (Figure 8, ventral view). A muscular dart sac with a constriction in its middle part is present; it is shorter than the mucous gland and opens in the atrium (Figure 7, dorsal view). A single club-shaped mucous gland is located between



Explanation of Figures 11 to 14

Figures 11, 12: *Epiphragmophora tucumanensis*. Figure 13: *E. argentina*. Figure 14: *E. hieronymi*. Figure 11. External morphology of the penis after cutting the double penis sheath. Note the position of the penial band; scale bar = 5 mm. Figure 12. Internal morphology of the penis after cutting penis sheath and penis wall; scale bar = 5 mm. Figure 13. Internal morphology of penis after cutting penis sheath. Note the position of the penis band in this species; scale bar = 6 mm. Figure 14. Internal morphology of penis after cutting penis sheath and wall; scale bar = 2 mm. Abbreviations: a, atrium; e, epiphallus; p, penis; pb, penial band.

the dart sac and the vagina. Internally (Figure 8, ventral view), the thin mucous gland duct opens at the base of the dart sac, at the junction between the dart sac and the atrium. This connection is externally overlapped by the muscular sheath that surrounds the basal part of the terminal genitalia (vagina, dart sac, mucous gland duct, penial complex, and atrium). The muscular sheath is fused basally with the atrium and loose in the upper portion, overlapping the basal part of the terminal genitalia. The penis is shorter than the epiphallus, making a basal loop (Figure 14) around the right ocular retractor. The penis has a basal muscular ring continued by a thin membranous penis sheath that covers $\frac{2}{3}$ of the length of the penis. From the basal muscular ring there is a short penial muscular band. This muscular band ends by inserting on the penis (Figure 14). Internally, the penis has five to six thin, longitudinal folds which are more conspicuous at the base. No verge is present, and the penial pore is terminal. The penial retractor inserts in the middle part of the epiphallus and in the lung floor. The epiphallus decreases in diameter to form the flagellum, which is half the length of the epiphallus. The atrium is long but does not form an atrial sac. Internally, the atrium presents short, thick, and smooth longitudinal folds along its internal wall.

In *E. argentina* (Figures 5, 6), the vagina is much longer than in *E. hieronymi*, being as much as half the length of the penis. The bursa copulatrix has a long, cylindrical, convoluted duct parallel to the last $\frac{1}{3}$ of the distal portion of the spermooviduct (Figure 4). No diverticulum is present. The bursal sac is ovoid. The vas deferens is long, straight, and attached to the vagina-penis angle by connective tissue. The diameter of the vas deferens is constant along its entire length. In this species, the vas deferens does not loop around the dart sac. The dart sac is cylindrical, muscular, shorter than in *E. hieronymi*, and seated on the vagina (Figure 5, ventral view). There are two mucous glands, equal in length and symmetrically located one on either side of the dart sac. The duct of one gland is basal while the other is medial to apical. As a consequence, the body of the first gland is directed toward the proximal genitalia, whereas the body of the second is directed toward the terminal part (Figures 5, 6). Both ducts are connected to the middle part of the dart sac. There is no muscular sheath overlapping the basal part of the terminal genitalia as in *E. hieronymi*.

The penis (Figure 6) is long, slender, and cylindrical in shape without making the basal loop observed in *E. hieronymi*. The penial pore is located at the apex of the

penis (terminal). The verge is absent. Internally, the upper half presents five to seven columns, radiating from the penial pore. The basal half of the penis has closer columns in a zig-zag pattern (Figure 13). The penial sheath encloses the entire penis. Basally, the penial sheath is muscular, forming a ring; distally, it is thin and transparent. The penial muscular band described in *E. hieronymi* is also present in *E. argentina*, but is thicker, being as long as $\frac{1}{4}$ of the penis length. It runs from the muscular basal ring and inserts apically in the penis wall (Figure 6, dorsal view). Apically, the penis sheath is attached to the vas deferens by connective tissue. There are also muscular strands attaching the upper part of the penis sheath to the vas deferens and epiphallus (retentor muscle). The penial retractor muscle is inserted in the middle part of the epiphallus and connected to the lung floor. The epiphallus is as long as the penis, with internal longitudinal folds. The flagellum is long and convoluted. The right ocular retractor passes through the penis-vagina angle. The atrium is well developed, with longitudinal smooth and deep ridges along its interior.

In *E. tucumanensis* (Figures 9, 10), the vagina is longer than the penis. The bursa copulatrix duct is cylindrical, shorter than in *E. argentina* and is half as long as the vagina. No diverticulum is present. The bursal sac is ovoid. The vas deferens is long and attached to the penis-vagina angle by connective tissue. A blind, muscular dart sac is present, seated in the middle part of the vagina (Figure 10). It is swollen at the base, decreasing in diameter toward the upper part. There are two mucous glands unequal in size. The smaller shows a basal thin duct, while the larger has the duct located close to the middle part of the gland. Both gland ducts end in the middle zone of the dart sac (Figure 10). No muscular sheath overlaps the basal part of the terminal genitalia as in *E. hieronymi*. The penis is enveloped by a double sheath; the inner one is thick and muscular, enclosing half of the penis (Figure 11). The penial muscular band is located under the muscular sheath and is as long as $\frac{3}{4}$ the length of the muscular sheath (Figure 11). The internal sculpture of the penis consists of a basal portion with smooth ridges intercalated with others in a zig-zag pattern. In the upper portion of the penis there are two central deep ridges and parallel to them zig-zag folds (Figure 12). The basal part of the penis forms a loop that surrounds the right ocular retractor. The verge is absent. The penial pore is terminal. The epiphallus is as long as the penis. The penial retractor muscle is thick and inserts in the middle of the epiphallus. The flagellum is thin and as long as the epiphallus. There is a short atrium with thin longitudinal folds in the interior.

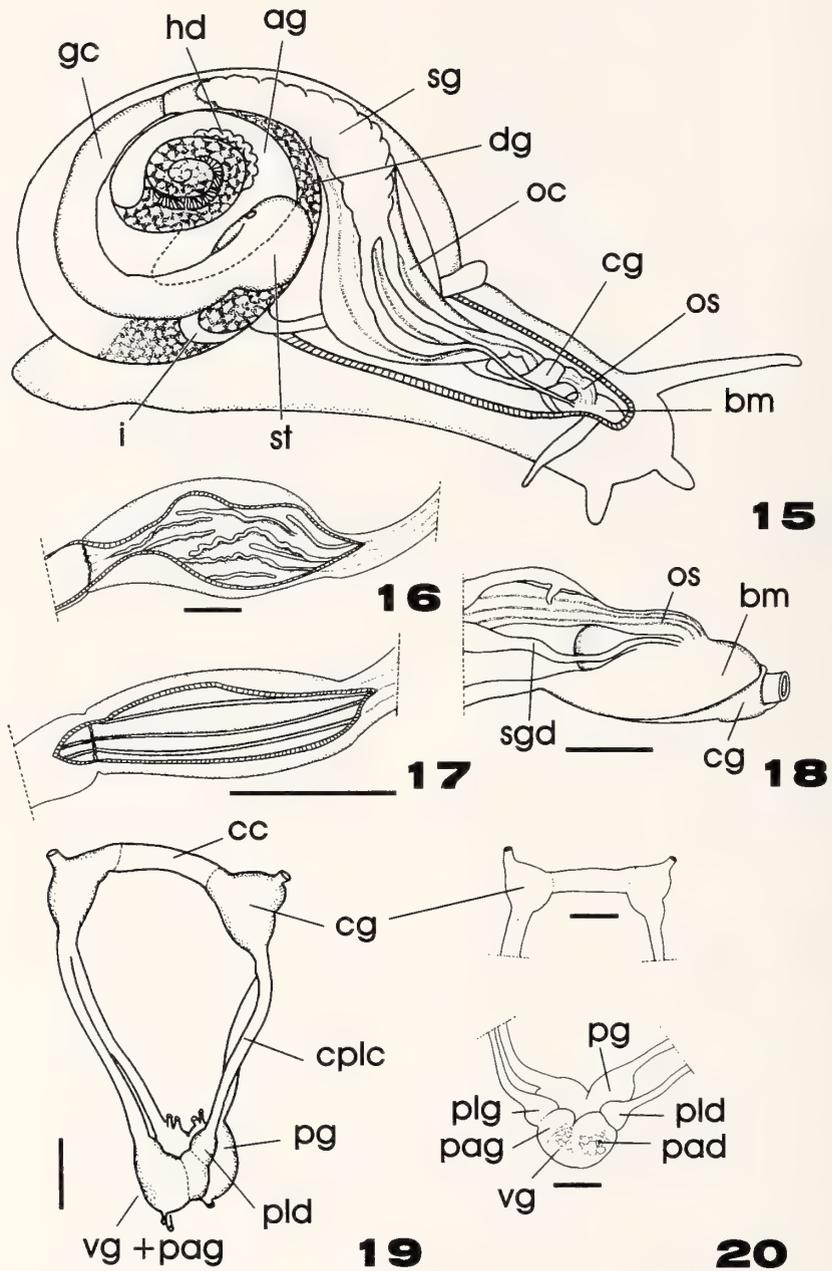
Digestive System

The arrangement of the digestive tract (Figure 15) follows the general patterns described for Stylommatophora (Tillier, 1984, 1989).

The jaw and radula are as described by Fernandez & Rumi (1984). The buccal mass is muscular, spheroidal to ovoid. The posterior portion behind the esophageal opening forms a small protuberance in relation to the size of the buccal mass (Figures 15, 18). The esophagus opens dorsally from the buccal mass and progressively increases in diameter, forming an esophageal crop. The internal morphology of the esophagus consists of longitudinal thin ridges widely separated at the level of the esophageal crop (especially in *E. hieronymi*) (Figures 16, 17). There are two long salivary glands spreading appressed to the esophageal crop with their main ducts ending on each side of the esophageal opening. At half the length of the esophageal crop, the glandular bodies join together. The esophageal crop is separated from the gastric crop by a transverse constriction internally marked by a wrinkled ridge (Figures 16, 17). The gastric crop is cylindrical and internally shows two ventral longitudinal ridges that delimit a groove. This is particularly marked in *E. tucumanensis*. The sculpture of the rest of the internal surface of the gastric crop consists of columns of very small pustules. Another transverse constriction separates the gastric crop from the stomach, which is located in the parietal side of the fourth whorl. The stomach is the portion of the digestive system that receives the posterior and anterior ducts of the digestive gland (Figure 15). The ventral groove of the gastric crop reaches the anterior duct opening of the digestive gland located in the stomach between the gastric crop and the proximal portion of the intestine. There is a short typhlosole running from the anterior duct opening to the proximal portion of the intestine. Another longer typhlosole runs from the posterior duct opening of the digestive gland, reaching the periaortic intestinal loop. The second, longer typhlosole is much deeper and more conspicuously marked than the first one. The intestine runs along the columellar side of the visceral mass turning down under the anterior portion of the gastric crop and then around the aorta (periaortic intestinal loop). The intestine is followed by the rectum, which runs parallel to the pulmonary cavity and ends through the anus into the mantle collar.

Central Nervous System

The central nervous system is entirely contained in the pedal cavity. It is composed of two dorsal ganglia and a ventral chain. Both ganglia are connected by a short cerebral commissure and typically located above the buccal mass at the point where the esophagus begins. This was different in several specimens of *E. hieronymi* where either a forward position on the proximal portion of the buccal mass (Figure 18) or a backward position on the proximal portion of the esophagus was observed (Figure 15), differences probably due to retraction of the buccal mass during fixation. The cerebro-pleural connectives run obliquely backward, connecting the dorsal ganglia to the



Explanation of Figures 15 to 20

Figures 15, 16, 20: *Epiphragmophora argentina*. Figures 17, 18, 19: *E. hieronymi*. Figure 15. Natural position of digestive and nervous systems. Shell and portion of the reproductive tract had been removed. Figure 16. Internal structure of the esophageal crop; scale bar = 5 mm. Figure 17. Internal structure of the esophageal crop; scale bar = 5 mm. Figure 18. Position of the central nervous system with respect to buccal mass; scale bar = 2.5 mm. Figure 19. General morphology of central nervous system. Note the fusion of the visceral ganglion with the left parietal ganglion; scale bar = 1 mm. Figure 20. General morphology of central nervous system. The visceral ganglion is not fused with the left parietal ganglion; scale bar = 1 mm. Abbreviations: ag, albumen gland; bm, buccal mass; cc, cerebral commissure; cg, cerebral ganglia; cplc, cerebro-pleural connective; dg, digestive gland; hd, hermaphroditic duct; i, intestine; gc, gastric crop; oc, esophageal crop; os, esophagus; pad, right parietal ganglion; pag, left parietal ganglion; pg, pedal ganglia; pld, right pleural ganglion; plg, left pleural ganglion; sg, salivary gland; sgd, salivary gland duct; st, stomach; vg, visceral ganglion.

Table 1
Summary of the most important characters in the three species treated.

Characters	<i>E. hieronymi</i>	<i>E. argentina</i>	<i>E. tucumanensis</i>
Sac of bursa copulatrix	round	ovoid	ovoid
Duct of bursa copulatrix	short, half the length of vagina	large, as long as vagina	large, half the length of vagina
Vagina	2/3 penis length	long, as long as the penis	longer than the penis
Muscular sheath over terminal genitalia	present	absent	absent
Vas deferens	looping around dart sac	does not surround dart sac	does not surround dart sac
Dart sac	with constriction in the middle	without constriction	without constriction
Mucous gland	one, open in the base of the dart sac	two, both open in middle zone of dart sac	two, both open in middle zone of dart sac
Atrium	long	long	short
Penial muscular band	short, 1/3 penis length	short, 1/4 penis length	long, 1/2 penis length
Penis	5-6 longitudinal, straight ridges along penis length	upper portion with 5-6 ridges and basal portion ridges in zig-zag	upper portion with two central ridges and basal portion ridges in zig-zag
Penial sheath	thin, membranous, enclosing 2/3 of the penis	thin, transparent, enclosing entire penis	double, inner thick, muscular, enclosing half of the penis. Outer thin, membranous
Flagellum	short, half of the epiphallus length	long and convoluted	long and convoluted, as long as the epiphallus
Diaphragm	thin, membranous	semithin, with some muscular strands	thick, muscular
Esophageal crop sculpture	thin, shallow, longitudinal ridges, rest of the wall smooth	thick, deep, longitudinal ridges, rest of the wall with pustules	thick, deep, longitudinal ridges, rest of the wall with pustules
Left parietal ganglion in relation with visceral ganglion	fused	in contact	in contact

ventral chain (Figure 15). This connection completes the ring around the digestive tract. The length of the cerebropleural connectives varied between specimens. However, the length of the cerebral commissure was constant (1.5 mm) regardless of the variability in the length of the cerebropleural commissure. The ventral chain is composed of the right and left pleurals, right and left parietals, and a visceral ganglion. Anterior to them two pedal ganglia are present. The visceral ganglion is positioned to the left of the median plane of the pedal ganglia. In *E. argentina* and *E. tucumanensis* the left parietal ganglion is in close contact with both the left pleural and visceral ganglion (Figure 20). In some specimens the visceral ganglion is very close to the left parietal giving the appearance of being fused. However, after pulling apart the ganglia, the separation of these ganglia is evident. The pedal ganglia are almost round and well separated. In *E. hieronymi*, however, a different disposition was found. The left parietal ganglion is fused with the visceral ganglion and in contact with the left pleural ganglion (Figure 19).

DISCUSSION

A comparison of the anatomical observations reported here on *Epiphragmophora hieronymi*, *E. tucumanensis*, and *E. argentina* (see Table 1 for summary) with published information reveals that the latter is scarce or misleading and that the genus is poorly defined. In fact, due

to the small number of species anatomically studied in detail, no single synapomorphy defining the genus *Epiphragmophora* or even the subfamily Epiphragmophorinae is evident at this time.

Although all the systems of the body were examined in this study (with the exception of the shell, radula, and muscle system), the genital system seems to offer more characters with phylogenetic potential than any other system.

In *E. hieronymi*, the type species of the genus, a muscular sheath overlapping the terminal genitalia was observed. This muscular sheath is not as well developed as that present in *Cepolis* Montfort, but both seem to be homologous because they are located in the same position, overlapping the terminal genitalia. This sheath, however, was not observed in *E. argentina* or in *E. tucumanensis*; in the latter species, a double penis sheath was found.

Another important character found is a single mucous gland present in *E. hieronymi* opening in the base of the dart sac, in disagreement with the observations made by Fernandez & Rumi (1984), who described a second mucous gland called "anexo I." The terms "appendix or anexo" in the published literature (Hylton Scott, 1951; Fernandez & Rumi, 1984) are used to designate either the mucous glands or dart sac, while the insertion of these structures are not clear in the figures.

The dart sac in the three species is a blind, muscular sac seated on the vagina in *E. tucumanensis* and *E. argentina* and on the atrium in *E. hieronymi*. In the latter species, a medial constriction is present. Also, in this species, the vas deferens makes a loop around the dart sac, a position not described previously for any other xanthonychid. All these differences between *E. hieronymi* and *E. tucumanensis*-*E. argentina* (Table 1) support the idea that subgroups could be established in the future after a phylogeny of the genus is proposed.

In *Epiphragmophora* a penial muscular band is present in all three species examined. The typical position of this penial muscular band is running from the muscular ring at the base of the penis to attach in the middle zone of the penis, concealed by the penis sheath. Through new dissections it was found that this new character is also present in other species of *Epiphragmophora*, eg., *E. tranquelleonis* (Gratoloup, 1851). *E. variegata* Hylton Scott, 1962, and *E. escoipensis* Cuezco, in press. In no other xanthonychid has this kind of penial band been described before. Although more studies are needed for both other species of the genus and other genera of Xanthonychidae, this type of retentor muscle could represent a synapomorphy for the genus *Epiphragmophora*.

The internal penial anatomy, a character presumably important in species recognition (Emberton, 1988), had never been examined before in *Epiphragmophora*. Again, differences between *E. hieronymi* and *E. argentina*-*E. tucumanensis* are noted. While in the first species it is not possible to recognize two internal regions, in the other two species the sculpture is clearly different in the upper and lower regions of the penis.

The diaphragm or lung floor is extremely thick and muscular in *E. tucumanensis*, this thickness remaining constant even in specimens of different sizes. In *E. argentina* the diaphragm is thinner but muscular, and in *E. hieronymi* it is thin and transparent.

In the digestive system the only difference that could be found between the species was the internal sculpture of the esophageal crop, which in *E. argentina* and *E. tucumanensis* consists of deep, longitudinal ridges intercalated with shallow pustules. In *E. hieronymi* the ridges are few, shallow, and the rest of the wall is smooth.

In the central nervous system, the length of the cerebral connectives was constant in each of the three species studied. The length of the cerebro-pedal connectives showed significant variation among the specimens dissected. For this reason, the length of the connectives should not be considered as good characters with phylogenetic potential in disagreement with Tillier (1989). The variations in length registered are the probable consequence of artifacts of fixation or preservation as stated by Emberton (1989) and Emberton & Tillier (1995). Nevertheless, the study of the pattern of fusion of the ganglia of the visceral chain of pulmonates provides valuable information for determining the direction of evolution in

particular lineages as stated by Bishop (1978). In the species of *Epiphragmophora* examined, two patterns of association between the left parietal and the visceral ganglion were observed. While in *E. hieronymi* both are fused, in the two other species the two ganglia are separate, although in contact. Emberton (1991) has mentioned differences in the type of association of these two ganglia of the visceral chain in two species of *Bradybana*.

In conclusion: (A) *E. hieronymi*, the type species of the genus, differs anatomically from *E. tucumanensis* and *E. argentina* in having (1) a muscular sheath overlapping the terminal genitalia, (2) shorter vagina, (3) single mucous gland opening at the base of the dart sac, (4) short bursa copulatrix duct, (5) dart sac with a constriction in the middle zone, (6) same internal penial sculpture along the entire penis length, (7) short flagellum, (8) thinner diaphragm, (9) esophageal crop sculpture consisting of thin longitudinal ridges, (10) left parietal ganglion fused with visceral ganglion and (11) smaller body size; (B) *E. tucumanensis* differs anatomically from *E. argentina* in: (1) length of the bursa copulatrix duct, (2) length of the vagina, (3) having mucous glands unequal in size, (4) length of the atrium, (5) having longer and thicker penial muscular band, (6) internal penial sculpture, (7) having a double penial sheath, (8) having a thicker, muscular diaphragm, and (9) presenting larger body size; (C) the presence of a penial muscular band is described and proposed as a possible synapomorphy for the genus.

Accurate descriptions of the anatomy of additional species of *Epiphragmophora* are necessary before a good understanding of the genus can be reached. Steps following the descriptions should include the construction of a phylogeny with strict methodology (Hennig, 1966; Farris, 1983) to clarify the relationship of *Epiphragmophora* with the rest of the Xanthonychidae.

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On the Morphology of the Magellanic Nudibranch *Anisodoris fontaini* (d'Orbigny, 1837) and Its Synonymy with *A. tessellata* Bergh, 1898

by

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Abstract. The poorly known nudibranch species *Anisodoris fontaini* (d'Orbigny, 1837) has been redescribed based on material collected in Chile and Argentina using SCUBA. Museum material of *A. fontaini* det. Odhner, 1926, has been re-examined. Since *A. fontaini* shows no morphological differences from *Anisodoris tessellata* Bergh, 1898, the latter is considered to be a junior synonym. The specimens described under the name *Neodoris carvi* by Muniaín et al. (1991) are shown to belong to *Anisodoris fontaini*; the synonymy of *Neodoris carvi* Marcus, 1959, and *Neodoris erinacea* Marcus, 1959, proposed by the same author, requires further confirmation.

INTRODUCTION

Within the genus *Anisodoris* Bergh, 1898, there are only two known species possessing triangular oral tentacles, *A. fontaini* (d'Orbigny, 1837) and *A. tessellata* Bergh, 1898 (Millen, 1982).

One specimen of *A. fontaini* was reported from Valparaíso, Chile, and externally described by d'Orbigny (1835–1846). Later, Odhner (1926) anatomically examined additional specimens of *A. fontaini* from Melinka, Chile, and from northern Argentina. Bergh (1898) established *A. tessellata* without any discussion and based on a single specimen found in the Bay of Molles, Chile, by L. Plate. Marcus (1959) thoroughly redescribed this species based on preserved material from Chiloé Island and Tumbes, Chile, collected during the Lund University Chile Expedition (1948–1949). Both species are very similar externally and internally, and the main differences were the apparent absence of spicules in the notum and longitudinal grooves in the oral tentacles of *A. fontaini*, according to Odhner (1926), whereas *A. tessellata* was known to possess spicules and grooved tentacles (Marcus, 1959).

In this study, *A. fontaini* is redescribed examining newly collected as well as museum material. Its taxonomy and geographic distribution are discussed.

MATERIALS AND METHODS

During 1991–1995, specimens of *A. fontaini* were collected in several localities of the Chilean and Argentinian coast

in 0–20 m depth using SCUBA (Table 1; Figure 1). Eighty-seven specimens were described in living condition; five of them were examined anatomically. Voucher specimens have been deposited in the Zoologische Staatssammlung München (Nos. 1901, 1902) and in the Swedish Museum of Natural History (SMNH, Nos. 1565, 1566). Six specimens of *A. fontaini* det. Odhner, 1926, from northern Argentina (SMNH, No. 576), three specimens of *A. fontaini* det. Odhner, 1926 (SMNH, No. 874) from Melinka, Chile, and one specimen of *A. fontaini* det. Muniaín, 1993, from Pta. Pardelas, Argentina were re-examined.

RESULTS

External Morphology

Living specimens reach 118 mm in length and 65 mm in breadth. The highly arched notum is covered by different-sized, rounded tubercles (Figure 2), the largest of which reach a diameter and a height of up to 5 mm. Large tubercles may be fused with others. Toward the border of the notum the tubercles become smaller. The tubercles of all recently collected specimens contain spicules, whereas spicules are absent in the preserved material of *A. fontaini* studied by Odhner (1926).

Living specimens from Chile are yellow, yellowish orange, or brownish (for color photograph see Schrödl, 1996). There is a network of more or less dark brown pigment between the tubercles. Large tubercles can have dark centers. Most, but not all of the Argentinian specimens are

Table 1
Known records of *A. fontaini*

Species	Locality
<i>A. fontaini</i> (d'Orbigny, 1837)	Near Valparaíso, Chile
<i>A. tessellata</i> Bergh, 1898	Bay of Molles, Chile
<i>A. fontaini</i> det. Odhner, 1926	North of Argentina (37°50'S, 56°11'W)
<i>A. tessellata</i> det. Marcus, 1959	Melinka, Guaitecas Islands, Chile
	5 stations north and east of Chiloé Island, Chile (41°30'06"S, 72°53'57"W; 41°43'00"S, 73°03'15"W; 41°51'57"S, 73°54'00"W; 41°50'10"S, 73°51'20"W; 41°49'24"S, 73°48'58"W)
	Montemar, Valparaíso (32°57'24"S, 71°33'25"W)
<i>Neodoris carvi</i> det. Muniaín et al., 1991	Pta. Gusano, Beagle Channal (54°55'22"S, 67°36'30"W)
	Pta. Maqueda (46°01'18"S, 67°34'43"W)
	Pta. Pardelas, Valdez (42°37'44"S, 64°16'00"W)
	Pta. Gales, Valdez (42°24'47"S, 64°32'16"W)
<i>A. fontaini</i> det. Schrödl, 1995 (see Schrödl, 1997)	Los Hornos (29°38'S, 71°29'W)
	Bahía de Coliumo (36°32'S, 72°57'W)
<i>A. fontaini</i> (this paper)	Queule (39°23'S, 73°13'W)
	Pta. Maqueda, near Comodora Rivadavia (46°02'S, 67°35'W)
	Pta. Pardelas, Valdez (42°38'S, 64°16'W)



Figure 2

Photograph of a living, 55 mm long specimen of *A. fontaini* from the Bahía de Coliumo.

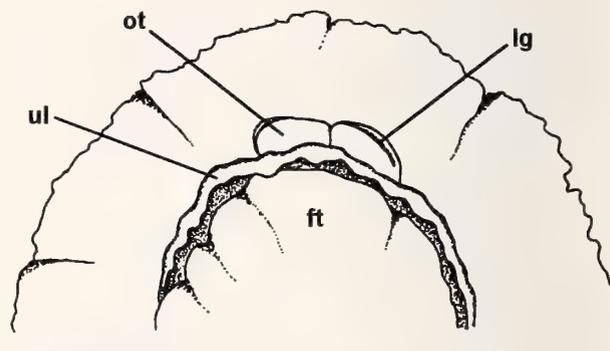


Figure 3

Preserved *A. fontaini* in frontal view (drawing from a photograph). Scale bar = 1 cm. Key: ft, foot; lg, longitudinal groove; ot, oral tentacle; ul, upper lip.

Table 2
List of specimens dissected

No. of specimens	Location and coordinates	Living color	Body size (preserved);		Radula dimensions, length × breadth (mm)	Radula formula
			l length, b breadth (mm)	length × breadth (mm)		
1	Pta. Pardelas	yellow, some dark pigmentation between tubercles	1 27, b 24	5 × 4.5	35 × 68.0.68	
2	Pta. Pardelas	yellow	1 30, b 35	6.2 × 5.7	36 × 74.0.74	
3	Comodora Rivadavia	yellow	1 34, b 24	5.8 × 5.4	39 × 69.0.69	
4	Queule	dark yellow with brown net between tubercles	1 34, b 22	5.9 × 5.6	35 × 63.0.63	
5	Bahía de Coliumo	yellowish orange with brown net between tubercles	1 47, b 30	6.3 × 5.8	37 × 70.0.70	



Figure 4

Radular morphology of *A. fontaini*. Inner lateral teeth of specimen No. 1. Scale bar = 0.2 mm.

bright yellow; the network of dark pigmentation is reduced or absent, and large tubercles may have yellowish centers. In preserved specimens, the coloration is lost, and the tubercles may become much flatter. There are five to seven large tri- to quadripinnate gills, which extended, reach a diameter of 45 mm in the largest specimen. The olive or dark yellow rhinophores possess up to about 30 lamellae and are surrounded by elevated sheaths covered with small tubercles. The head bears triangular, grooved oral tentacles (Figure 3). Tentacle grooves are also detectable in seven of the nine re-examined specimens of *A. fontaini det.* Odhner, 1926. In two of Odhner's specimens, the mouthparts are too contracted to allow a statement about the presence of grooved tentacles. The dark yellow to orange-colored foot is broad and anteriorly bilabiate, but not notched in living specimens. In some preserved specimens, the superior lip appears to be notched due to contraction.

Digestive Tract

The lip cuticle is smooth. The radulae consist of 35–39 rows with 63 to 74 simply hooked teeth per half row (Table 2; Figure 4). The width of the toothless rhachis varies between individuals; it may be rather broad or hardly detectable. The innermost laterals are small and have a rounded shape. Toward the middle of the half rows the teeth increase in size and become straighter and more slender, reaching 0.3 mm in height. The outermost teeth are reduced to small hooks. The salivary glands are long ribbons with a granular appearance. The large stomach has an oval shape and covers the anterior left portion of the digestive glands. Ventrally, left of the esophagus entrance, the stomach bears a short, bulbous caecum, which is covered by the stomach in dorsal view. The intestine leaves the stomach anteriorly and goes posteriorly on the surface of the digestive gland as a straight and thin tube.

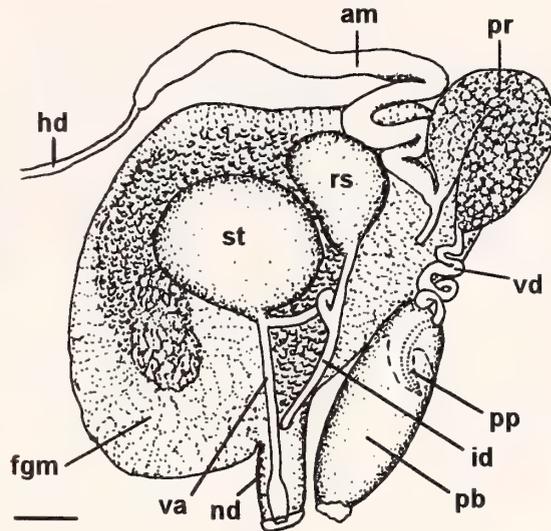


Figure 5

Reproductive system of *A. fontaini* (specimen No. 3). Scale bar = 2 mm. Key: am, ampulla; fgm, female gland mass; hd, hermaphroditic duct; id, insemination duct; nd, nidamental duct; pb, penial bulb; pp, penial papilla; pr, prostate; rs, receptaculum seminis; st, spermatheca; va, vagina; vd, vas deferens.

Reproductive System

The position and shape of the genital organs of all specimens examined are similar to each other, but their dimensions vary individually and due to maturity. The female organs of the small specimens No. 1 and No. 4 were not fully developed. A drawing of the genital system of specimen No. 3 is given in Figure 5. The curved and flattened hermaphroditic ampulla divides into a short oviduct and a short sperm duct leading into the prostate. This is a massive, somewhat U-shaped organ which has a granular appearance. Distally, the prostate passes more or less gradually into the short and convoluted vas deferens, which enters the male atrium as a large, muscular penial papilla.

The vagina is a long and thin duct leading into the spherical spermatheca. Where the vagina enters the spermatheca the fertilization duct emerges. After some curving, it divides into the stalk of the oval to pear-shaped receptaculum seminis and the insemination duct, which enters the female gland mass near the insertion of the nidamental duct. This wide duct opens separately below the female opening.

Other Organs

The blood gland consists of two flatish lobes; one lying anterior and one posterior above the central nervous system. The cerebral and pleural ganglia are completely fused, the eyes nestling directly on the cerebral ganglia.

Ecology

This species has been found to be abundant in some localities of the Chilean and Argentinian shallow subtidal, mainly on vertical rocks covered with yellowish encrusting demosponges. Specimens are present year-round in the Bahía de Coliumo, central Chile. In January, spawning occurred in the laboratory. The spawn of a 115 mm long specimen are six spirals from a 15 mm broad ribbon, and have a diameter of 7 cm. The translucent egg capsules are rounded to oval in shape, up to 0.3 mm long, and contain one to eight, but usually three or four white eggs, which, in preserved condition, have a diameter between 0.11 and 0.13 mm. Free-swimming veligers hatched after 13 days in the aquarium (16–17°C).

DISCUSSION

There is considerable color variation within the specimens examined here. Living specimens from Argentina are usually brighter than Chilean ones, mostly lacking the dark pigmentation between the tubercles. Because a few Argentinian specimens were found to possess some dark dorsal pigmentation and because anatomical features are almost identical within the examined Chilean and Argentinian specimens, they all are considered to belong to the same species. According to its highly arched tuberculate notum, large tri- to quadripinnate gills, smooth lip cuticle, numerous smooth, hook-shaped radular teeth, the presence of a massive prostate, a large penis, and a long, unarmed vagina, this species fits into the genus diagnosis of *Anisodoris* Bergh, 1898 by Millen (1982). Due to its triangular oral tentacles and very large tubercles, this species can be easily distinguished from all known members of this genus except *A. fontaini* and *A. tessellata*. Anatomically it agrees well with the descriptions of both species, but the presence of spicules and the clearly grooved tentacles only coincide with the descriptions of *A. tessellata*. According to Odhner (1926), *A. fontaini* does not possess spicules and has ungrooved oral tentacles. However, d'Orbigny's (1835–1846) original description of *A. fontaini* having "two very short oral tentacles" gives no details about their shape, and the re-examination of the specimens assigned to *A. fontaini* by Odhner (1926) shows that their tentacles in fact are triangular and grooved. The absence of spicules within material preserved for a long time is a common artifact and also occurs in several other Magellanic species studied by Odhner (1926), for example, in his material of *Gargamella immaculata* Bergh, 1894 (own observation). Marcus (1959) mentioned certain differences regarding the lengths of the vas deferens, vagina, and fertilization ducts between *A. tessellata* and *A. fontaini*. These differences are within the ranges of variation found in the examined specimens here. Thus slight differences in the dimensions of reproductive organs are considered to vary intraspecifically and are influenced by maturity and artificial contraction due to fixation. Lacking further distinguishing features between

A. fontaini and *A. tessellata*, the latter species must be regarded as a junior synonym.

Strikingly similar to the Chilean and Argentinian material of *A. fontaini* examined during this study are some specimens which were identified as *Neodoris carvi* by Muniaín et al. (1991). Based on apparently intermediate characters of their material, they synonymized *Neodoris carvi* Marcus, 1959, with *Neodoris erinacea* Marcus, 1959. However, Muniaín et al. (1991) mentioned the presence of a penial papilla and a massive prostate within their specimens, which has been confirmed by the re-examination of a specimen kindly made available by C. Muniaín. As Marcus (1959) characterized the species belonging to the genus *Neodoris* by the absence of a penial papilla and by a prostate consisting of a convoluted, thickened vas deferens, these specimens cannot belong to *Neodoris*, but to *Anisodoris fontaini*. Consequently, it must be suggested not to fuse *N. carvi* and *N. erinacea* until a proper redescription based on adequate material will show that both anatomically similar species really are conspecific.

Zoogeography

Along with the conspecific *A. tessellata* Bergh, 1898, and *Neodoris carvi* det. Muniaín et al. (1991), *Anisodoris fontaini* is known from northern Argentina, 37°50'S, 56°11'W (Odhner, 1926) through Argentinian and Chilean Patagonia (Muniaín et al., 1991; Odhner, 1926; this paper) to Chiloé Island (Marcus, 1959) and also occurs in central Chile (d'Orbigny, 1835–1846; Bergh, 1898; Marcus, 1959; this paper) north to Los Hornos (Schrödl, 1997). All known records are listed in Table 2 and are indicated on the map (Figure 1). Thus *A. fontaini* shows a wide Magellanic distribution occurring within cold temperate and subantarctic waters of the Atlantic and the Pacific Oceans. In Chile, the occurrence of *A. fontaini* extends considerably into the warm temperate waters of the Peruvian faunal province north of Chiloé Island, a pattern which recently has been shown to be common among Magellanic nudibranch species (Schrödl, 1997).

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First Record of the Genus *Janolus* Bergh, 1884
(Opisthobranchia: Arminacea: Zephyrinidae) from the
Pacific Coast of South America, with the
Description of a New Species

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Abstract. A new species of the nudibranch genus *Janolus* Bergh, 1884, from the Chilean coast is described. The external and internal anatomy and coloration are described. The species, *Janolus chilensis* sp. nov., is compared with those most similar to it. *Janolus chilensis* constitutes the first record of the genus on the Chilean and South American Pacific coasts.

INTRODUCTION

The genus *Janolus* Bergh, 1884, includes only two known species from the American Pacific coast: *J. barbarentis* (Cooper, 1863) and *J. fuscus* (O'Donoghue, 1924). Behrens (1991) illustrated a third undescribed species identified as *Janolus* sp. 1. The known geographical range for these species extends more or less along the North American Pacific coast, depending on the species, but never south of the Gulf of California (Behrens, 1991).

On the Chilean coasts the suborder Arminacea is represented by only one species, *Armina cuvieri* (d'Orbigny, 1837). In this paper we describe a new species of zephyrinid nudibranch, recently illustrated and identified as *Janolus* sp. 1 by Schrödl (1996: tab. 6, fig. 34), from two specimens collected on the north Chilean coast.

SYSTEMATIC DESCRIPTION

Suborder ARMINACEA Odhner, 1934

Family ZEPHYRINIDAE Iredale & O'Donoghue,
1923

Genus *Janolus* Bergh, 1884

Janolus chilensis Fischer, Cervera & Ortea,
sp. nov.

(Figures 1–5)

Material: Holotype: One specimen, 45 mm in length, collected on hydrozoan and bryozoan colonies attached to floats and culture lines substrates, at 3 m depth, Iquique (20°20'S;70°05'W), north coast of Chile, 10 August 1993,

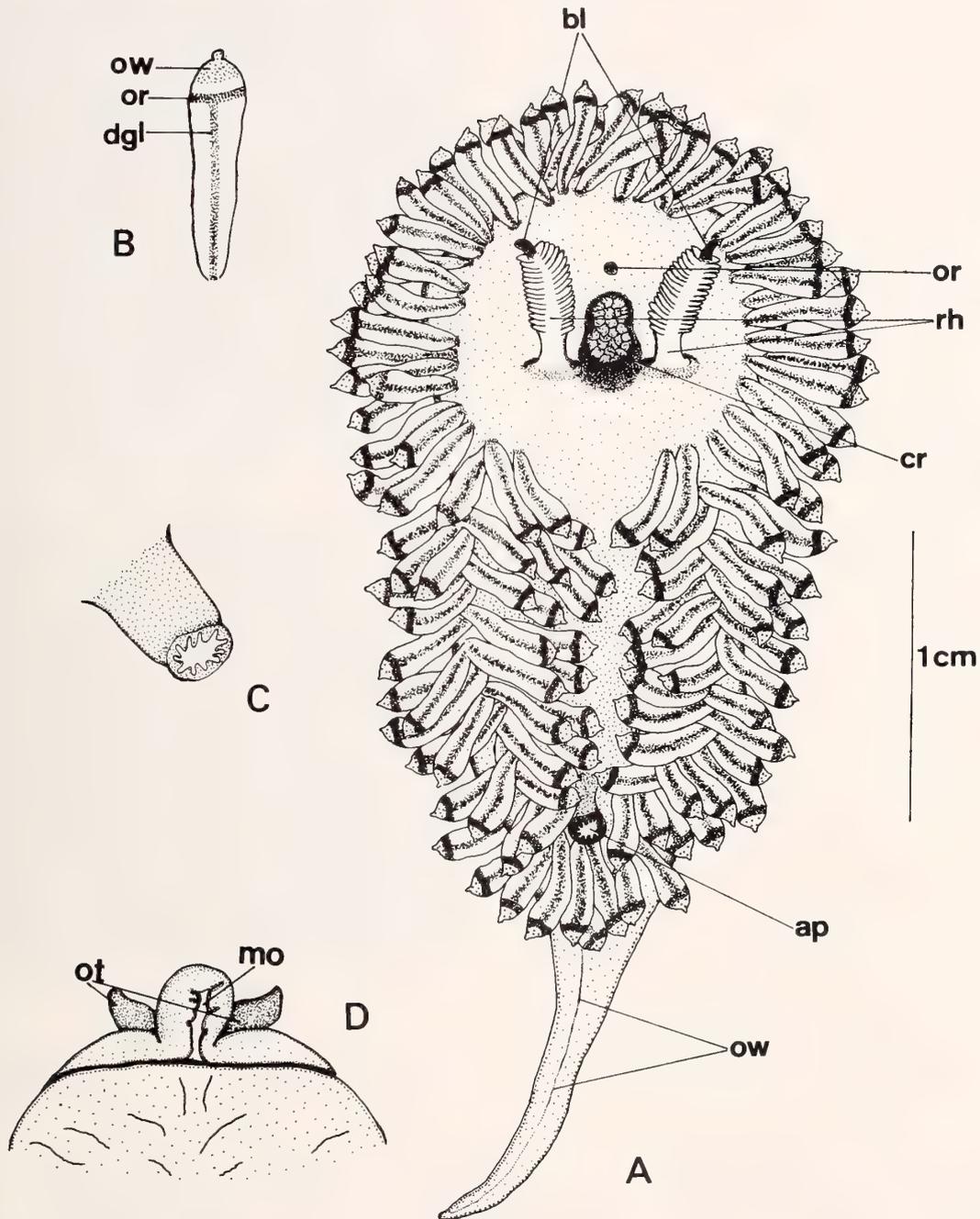


Figure 1

Janolus chilensis Fischer, Cervera & Ortea, sp. nov. A. Dorsal view of the living animal. B. Color pattern of a ceras. C. Detail of the anal papilla. D. Ventral view of the anterior part of the animal. Key: ap, anal papilla; bl, blue; cr, caruncle; dgl, digestive gland; mo, mouth; or, orange; ot, oral tentacle; ow, opaque white; rh, rhinophore.

M. Angelica Fischer coll. This specimen, which is not dissected, has been deposited in the collections of the Museo Nacional de Historia Natural (MNHN) de Santiago de Chile, catalogue number 201621.

Paratype: One specimen dissected, 40 mm in length, collected concurrently with the holotype, has been also deposited in the collections of the MNHN, catalogue number 201622.

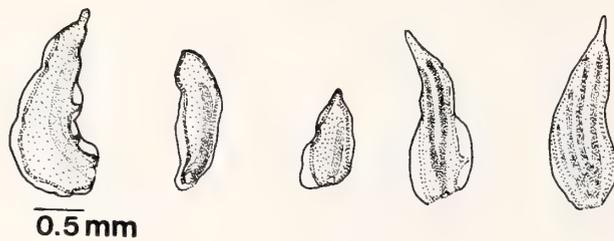


Figure 2

J. chilensis Fischer, Cervera & Ortea, sp. nov. Several cerata showing branching of digestive gland.

Description: Body stout, broadest anteriorly, narrower behind rhinophores, and ending in long, fine tail. Body of live animal translucent white; rhinophores also translucent with blue apex (Figure 1A). Cerata translucent with opaque white apical band, orange subapical band, and narrow translucent band between them (Figure 1B). Branches of digestive gland in cerata translucent brown. Tail translucent with thin central opaque white line. Head wider than rest of body. Pair of short, pointed oral tentacles present in front of head, near mouth. Edge of foot smooth and anteriorly rounded with deep transverse groove (Figure 1D). Rhinophores perfoliate, with 16 thin complete or incomplete transverse lamellae, shortest at base of club. Between rhinophores is an obvious orange bilobed caruncle formed by many lumpy groups (Figure 1A). Anterior to it is also an orange spot. Anus at end of body, where tail begins; anus a short tube opening like flower with nine folds (Figure 1A, C). No anal gland observed. Cerata arranged dorsoventrally around body, 36 on each side. At head, are two alternating ceratal rows. In middle of body are three alternating ceratal rows. Behind anus, cerata form only single row. Cerata shorter and thinner anteriorly and longer and thicker in central body region. Cerata smooth, digitiform, inflated in apical zone with little nipple-shaped end. Digestive gland in cerata appears as slender mostly unbranched tributary, but some have two to five branches that terminate in subapical zone (Figure 2).

Jaws strong, roughly triangular in shape, each side with six broad teeth (Figure 3A, B). Radula broad and well developed. Radular formula of 40 mm specimen $18 \times 18-24.1.18-24$. Rachidian tooth smooth, straight, large, winged, with two small denticles on each side (Figure 4A, B,r). Lateral teeth sickle-shaped. Cusp of lateral teeth becomes shorter from inner portion toward outer edge of radula. Three inner lateral teeth possess two to four denticles (Figure 4A, B).

Reproductive system diallic (Figure 5A). Penis smooth, muscular, broad, and elongate with pointed end (Figure 5B). Penial sac thick and muscular. Vas deferens narrow, relatively short, and coiled twice, without differentiated prostatic portion. Junction of vas deferens and

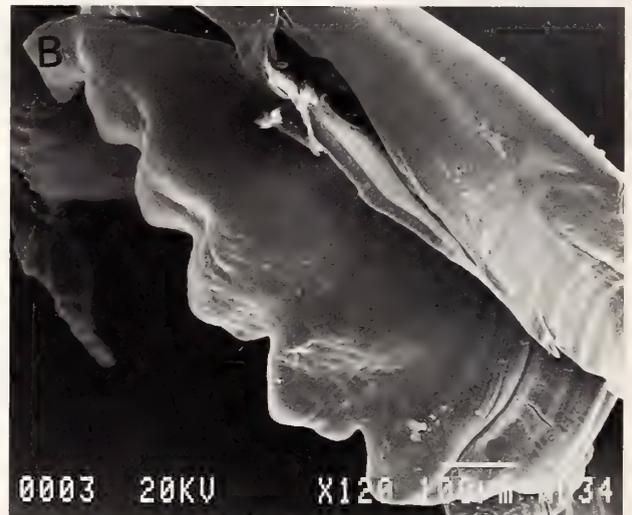


Figure 3

J. chilensis Fischer, Cervera & Ortea, sp. nov. Paratype, MNHN 201622. A, Jaws (scanning electron micrograph). B, Detail of the denticles of the jaws (scanning electron micrograph).

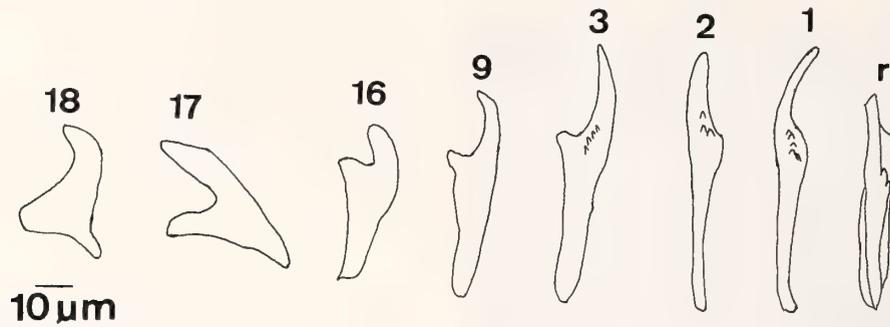
ampulla inside female gland. Ampulla thin, elongate, and refringent, continuing distally as slender hermaphroditic duct, which branches into three ducts. Female gland massive, surrounding bursa copulatrix. Bursa rounded joining female gland via relatively long vagina. Both bursa copulatrix and vagina represented by discontinuous line in figure 5A, according to their arrangement.

DISCUSSION

Janolus chilensis can be separated from the other two American Pacific *Janolus* species (see Table 1). Thus, *J. barbansensis* differs from our species by having an anal gland and a receptaculum seminis. It also lacks lateral

Table 1
Comparative morphology of *Janolus chilensis* sp. nov. and its most similar Pacific species.

Species	Color	Digestive ceratal branches	Anal gland	Jaws	Radular formula and teeth	Receptaculum seminis	Bursa copulatrix	Penis	References
<i>Janolus barbarensis</i> (Cooper, 1863)	body translucent white; cerata with gold sub- apical ring and blue tips, branches of di- gestive gland brown; rhino- phores with lemon yellow subapical ring and blue tip; or- ange caruncle	branched	present	7-9 denticles	16 × 27.1.27; ra- chidian narrow, without denti- cles; inner later- al teeth about 6 denticles; remaining later- al smooth	spherical, thin- walled, dis- tal	short, spheri- cal, serial, proximal	large, muscu- lar, thickest near the middle	Cockerell & Eliot (1905); MacFarland (1966); Gos- liner (1981, 1982)
<i>J. fuscus</i> O'Dono- ghue, 1924	body translucent white, with mid- dorsal red- brown lines; cerata with sub- apical yellow and apical opaque white bands, branches of the digestive gland brown; rhinophores pink and opaque white tip; red- brown caruncle	unbranched	absent	10-13 denticles	21-26 × 22- 25.1.22-25; ra- chidian broad, denticulate; inner laterals 2 denticles; re- maining laterals smooth	pyriform, dis- tal	elongate, semi-serial, proximal	conical, thickened posteriorly	O'Donoghue (1924); MacFarland (1966); Gos- liner (1981, 1982)
<i>J. chilensis</i> sp. nov.	body translucent white; cerata with opaque white tip and orange subapi- cal ring; branch- es of the diges- tive gland pale brown; rhino- phores tip dark blue; or- ange caruncle	branched	absent	6-7 denticles	18 × 18-24.1.18- 24; rachidian narrow, denticu- late; inner three lateral with 2-4 denticles; re- maining lateral smooth	absent	spherical, semi-serial	thick, muscu- lar, conical, pointed	present study



A

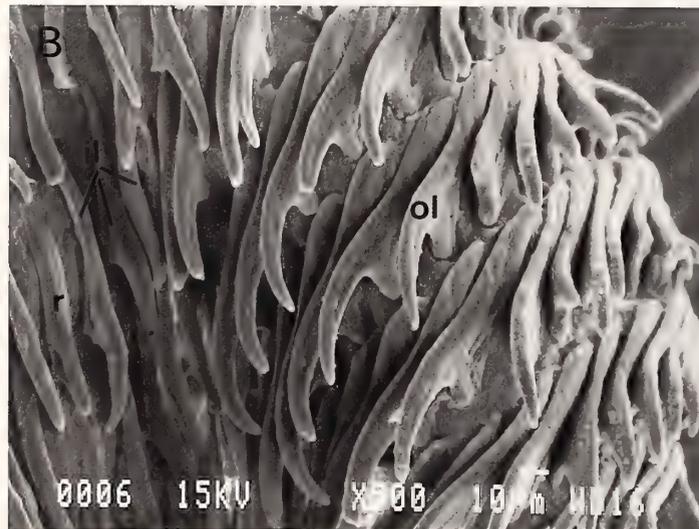


Figure 4

J. chilensis Fischer, Cervera & Ortea, sp. nov. Paratype, MNHN 201622. A. Schematic view of the radular teeth in a half-row. B. Scanning micrograph of several half-rows of the radula. Key: il, inner lateral teeth; ol, outer lateral teeth; r, rachidian tooth.

denticles on the rachidian tooth. On the other hand, *J. fuscus* also has a receptaculum seminis. In the genus *Janolus*, the presence of one or two receptacles varies intraspecifically. Following the revisions of Gosliner (1981, 1982) and Miller & Willan (1986), the species recognized as having only a bursa copulatrix are *J. comis* Marcus, 1955 (has a bursa/vagina), *J. mucloc* (Marcus, 1958), *J. toyamensis* Baba & Abe, 1970, and *J. eximius* Miller & Willan, 1986; and the species recognized as having only a receptaculum seminis is *J. hyalinus* (Alder & Hancock, 1854). There are also other species that have both types of receptacles: *J. cristatus* (Delle Chiaje, 1841), *J. barbarensis* (Cooper, 1863), *J. novozealandicus* (Eliot, 1907), *J. fuscus* O'Donoghue, 1924, *J. capensis* Bergh, 1907, *J. longidentatus* Gosliner, 1981, *J. ignis* Miller & Willan, 1986 (has a bursa/vagina), and *J. mokohinau* Mil-

ler & Willan, 1986 (has a bursa/vagina). However, there are several species whose reproductive systems remain unknown: *J. australis* Bergh, 1884, *J. indicus* (Eliot, 1909), *J. mirabilis* Baba & Abe, 1970, *J. preclarus* (Bouchet, 1975). After the Gosliner and Miller & Willan papers, Ortea & Llera (1988) described *J. faustoi* from the Canary Islands, but with no details of the reproductive system. A bursa copulatrix surrounded by the female gland was also described in *J. mucloc* by Marcus (1958), similar to *J. chilensis*.

On the other hand, the coloration in some representatives of the Zephyrinidae is variable, like *Bonisa nakaza* Gosliner, 1981. This species is recorded with three different patterns of coloration, but in *Janolus* this variability has not been described. *J. chilensis* has a distinct pattern of coloration. It is clearly different from the other

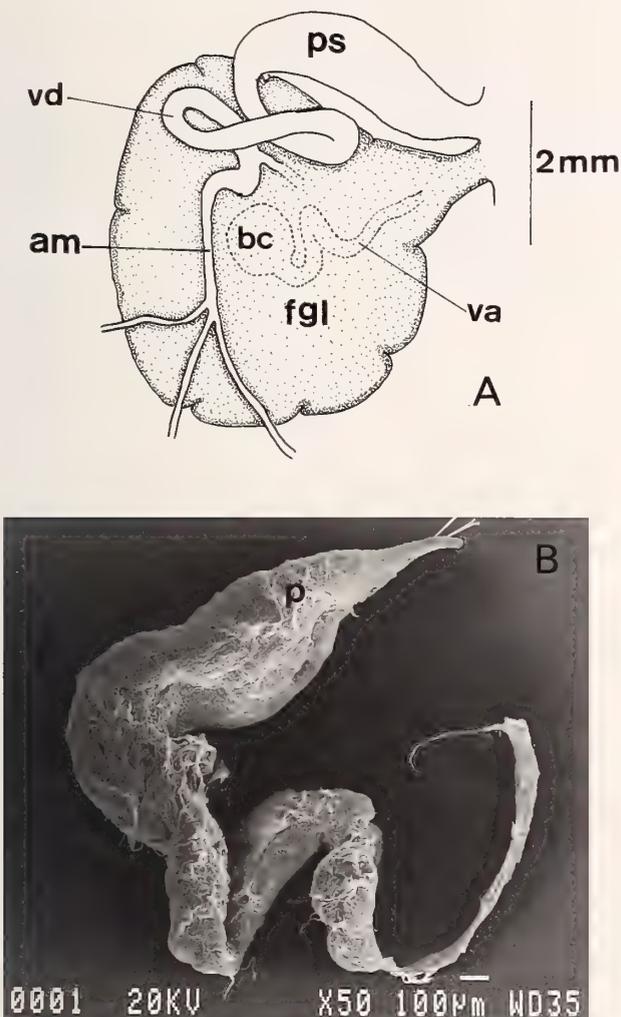


Figure 5

J. chilensis Fischer, Cervera & Ortea, sp. nov. Paratype, MNHN 201622. A. Reproductive system. B. Detail of the penis. Key: am, ampulla; bc, bursa copulatrix (discontinuous line), fgl, female gland; ps, penial sheath; va, vagina (discontinuous line); vd, vas deferens.

species of *Janolus* from the American Pacific. *Janolus fuscus* has mid-dorsal lines of red-brown, yellow and white cerata, and pink and opaque white rhinophores. *Janolus barbarentis* has cerata with a subapical gold ring, and rhinophores with a subapical lemon-yellow ring and blue tip. *J. chilensis* has opaque white ceratal tips, a subapical orange ring, and the tips of the rhinophores are blue (Table 1). The coloration of the remaining species

of *Janolus* is clearly different. The rachidian teeth of *J. chilensis* are similar to the rachidian teeth of *J. barbarentis*. The two inner lateral teeth of *J. barbarentis* are denticulate, whereas in *J. chilensis* the three inner teeth are denticulate.

Etymology: The specific name, *chilensis*, is from Chile, where the new species was collected.

ACKNOWLEDGMENTS

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Review of the genus *Doriopsilla* Bergh, 1880 (Gastropoda: Nudibranchia) in the Atlantic Ocean

by

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Abstract. Three valid species of the nudibranch genus *Doriopsilla* Bergh, 1880, inhabit the Atlantic Ocean, including the Mediterranean and the Caribbean Sea: *Doriopsilla areolata* Bergh, 1880 (with three subspecies: *D. areolata areolata* Bergh, 1880; *D. areolata albolineata* Edmunds, 1968; and *D. areolata nigrolineata* Meyer, 1977); *Doriopsilla pelseneeri* d'Oliveira, 1895; and *Doriopsilla pharpa* Marcus, 1961. The other eight nominal species previously assigned to *Doriopsilla* in the Atlantic Ocean: *Doriopsilla pusilla* Pruvot-Fol, 1951; *Doriopsilla rarispinosa* Pruvot-Fol, 1951; *Doriopsilla fedatae* Pruvot-Fol, 1953; *Doriopsilla leia* Marcus, 1961; *Doriopsilla albolineata* Edmunds, 1968; *Doriopsilla nigrolineata* Meyer, 1977; *Doriopsilla evanae* Ballesteros & Ortea, 1980; and *Doriopsilla ciminoi* Ávila, Ballesteros & Ortea, 1992, are synonyms of the former. The species *Doris reticulata* Schultz in Philippi, 1836, is a junior subjective synonym of *Doriopsilla areolata*, but the name is preoccupied by *Doris reticulata* Quoy & Gaimard, 1832.

Additional data about the anatomy, geographical distribution, and variability of these species are presented. Neotypes are designated for nominal species whose type material is untraceable.

The major diagnostic features utilized to separate species are body color, dorsal tubercular morphology, shape of the oral tentacles, morphology of the reproductive system, and shape of the penial hooks.

INTRODUCTION

Bergh (1880) described the new genus *Doriopsilla*, which differs from *Dendrodoris* (cited under the name *Doriopsis*) by its somewhat rigid and granulated mantle, and by the position of the buccal ganglia, which is located some way back from the central nervous system.

Eliot (1906a) misinterpreted Bergh's description and considered that in *Doriopsilla* the buccal ganglia lie immediately behind the rest of the nervous system, whereas in *Dendrodoris* (cited under the name *Doridopsis*) they are situated some way back. Steinberg (1961) followed Eliot's paper and included his material from California in the genus *Dendrodoris*, and argued that both genera must be considered synonyms.

However, other authors (Pruvot-Fol, 1954; Burn, 1962) reaffirmed *Doriopsilla* as valid and different from *Dendrodoris* and their synonyms, based on the distinctive fea-

tures proposed by Bergh (1880). Valdés et al. (1996) included additional anatomical features to distinguish these two genera, such as the absence of ptyaline glands, a flat, non-tubular prostate, and a proximal connection between seminal receptacle and gametolytic glands in *Doriopsilla*. Also, the eccentric position of the anus in *Doriopsilla* has been used as diagnostic (Ballesteros & Ortea, 1980).

A review of the literature shows that, since its original description, 13 species have been assigned to the genus *Doriopsilla* Bergh, 1880, in the Atlantic Ocean. Bergh (1880) included in his new genus the species *Doriopsilla areolata* Bergh, 1880 (type species by monotypy), collected from the Mediterranean Sea and, with a question mark, *Doriopsis granulosa* Pease, 1860, from the Indo-Pacific. Several years later, d'Oliveira (1895) described the new species *Doriopsilla pelseneeri* d'Oliveira, 1895, collected from Portugal. Since then, three additional spe-

cies have been described from the Mediterranean Sea: *Doriopsilla pusilla* Pruvot-Fol, 1951; *Doriopsilla rarispinosa* Pruvot-Fol, 1951; and *Doriopsilla evanae* Ballesteros & Ortea, 1980; and another three from West Africa: *Doriopsilla fedalae* Pruvot-Fol, 1953; *Doriopsilla ciminoi* Ávila, Ballesteros & Ortea, 1992; and *Doriopsilla albolineata* Edmunds, 1968.

More recently, Valdés et al. (1996) proposed the inclusion of the Mediterranean species *Dendrodoris racemosa* Pruvot-Fol, 1951; and *Dendrodoris minima* Pruvot-Fol, 1951, in the genus *Doriopsilla*.

The first record of the genus *Doriopsilla* from the Atlantic coast of America was in the paper by Marcus (1961) which described two new species: *Doriopsilla leia* Marcus, 1961, and *Doriopsilla pharpa* Marcus, 1961, both from North Carolina. A later paper by Meyer (1977) described *Doriopsilla nigrolineata* Meyer, 1977, from the Caribbean coast of Panama.

In the present paper, we review all the species reported from the Atlantic Ocean and propose a list of valid species for this area.

MATERIALS AND METHODS

Most of the specimens studied in this paper were provided by a number of colleagues. The type material and additional specimens were deposited in several natural history museums. The following abbreviations are used to denote these institutions: USNM, National Museum of Natural History, Washington D. C., USA; BMNH, The Natural History Museum, London, United Kingdom; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; ZMUC, Zoologisk Museum, København Universitet, Copenhagen, Denmark; MCNB, Museo de Ciencias Naturales de Barcelona, Barcelona, Spain; IPM, Instituto Português de Malacologia, Estoril, Portugal; MCNT, Museo Insular de Ciencias Naturales, Tenerife, Spain.

Additional material is in the Universidad de Oviedo: Laboratorio de Zoología, Departamento de Biología de Organismos y Sistemas (LZUO).

Features of living animals were recorded from original notes, drawings, and photographs taken by collectors. At least one specimen from each locality was dissected, the penis was isolated and mounted for microscopical examination, and the penial hooks were drawn with the aid of a camera lucida. Particularly interesting soft parts were critical point dried for scanning electron micrography (SEM). Diagnostic differences among the taxa are summarized in Table 1.

SYSTEMATIC DESCRIPTIONS

Family DENDRODORIDIDAE O'Donoghue, 1924

Genus *Doriopsilla* Bergh, 1880

Diagnosis: Mantle hard, stiffened by calcareous spicules. Dorsum covered by tubercles of different shapes and

sizes. Gills tripinnate, disposed in a circle closed by the anus, which is eccentric to the left. Oral tentacles reduced, sometimes fused together.

Digestive system lacking ptyaline glands. A pyloric gland may be present. Reproductive system with a flat, non-tubular prostate, and a proximal connection between seminal receptacle and gametolytic glands. Penis eversible, with numerous internal hooks.

Nervous system with the buccal ganglia some way back from the central nervous system.

Doriopsilla areolata Bergh, 1880

(Figures 1, 2A, 3A, 4, 5)

Diagnosis: Background color varies from yellow to light brown (or pearl grey), with a pattern of white rings or lines. The edge of the gill pocket does not have a white ring. Dorsum covered with low and simply rounded tubercles stiffened by spicules, larger in the center of the dorsum. Oral tentacles fused together, with only the tips separated.

Muscular pharyngeal bulb quite long. Intestine without a pyloric gland on its proximal part. Penial hooks with a long cusp (about 300 μm long), curved in the basal hooks, and a narrow base.

External morphology: The background color of the body varies from yellow, in the smallest specimens, to light brown (or pearl grey) in the largest. The border of the mantle is translucent and poorly pigmented in juvenile specimens, and pale yellow to light brown (or grey) in adults. There is a darker brown or black area in the middle of the body whose center is lighter again. There is a pattern of white rings or lines on the dorsum which varies in different subspecies (Figure 1). Rhinophores and gills have the same color as the body.

The dorsum is covered by low and simply rounded tubercles (Figure 2A), stiffened with spicules. The largest tubercles are along two rows between rhinophores and gills. Tubercles of the center of the dorsum are larger, decreasing in size toward the border of the mantle and absent near the edge. They are arranged in irregular longitudinal rows and clustered separately from each other.

The entire body is stiffened by a subepidermal network of strong spicules, whose shape and variability have been fully described by García et al. (1986).

Four to six tripinnate gills form a circle, completed by the anus on the left. The rhinophores have seven to 30 lamellae.

Ventrally, the border of the mantle shows a strong network of spicules. The oral tentacles are small and fused together with only the tips separated (Figure 3A). The anterior border of the foot is notched and covers the bases of the oral tentacles.

Anatomy: The muscular pharyngeal bulb is quite long, and its length is 4 to 5 times its breadth (Figure 4A). The

Table 1
Comparative table of the species and subspecies of the genus *Doriopsilla* in the Atlantic Ocean.

	Body color	Dorsal tubercles	Oral tentacles	Pharyngeal bulb	Penial hooks	Geographical range
<i>Doriopsilla areolata</i>	—	low and simply rounded tubercles, larger in two rows between rhinophores and gills	small and fused together with only the tips free	several times longer than wide	cusps very long (about 300 μm) curved in the proximal hooks, base narrow	Atlantic Ocean, in tropical and temperate areas
<i>D. areolata areolata</i>	yellow to pale brown with white rings or lines forming a frayed network, center of the dorsum pale brown	↔	↔	↔	↔	Mediterranean Sea to Cape Verde Islands, and Atlantic coast of Spain and Portugal
<i>D. areolata albolineata</i>	pearl grey with white lines most of which are transverse, brown lines in the mantle margin	↔	↔	↔	↔	West Africa, from Ghana to Angola
<i>D. areolata nigrolineata</i>	light to dark orange with white rings around tubercles and black lines forming a frayed network	↔	↔	↔	↔	Caribbean coast of Panama
<i>Doriopsilla pelseneeri</i>	white, yellow, orange or red, with a white ring in the gill pocket edge	large, irregular warts, larger in the center of the dorsum	small, separated and ventrally grooved	twice as long as wide	cusps long (200 to 300 μm) and straight, base very elongated	Iberian Peninsula
<i>Doriopsilla pharpha</i>	yellow with numerous dark brown spots on the whole surface of the dorsum	numerous and minute tubercles, all of them of a similar size	very long and fused together with only the tips free	several times longer than wide	cusps very curved, base narrow	Atlantic coast of the USA (Massachusetts to Florida) and Cuba

tubular pharynx leads from the pharyngeal bulb. At this point, two thin retractor muscles insert onto the posterior of the bulb. The pharynx is very long and convoluted, and passes directly through the central nerve ring. The esophagus is shorter than the pharynx (the latter is about 2 times the length of the former). Posteriorly, the esophagus broadens into a muscular portion. The intestine has a dilated proximal part, then narrows and runs posteriorly down in the usual position.

The female gland (Figure 4B) is very large in mature specimens; it can be as large as the digestive gland. The rounded gametolytic gland connects by a long duct with the seminal receptacle; at the point where this duct connects with the gametolytic gland, there are two other ducts; one of them connects with the female gland, and the other one is the vagina. The ampulla is large and elongated. There is a flat, granular, and very large prostate overlying all of these organs. The deferent duct is long and as wide as the vagina; both open in a common atrium. The penis is covered with numerous large hooks (about 300 μm long); they have a long cusp, curved in the basal hooks, and a narrow base (Figure 4C). As result of a teratism, one specimen has penial hooks with two cusps and denticles.

The small triangular heart is connected with the blood gland by the aorta. Close to the heart and connected with the pericardium there is a rounded renal sac.

Biology: The egg mass is spirally coiled. The yellow eggs are spherical, arranged in parallel lines, and each one enclosed in a much larger spherical capsule. Eggs measure 96–121 μm (mean: 106 \pm SD μm). Capsules measure 173–201 (mean: 189 \pm SD).

Most of the preserved animals show hard ochre balls on the dorsum, which could be the result of secretions. Spinella et al. (1994) investigated the chemicals of *Doriopsilla areolata*, finding new acetoxo-*ent*-pallascensin-A sesquiterpenoids from the skin of this species.

Geographic range: In the Atlantic Ocean, this species has been recorded (under different names) from the north coast of Spain (Ballesteros & Ortea, 1980); Portugal (d'Oliveira, 1895; Nobre, 1932); Morocco (Pruvot-Fol, 1953); Senegal (White, 1955); Cape Verde Islands (Eliot, 1906b; Ávila, et al., 1992); Nigeria (Marcus & Marcus, 1966); Ghana (Edmunds, 1968); Angola (present paper); in the Mediterranean Sea from Spain (Ballesteros & Ortea, 1980; García-Gómez, 1983); France (Vayssière, 1901; Pruvot-Fol, 1951); Palestine (O'Donoghue & White, 1940); and Israel (Barash & Danin, 1971). In the West Atlantic, it has only been recorded from the Caribbean Sea (Marcus & Marcus, 1962; Meyer, 1977).

Remarks: *Doriopsilla areolata* is externally characterized by the low and simply rounded tubercles of the dorsum, larger in two rows between the rhinophores and the gills. The yellow, pale brown or grey background color

with a central dark brown or black area whose center is lighter is also characteristic of this species, and remains in preserved specimens. On the dorsum there is white pigment forming a pattern of lines or rings. The oral tentacles are fused, being free only at the tips. No other Atlantic species has this combination of characters. Nevertheless, *Doriopsilla areolata* shows a considerable local variability in the color pattern. We have observed three different geographical color forms, described here as subspecies: *Doriopsilla areolata areolata* Bergh, 1880, *Doriopsilla areolata albolineata* Edmunds, 1968, and *Doriopsilla areolata nigrolineata* Meyer, 1977.

The species *Doris reticulata* was described by Schultz in Philippi (1836) from Sicily as having the center of the dorsum black with white spots and a network of lines "in relief" which are branched toward the border of the mantle (spicules?). There are six or seven narrow gills and small oral tentacles. Ventrally there are branched lines in relief (spicules?). Unfortunately, the type material of this species is untraceable, but in the knowledge of the Mediterranean fauna it is acceptable to consider *Doris reticulata* a senior subjective synonym of *Doriopsilla areolata*. However, the former name is preoccupied by *Doris reticulata* Quoy & Gaimard, 1832, described from the Indo-Pacific.

Specimens of *Doriopsilla* reported from the Indo-West Pacific which have a network of white lines on the dorsum have been assigned to the species *Doriopsilla miniata* Alder & Hancock, 1864, by several authors (Baba, 1949; Thompson, 1975; Gosliner, 1987). Thompson (1975) and Gosliner (1987) have proposed that *Doriopsilla areolata* could be a junior synonym of *D. miniata*. However, the original description of *D. miniata* was based on an undetermined number of specimens of roughly 30 mm length which did not have white pigment (lines or spots) on the dorsum, whereas specimens of *D. areolata* have white pigment even as juveniles. It is probable that *D. areolata* has a tropical and subtropical distribution throughout the world, but the name *D. miniata* should be applied to a different Indo-Pacific species. On the contrary, *Doriopsilla davisii* (Allan, 1933) described from Australia as having white lines around the dorsal tubercles (Allan, 1933) could be a subjective junior synonym of *D. areolata*.

Doriopsilla areolata areolata Bergh, 1880

(Figure 1A–D)

Doris reticulata Schultz in Philippi, 1836: 105 (non *Doris reticulata* Quoy & Gaimard, 1832).

Doriopsilla areolata Bergh, 1880: 318–326, pl. 11, 3–11.

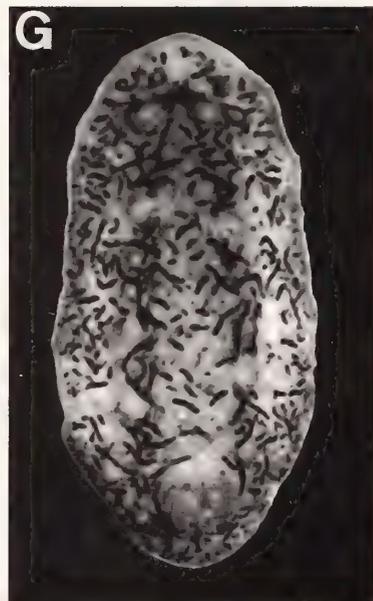
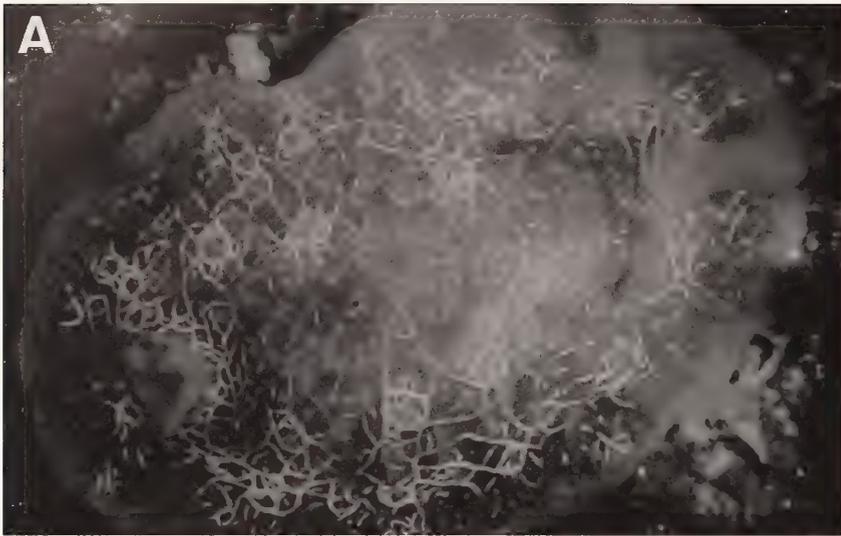
Doriopsilla pusilla Pruvot-Fol, 1951: 41–42, pl. 2, 1–2.

Doriopsilla rarispinosa Pruvot-Fol, 1951: 40–41, fig. 22.

Doriopsilla fedalae Pruvot-Fol, 1953: 92–93, fig. 34, pl. 2, 32.

Doriopsilla evanae Ballesteros & Ortea, 1980: 26–30, figs. 1–2.

Doriopsilla ciminoi Ávila, et al., 1992: 24–30, figs. 1–3.



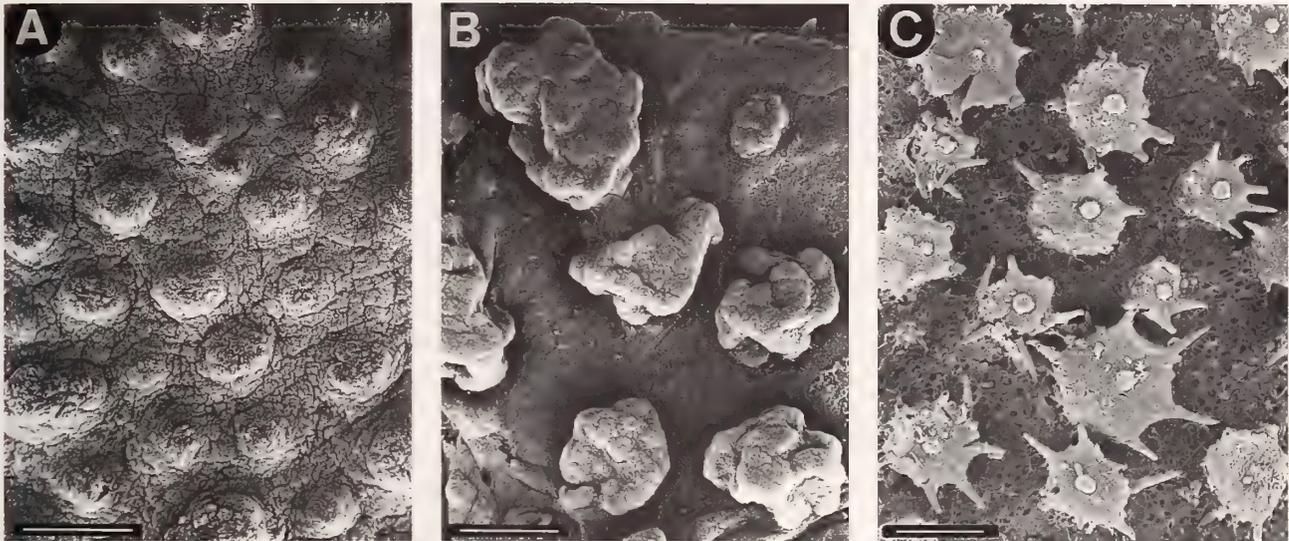


Figure 2

Scanning electron micrographs using critical point drying technique, A. dorsal tubercles of *Doriopsilla areolata* (scale bar = 1 mm), B. dorsal tubercles of *Doriopsilla pelseneeri* (scale bar = 1 mm), C. dorsal tubercles of *Doriopsilla pharpa* (scale bar = 100 µm).

Type material:

Doris reticulata. The type material of this species is untraceable. Neotype (here designated): ZMUC GAS-234, Villefranche, France, 1954, 37 mm preserved length, coll. Barrois, formerly deposited at MNHN.

Doriopsilla areolata. The two syntypes of this species collected by Dr. v. Marenzeller from the Dalmation coast (Lessina Island) are untraceable at ZMUC (Tom Schiøtte, personal communication). Neotype (here designated): ZMUC GAS-234, Villefranche, France, 1954, 37 mm preserved length, coll. Barrois, formerly deposited at MNHN.

Doriopsilla pusilla. The type material of this species could not be located in MNHN and it is presumed lost; the type locality is Banyuls, France. Neotype (here designated): ZMUC GAS-234, Villefranche, France, 1954, 37 mm preserved length, coll. Barrois, formerly deposited at MNHN.

Doriopsilla rarispinosa. The type material of this species could not be located in MNHN and it is presumed lost; the type locality is Banyuls, France. Neotype (here designated): ZMUC GAS-234, Villefranche, France, 1954,

37 mm preserved length, coll. Barrois, formerly deposited at MNHN.

Doriopsilla fedalae. The type material of this species could not be located in MNHN and it is presumed lost; it was collected from Fedala and Temara, Morocco. Neotype (here designated): ZMUC GAS-234, Villefranche, France, 1954, 37 mm preserved length, coll. Barrois, formerly deposited at MNHN.

Doriopsilla evanae. According to the original description (Ballesteros & Ortea, 1980) the type material of this species includes one lectotype (selected by Ballesteros & Ortea, 1980) and one paralectotype, both in MCNB. However, these specimens must be considered as holotype and paratype. At present, the holotype (San Antonio, Ibiza, Spain, Ago. 1978) and one paratype (Islas Formiges, Girona, Spain, July 1979) are deposited at MNCN with the registration numbers 15.05/23763 and 15.05/23746, respectively. The other paratype is lost.

Doriopsilla cimini. Holotype (by original designation): MCNT Mo 135, Sal Rei, Boavista Island, Cape Verde, 23 August 1985, 1 specimen 20 mm preserved length. Paratypes: Cape Verde Islands (several localities), 4

Figure 1

Photographs of specimens of *Doriopsilla areolata* showing external features, A. *D. areolata areolata*, 30 mm long, Mediterranean Sea, B. *D. areolata areolata*, 15 mm long (MNCN 15.05/23784), C. *D. areolata areolata*, 25 mm long, Asturias, North of Spain, D. *D. areolata areolata*, 15 mm long (MNCN 15.05/23783), E. *D. areolata albolineata*, 18 mm long (MNCN 15.05/23774), F. *D. areolata albolineata*, 16 mm long, Angola, G. *D. areolata nigrolineata*, preserved holotype (USNM 760618).

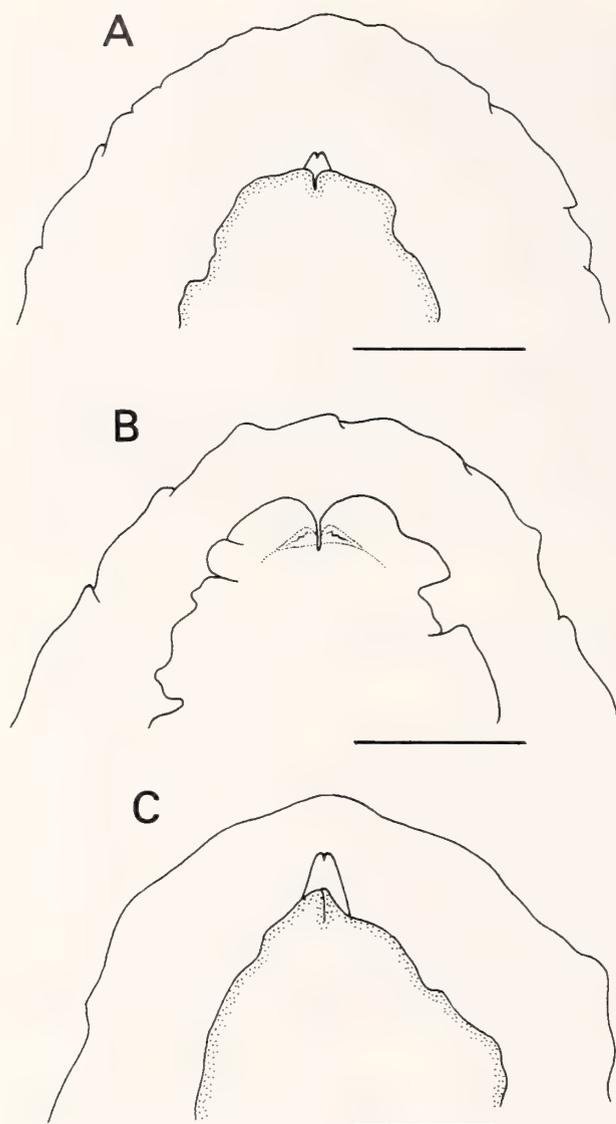


Figure 3

Ventral view of preserved specimens showing oral tentacles. A. *Doriopsilla areolata* (scale bar = 5 mm), B. *Doriopsilla pelse-neeri* (scale bar = 5 mm), C. *Doriopsilla pharpa* (scale bar = 2 mm).

specimens 14–20 mm preserved length (MNCN 15.05/23772) formerly at LZUO; other 4 specimens at MCNB.

Diagnosis: Background color varies from yellow to pale brown. Mantle margin without radial and branched brown lines. Specimens smaller than 5 mm without white pigment. Larger animals with white rings around several tubercles (Figure 1B), sometimes joined in groups of two, three, or more. Specimens larger than 20 mm can have the white rings broken and joined, forming a network

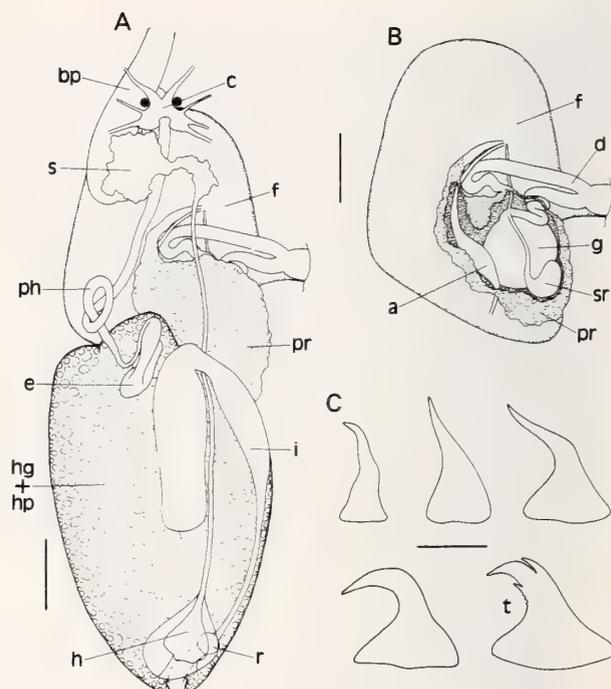


Figure 4

Anatomy of *Doriopsilla areolata* (MNCN 15.05/23780), A. Dorsal view of the anatomy (scale bar = 2 mm): bp, pharyngeal bulb; c, central nervous system; e, esophagus; f, female gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; ph, pharynx; pr, prostate; r, renal sac; s, blood gland, B. Reproductive system (scale bar = 2 mm): a, ampulla; d, deferent duct; f, female gland; g, gametolytic gland; pr, prostate; sr, seminal receptacle, C. Detail of the penial hooks (scale bar = 200 μ m): t, deformed hook.

(more or less frayed) which never reaches the border of the mantle (Figure 1A, C, D).

Remarks: Specimens from the Atlantic coast of Spain and Portugal differ from *Doriopsilla areolata areolata* collected in the Mediterranean and North Africa in the ontogenetic evolution of the white color pattern. In specimens from the Atlantic coast of Spain and Portugal, the white rings around the tubercles change rapidly to a frayed network (at 10 mm), whereas in the Mediterranean and North Africa material, white rings remain in quite large animals (25 mm). Also, specimens from the Atlantic coast of Spain and Portugal have a white network which is not frayed, and the center of the dorsum is very dark, sometimes black, whereas in Mediterranean and North African specimens, the dorsal network is frayed, and the center of the dorsum is brown. However, around Gibraltar Strait, the separation of both color patterns is not clear, and Ballesteros (personal communication) has collected specimens in the Mediterranean Sea with a non-frayed network and dorsum with a black center.

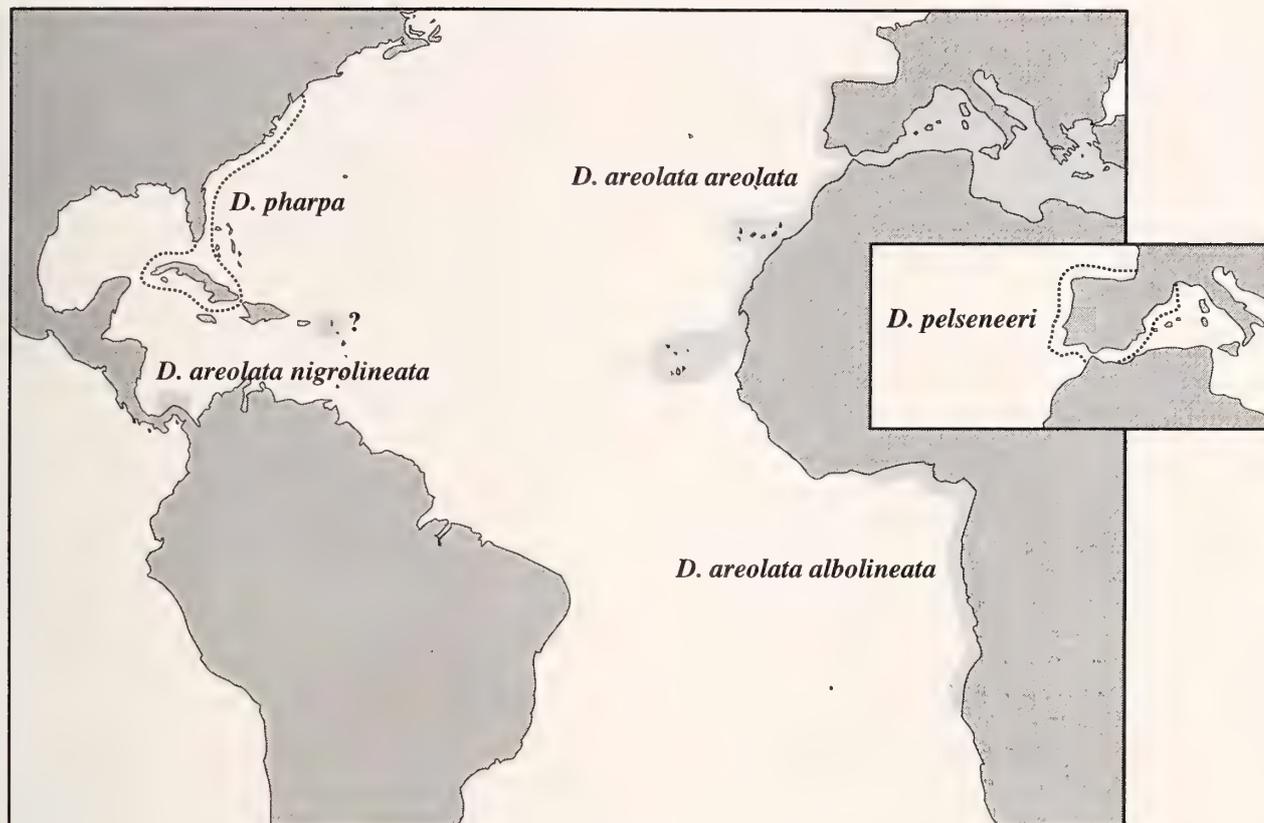


Figure 5

Distribution map of the Atlantic species of the genus *Doriopsilla*.

Doriopsilla pusilla and *Doriopsilla rarispinosa* were described by Pruvot-Fol (1951) from the Mediterranean Sea based on small preserved specimens with no trace of the white lines. All of the few external and internal features originally described by Pruvot-Fol (1951) and later redescribed by Pruvot-Fol (1954) are identical to those of *D. areolata areolata*, such as the shape of the penial hooks and the anterior digestive system, of *D. rarispinosa*, and the dorsal external morphology of both species.

Doriopsilla evanae described by Ballesteros & Ortea (1980) from the Mediterranean Sea and *Doriopsilla ciminoi* described by Ávila, et al. (1992) from Cape Verde Islands, were based on small specimens of *Doriopsilla areolata areolata*, with the typical white rings around the tubercles of this subspecies. All the internal and external features of both these nominal species are identical to those of *D. areolata areolata*. Ballesteros & Ortea (1980) described egg sizes of 209–266 µm, which contrasts with the values given here for *D. areolata* (96–121 µm). This difference could be explained by an erroneous measuring because all the other external and internal features of *D. evanae* are identical to those of *D. areolata*.

Doriopsilla fedalae was described by Pruvot-Fol

(1953) from the Atlantic coast of Morocco, as having a yellow-orange background color with “filigrane blanches” (white filigree). These external features are identical to those of *Doriopsilla areolata areolata*.

Geographic range: This subspecies ranges from the North coast of Spain to Cape Verde Islands, including the Mediterranean Sea (Figure 5).

Material examined: Laredo, Spain, April 1983, 1 specimen 15 mm preserved length, coll. Templado (MNCN 15.05/18276); Ribadesella, Spain, May 1977, 1 specimen 30 mm preserved length, with the egg mass (MNCN 15.05/23796); Luanco, Spain, 22 November 1984, 2 specimens 26–38 mm preserved length (MNHN). Setubal, Portugal, 31 March 1995, 1 specimen 14 mm preserved length (IPM R311621). Sagres, Portugal, 27 May 1986, 2 specimens 20–22 mm preserved length; 12 May 1988, 2 specimens 18–27 mm preserved length; 1 specimen 10 mm preserved length. Fuengirola, Spain, 26 May 1985, 1 specimen 20 mm preserved length (MNCN 15.05/23775). Alborán, Spain, 12 July 1989, 80 m depth, 1 specimen 9 mm preserved length (MNCN 15.05/23776). Measina Island, Italy, 13 July 1978, 1 specimen 18 mm

preserved length (MNCN 15.05/23780). Staguone di Marsala, Santa Maria, Italy, July 1987, 4 specimens 10–14 mm preserved length (MNHN). Villefranche, France, 1 specimen 37 mm preserved length, NEOTYPE of *Doris reticulata*, *Doriopsilla areolata areolata*, *Doriopsilla pusilla*, *Doriopsilla rarispinosa*, and *Doriopsilla fedatae*, coll. Barrois (ZMUC GAS-234); 1 specimen 29 mm preserved length, coll. Barrois (MNHN). Acitrezza, Italy, 3 May 1990, 1 specimen 4 mm preserved length (MNHN); 4 May 1990, 12 m depth, 1 specimen 9 mm preserved length (LZUO 113-35). Fauna III expedition, sta. 182A (39°44.33'N, 2°31.86'E), Mallorca, Spain, 72–74 m depth, 1 specimen 13 mm preserved length (MNCN 15.05/19403); sta. 186A (39°49.66'N, 2°38.71'E), Mallorca, 59–61 m depth, 1 specimen 31 mm preserved length (MNCN 15.05/19349); sta. 222A (39°19.30'N, 3°17.20'E), Mallorca, 92–97 m depth, 1 specimen 16 mm preserved length (MNCN 15.05/18553). Santa Ponsa, Mallorca, 11 June 1981, 1 specimen 15 mm preserved length, coll. Ballesteros (MNCN 15.05/23765). San Antonio, Ibiza Island, Spain, 26 August 1978, 1 specimen 11 mm preserved length, HOLOTYPE of *Doriopsilla evanae*, coll. Ballesteros (MNCN 15.05/23763). Formigues Islands, Gerona, Spain, June 1979, 1 specimen 8 mm preserved length, PARATYPE of *Doriopsilla evanae*, coll. Ballesteros (MNCN 15.05/23764). Cadaqués, Gerona, date unknown, 2 specimens 9–10 mm preserved length, coll. Ballesteros (MNCN 15.05/23766). Peñon del Fraile, Granada, Spain, 28 August 1981, 4 specimens 17–21 mm preserved length (MNCN 15.05/1989). La Herradura, Granada, 31 March 1983, 1 specimen 15 mm preserved length (MNCN 15.05/1990); 11 June 1983, 1 specimen 15 mm preserved length (MNCN 15.05/17709); 5 September 1993, 1 specimen 16 mm preserved length (MNCN 15.05/17217). Fuengirola, Spain, July 1982, 1 specimen 19 mm preserved length (MNCN 15.05/2981); 1 specimen 17 mm preserved length (MNCN 15.05/18269). Fauna I expedition, sta. 23A (36°24.05'N, 5°00.99'W), Málaga, Spain, 30 m depth, 13 July 1989, 2 specimens 7–11 mm preserved length (MNCN 15.05/23783). Ceuta, Spain, 27 May 1986, 2 specimens 19–21 mm preserved length (MNHN). Gibraltar, Spain, 17 June 1993, 1 specimen 24 mm preserved length (MNCN 15.05/17739). Algeciras, Spain, 18 June 1993, 4 specimens 5–19 mm preserved length (MNCN 15.05/17725). Puerto del Carmen, Lanzarote, Spain, 7 January 1993, 1 specimen 25 mm preserved length (MNCN 15.05/23782). São Vicente (May 1980), Boavista (27 May 1986) and Sal (3 May 1987), Cape Verde Islands, 4 specimens 14–20 mm preserved length, PARATYPES of *Doriopsilla ciminoi* (MNCN 15.05/23772), formerly deposited at the Universidad de Oviedo, Spain. Sal, Cape Verde Islands, 6 August 1985, 2 specimens 16–17 mm preserved length (MNHN); 9 August 1985, 2 specimens 15–20 mm preserved length; 10 August 1985, 1 specimen 11 mm preserved length (MNCN 15.05/23784). Boavista, 23 August

1985, 1 specimen, 17 mm preserved length (MNCN 15.05/23781). Guinea Conakry, 1953, 1 specimen, 29 mm preserved length, coll. Forest (MNHN).

Doriopsilla areolata albolineata Edmunds, 1968

(Figure 1E, F)

Doriopsilla albolineata Edmunds, 1968:93–95, fig. 9.

Type material: Holotype (by original designation): BMNH 19678W, Tema, Ghana, 22 January 1965, 6 mm preserved length.

Diagnosis: Background color varies from bright yellow to pearl grey. Mantle margin with radial and branched brown lines which lead from the center of the dorsum (Figure 1E, F). Irregular white lines cover the dorsum, the majority of which (90%) are transverse.

Remarks: *Doriopsilla albolineata* was the first well described Atlantic *Doriopsilla* species (Edmunds, 1968), but both the external and internal features are identical to specimens of *Doriopsilla areolata* from the Mediterranean Sea (previously described), except for the grey background color and the distribution of the white lines, most of which are transverse.

All the specimens collected from West Africa showed a similar color pattern, different from specimens collected in the Mediterranean. But in our opinion, a few color differences cannot be used to separate two species of this genus. However, specimens from West Africa have enough distinctive features to be recognized as a subspecies, such as the disposition of the white lines of the dorsum, the majority of which (90%) are transverse, whereas in the Mediterranean specimens they form a network. Another difference is the presence of radial and branched brown lines which lead from the center of the dorsum in the mantle margin of West African specimens.

Specimens from Angola are very similar to those collected from Ghana, with frayed white lines on the dorsum, most of which are transverse. But they differ in the background color, which is bright yellow in the former and grey, sometimes yellowish, but never yellow (M. Edmunds, personal communication), in the latter.

Geographic range: This subspecies is known from Ghana, São Tomé, and Angola, on the west coast of Africa (Figure 5).

Material examined: Tema, Ghana, 22 January 1965, 1 specimen, 6 mm preserved length, HOLOTYPE of *Doriopsilla albolineata*, coll. Pople (BMNH 19678W). Takoradi, Ghana, 5 March 1993, 1 specimen, 13 mm preserved length, coll. Templado (MNCN 15.05/23774). Miemia, Ghana, 9 March 1993, 1 specimen 12 mm preserved length, coll. Templado (MNCN 15.05/23773). Luanda, Angola, 28 January 1989, 1 specimen, 16 mm preserved length, coll. Rolán (MNCN 15.05/23786); 14 July

1989, 1 specimen, 15 mm preserved length, coll. Rolán (MNCN 15.05/23795); 18 July 1989, 1 specimen, 6 mm preserved length, col. Rolán (MNCN 15.05/23794); 23 July 1989, 1 specimen, 14 mm preserved length, coll. Rolán (MNCN 15.05/23791); 8 August 1989, 1 specimen, 11 mm preserved length, coll. Rolán (MNCN 15.05/23785); 20 August 1989, 2 specimens, 7–10 mm preserved length, coll. Rolán (MNCN 15.05/23790); 17 August 1989, 1 specimen, 11 mm preserved length, coll. Rolán (MNCN 15.05/23788). Corimba, Angola, 15 January 1989, 4 specimens 5–18 mm preserved length, coll. Rolán (MNCN 15.05/23792); 4 September 1989, 20 m depth, 1 specimen 19 mm preserved length, coll. Rolán (MNCN 15.05/23793). Praia Amelia, Angola, 17 November 1990, 1 specimen 26 mm preserved length, coll. Rolán (MNCN 15.05/23771); 1 specimen 19 mm preserved length, coll. Rolán (MNCN 15.05/23789); 21 November 1990, 1 specimen 30 mm preserved length, coll. Rolán (MNHN). São Tomé, 11 February 1989, 2 specimens 4–7 mm preserved length, coll. Rolán (MNCN 15.05/23787).

Doriopsilla areolata nigrolineata Meyer, 1977

(Figure 1G)

Doriopsilla nigrolineata Meyer, 1977:304–305, fig. 3.

Type material: Holotype (by original designation): USNM 760618, Galeta Point, Panama, 24 May 1971, 6 m depth, 23 mm long, 15 mm preserved length. Paratype: USNM 760619, Galeta Point, 24 October 1971, 1 specimen, 20 mm long.

Diagnosis: Background color varies from light to dark orange. Mantle margin without radial and branched brown lines. Covering the dorsum there is a frayed network of black lines (Figure 1G). Tubercle bases densely speckled with white.

Remarks: We have observed only one specimen (the holotype) of this uncommon nominal species. In the preserved specimen, the entire body is covered by a frayed network of black lines (Figure 1G). In life, following the description of Meyer (1977), specimens have “tubercle bases densely speckled with white” and “opaque white speckling over whole surface except margin and along the two lines where the large tubercles lie.” The background color of the body is light to dark orange in life and in the preserved holotype, there is a central dark area whose center is lighter.

Doriopsilla areolata nigrolineata differs most notably from the other subspecies of *D. areolata* by the presence of a network of black lines on the dorsum. However, all other external features of this subspecies are identical to those of eastern Atlantic material, such as the low and simply rounded tubercles (larger along two rows between rhinophores and gills), the yellow to pale brown background color (with a central dark area whose center is

paler), and the oral tentacles fused with only the tips free. Also, Meyer (1977) described “tubercle bases densely speckled with white” in *D. nigrolineata* exactly as occurs in specimens of *Doriopsilla areolata areolata* of similar size (roughly 25 mm). However, since we have not studied the reproductive system or the penial hooks of *D. nigrolineata*, this synonymy must remain open to question.

Marcus & Marcus (1967a) studied one specimen of *Doriopsilla areolata* from the Caribbean Sea (Virgin Islands), but it was preserved, and no white or black color remained on the skin. The subspecific allocation of this specimen remains uncertain.

Geographic range: At present, this subspecies is only known from the Caribbean coast of Panama (Figure 5).

Material examined: Galeta Point, Panama, 24 May 1971, 6 m depth, 1 specimen 23 mm long, HOLOTYPE of *Doriopsilla nigrolineata* (USNM 760618).

Doriopsilla pelseneeri d'Oliveira, 1895

(Figures 2B, 3B, 5–7)

Doriopsilla pelseneeri d'Oliveira, 1895: 12–13.

Dendrodoris minima Pruvot-Fol, 1951: 47.

Dendrodoris racemosa Pruvot-Fol, 1951: 44, figs. 28–29, pl. 2, 11–12.

Type material:

Doriopsilla pelseneeri, the type material is untraceable, it was collected from Sines, Portugal. Neotype (here designated): Muros de Nalón, Spain, 16 May 1992, 30 mm preserved length, coll. Rodríguez (MNHN).

Dendrodoris minima, the holotype of this species is presumed lost; it could not be located in MNHN; it was collected from Banyuls (France) or from the Spanish Mediterranean coasts. Neotype (here designated): Muros de Nalón, Spain, 16 May 1992, 30 mm preserved length, coll. Rodríguez (MNHN).

Dendrodoris racemosa, the type material of this species is presumed lost; it could not be located in MNHN; the type locality is Banyuls, France. Neotype (here designated): Muros de Nalón, Spain, 16 May 1992, 30 mm preserved length, coll. Rodríguez (MNHN).

Diagnosis: Background color varies from white to red as the animal grows. The edge of the gill pocket has a white ring. Dorsum covered with large, irregular warts stiffened by spicules, larger in the center of the dorsum. Oral tentacles separated, with a ventral groove.

Muscular pharyngeal bulb very short. Intestine with a pyloric gland on its proximal part. Penial hooks with a straight and very long cusp (200 to 300 µm) and a long narrow base.

External morphology: The background color varies as the animal grows. Juvenile specimens are uniformly

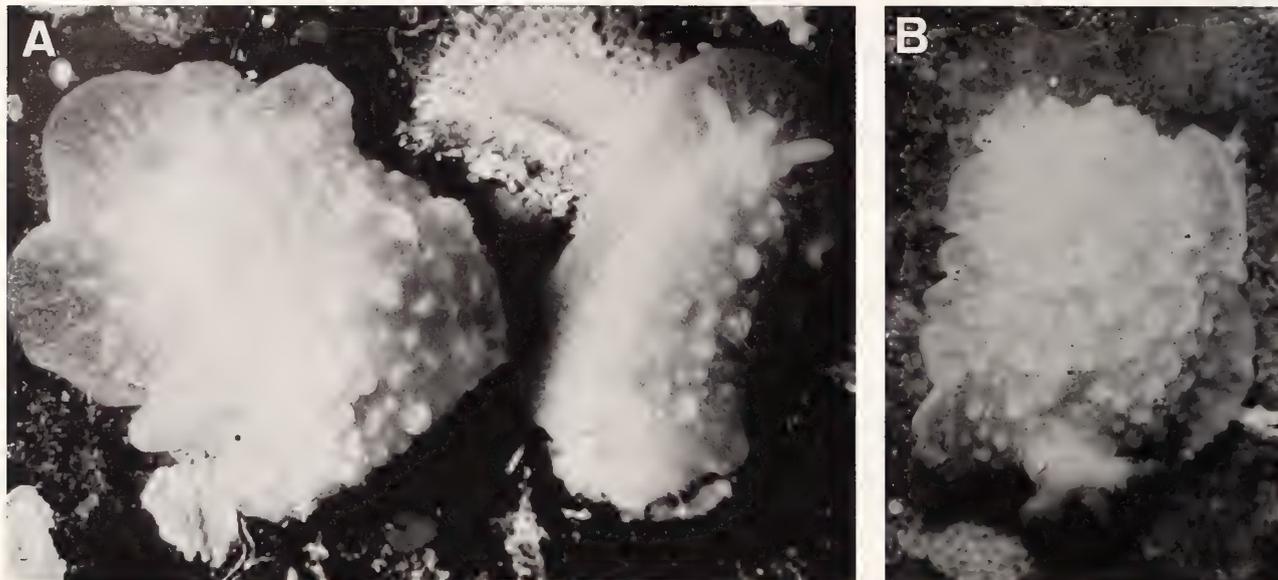


Figure 6

Photographs of specimens of *Doriopsilla pelseeneeri* showing external features, A. Specimens 15 and 30 mm long (MNCN 15.05/23779), B. Specimen 22 mm long (MNCN 15.05/23777).

white, larger ones are yellow or orange, and the largest are red. There is always a white ring around the edge of the gill pocket (Figure 6).

The whole center of the dorsum is covered by large and irregular tubercles (Figure 2B), similar to warts and stiffened with spicules. In general, tubercles are larger in the center of the dorsum, but there are small tubercles scattered between the largest. In the mantle margin only small tubercles remain, which disappear toward the edge.

The rhinophores are the same color as the body. Each rhinophoral clavus has eight to 25 lamellae. There are four to five tripinnate gills, similar in color to the body. They form a circle completed by the anus on the left.

Ventrally, the border of the mantle shows a strong network of spicules. The oral tentacles are small and separated, having a ventral groove (Figure 3B). The border of the foot covers the oral tentacles anteriorly and extends widely with a deep notch.

Anatomy: The muscular pharyngeal bulb is short (Figure 7A), its length is about twice its breadth. The tubular pharynx leads from the pharyngeal bulb. At this point, two thin retractor muscles insert onto the posterior of the bulb. The pharynx is very long and passes directly through the central nerve ring, it leads into the short and broad esophagus. The intestine has a pyloric gland on its proximal part.

The female gland is very large in mature specimens (Figure 7B); it can be larger than the digestive gland. The rounded gametolytic gland connects by a short duct with the seminal receptacle. At the point where this duct con-

nects with the gametolytic gland, two other ducts arise; one of them connects with the female gland, and the other one is the vagina. The ampulla is very large and elongated. There is a flat, granular, and very large prostate overlying all the former organs. The deferent duct is long and wider than the vagina; both open in a common atrium. The penis is covered by numerous hooks with a straight and very long cusp (200 to 300 μm) and a long narrow base (Figure 7C).

The large triangular heart is connected with the bilobed blood gland by the aorta. There is a rounded renal sac close to the heart and connected with the pericardium.

Geographic range: This species is at present known from the Iberian Peninsula (Figure 5), from the north Atlantic coast of Spain to Portugal and the Mediterranean coast of Spain and France (Ortea & Urgorri, 1979; d'Oliveira, 1895; Hidalgo, 1916; Ballesteros & Ortea, 1980; Cervera & García-Gómez, 1986; Pruvot-Fol, 1951).

Remarks: *Doriopsilla pelseeneeri* was originally described as being red or yellow in color, paler on the mantle margin, and having large, irregular tubercles on the dorsum (d'Oliveira, 1895). External features of our material are identical to this description, and no other Atlantic species of the genus *Doriopsilla* has this combination of characters.

Marcus & Marcus (1962) suggested that *Doriopsilla pelseeneeri* could be a local variety of *Doriopsilla areolata*. However, external features, such as the lack of white

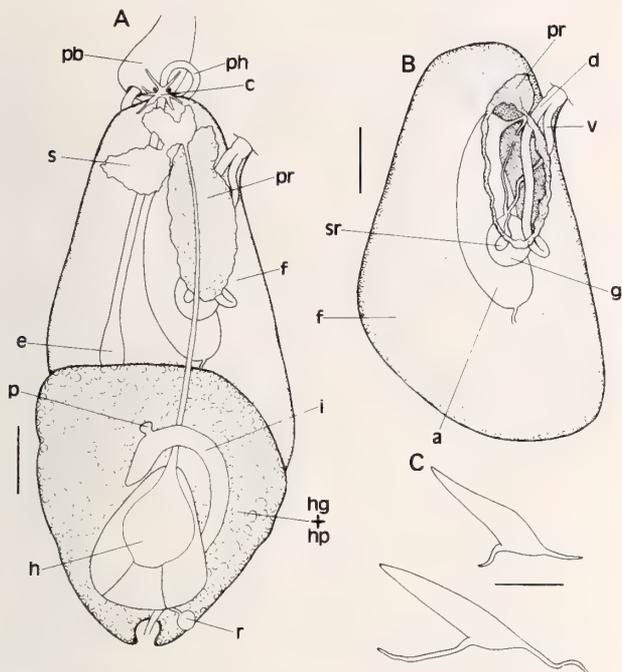


Figure 7

Anatomy of *Doriopsilla pelseneeri* (MNHN). A. Dorsal view of the anatomy (scale bar = 4 mm): bp, pharyngeal bulb; c, central nervous system; e, esophagus; f, female gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; ph, pharynx p, pyloric gland; pr, prostate; r, renal sac; s, blood gland. B. Reproductive system (scale bar = 4 mm): a, ampulla; d, deferent duct; f, female gland; g, gametolytic gland; pr, prostate; sr, seminal receptacle; v, vagina. C. Detail of the penial hooks (scale bar = 200 µm).

pigment in the dorsum of *D. pelseneeri* (except the white ring of the gill pocket), the shape of the dorsal tubercles (large, irregular warts in *D. pelseneeri*, and low, simply rounded tubercles in *D. areolata*), and the morphology of the oral tentacles, separated, grooved, and covered by the anterior edge of the foot in *D. pelseneeri*, and fused, ungrooved, and uncovered in *D. areolata*, clearly separate the two species.

Internally, the differences between both species are the relative length of the pharyngeal bulb, much longer in *Doriopsilla areolata* than in *Doriopsilla pelseneeri*, the presence of a pyloric gland in the intestine of *D. pelseneeri*, and the shape of the penial hooks, with a long base and straight cusp in *D. pelseneeri*, and short base and curved cusp in *D. areolata*.

Pruvot-Fol (1951) described the Mediterranean species *Dendrodoris racemosa* Pruvot-Fol, 1951, and *Dendrodoris minima* Pruvot-Fol, 1951, as having the dorsum covered by large, irregular warts. Valdés et al. (1996) suggested that these two species must be included in the genus *Doriopsilla* and considered synonyms of *Doriopsilla pelseneeri*. Pruvot-Fol (1951) described *D. racemosa*

as being yellow in color and lacking oral tentacles; this is similar to *D. pelseneeri*, which can be yellow and has the oral tentacles covered by the border of the foot. *Dendrodoris minima* was characterized by two large lobules in the anterior border of the foot (Pruvot-Fol, 1951), again similar to *D. pelseneeri*. Also, the drawings by Pruvot-Fol (1951, pl. 2: 11–12, figs. 28, 29) of *D. racemosa* show an external morphology and anatomy identical to *D. pelseneeri*. The type material of these two species is lost, but all evidence indicates that they must be considered synonyms of *D. pelseneeri*. Two unnamed species described in the same paper (Pruvot-Fol, 1951) and included in the genus *Dendrodoris*, as *Dendrodoris* sp. 1 and *Dendrodoris* sp. 2, are externally very similar to our material of *D. pelseneeri* and probably belong to this species.

Material examined: Muros de Nalón, Spain, 16 May 1992, 1 specimen, 30 mm preserved length, NEOTYPE of *Doriopsilla pelseneeri*, *Dendrodoris minima*, and *Dendrodoris racemosa*, coll. Rodríguez (MNHN); 10 August 1991, 7 m depth, 1 specimen, 35 mm preserved length, coll. Rodríguez (MNHN). Setubal, Portugal, 4 May 1995, 6 m depth, 1 specimen 19 mm preserved length, coll. Calado (IMP R311622). Fauna Ibérica I expedition, sta. 23A (36°24.05'N, 5°00.99'W), Málaga, Spain, 30 m depth, 13 July 1989, 2 specimens 11–14 mm preserved length (MNCN 15.05/23777); sta. 56A (36°09.81'N, 6°09.21'W), Trafalgar, Spain, 24 m depth, 20 July 1989, 1 specimen 2 mm preserved length (MNCN 15.05/23778); sta. 58A (36°08.60'N, 6°01.20'W), Trafalgar, Spain, 34 m depth, 2 specimens 14–26 mm preserved length (MNCN 15.05/23779).

Doriopsilla pharpa Marcus, 1961

(Figures 2C, 3C, 5, 8)

Doriopsilla leia Marcus, 1961: 144–146, figs. 15–18.

Doriopsilla pharpa Marcus, 1961: 146, figs. 19–21.

Type material: The type material of *Doriopsilla leia* and *Doriopsilla pharpa* was recorded from North Carolina (U.S.A.) by Dr. Harry W. Wells and returned to him after its study (Marcus, 1961). Later, Dr. Wells donated this material to the USNM.

Doriopsilla leia. Marcus (1961) originally designated a holotype (an 8 mm specimen) for this species. However, the three specimens collected by Dr. Wells were together in the same vial with the label “holotype+paratype and therefore all of them are considered syntypes.” We have selected one specimen as lectotype: USNM 575616, Beaufort, North Carolina, USA, 20 July 1955, 8 mm preserved length, dissected. Paralectotypes: USNM 880115, Beaufort, 20 July 1955, 2 specimens 7–8 mm preserved length, dissected.

Doriopsilla pharpa. Lectotype (here selected): USNM

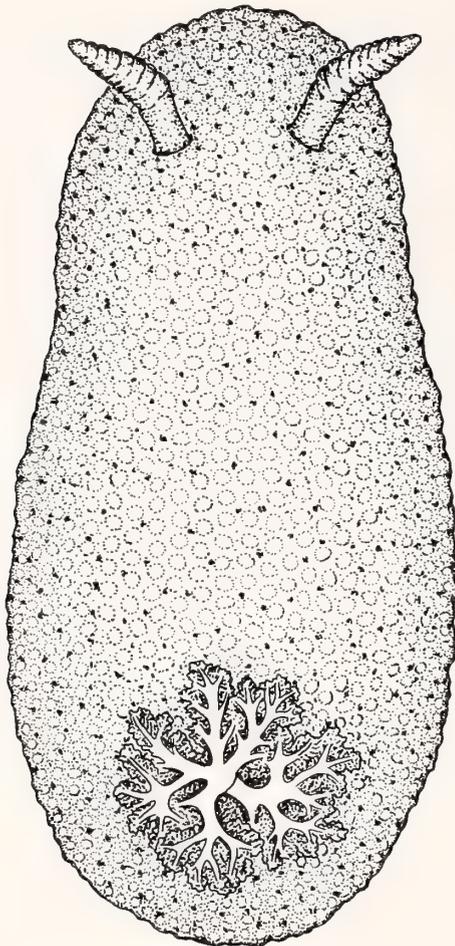


Figure 8

Dorsal view of a living animal of *Doriopsilla pharpa* from Cuba (scale bar = 3 mm).

575617, Beaufort, North Carolina, USA, date unknown, 15 mm preserved length, dissected; paralectotypes: USNM 880116, Beaufort, date unknown, 5 specimens 5–9 mm preserved length, three of them dissected.

Diagnosis: Background color yellow with numerous dark brown spots. The edge of the gill pocket does not have a white ring. Dorsum covered with numerous small tubercles stiffened by spicules which project out of the tubercles. Oral tentacles fused together, with only the tips free.

Penial hooks elongated with a short base and a very curved cusp.

External morphology: The background color of the living animals is yellow. Numerous dark brown spots (chromatophores) are scattered over the entire dorsum (Figure 8). The rhinophores and the gills have the same color as the body.

The whole surface of the dorsum, including the edge of the mantle margin, is covered with numerous small tubercles stiffened by spicules which project out of the tubercles. All tubercles have a similar size; they are scattered very close together, never forming rows.

Ventrally, the oral tentacles are long and fused together, with only the tips free. The anterior border of the foot is a little notched, and it never overlies the oral tentacles.

Anatomy: Marcus (1961: figs. 17, 21) studied and drew the reproductive system of this species. Our specimens were too small for anatomical studies, and the type specimens were all previously dissected, having the reproductive systems destroyed. Following Marcus' drawing, the female gland is very small. From the elongated gametolytic gland lead two ducts; one of them is branched and connects with the seminal receptacle and the female gland; the other is the vagina. The ampulla is very large and elongated. The prostate is very small and tubular shaped; however, the later described specimens from Georgia by Marcus & Marcus (1967c), have the prostate "considerably wider" than in the original description. The deferent duct is longer and as wide as the vagina in the distal part. The penis is covered by numerous hooks elongated with a short base and a very curved cusp.

Biology: Eyster & Stancyk (1981) reported this species eating the sulfur burrowing sponge *Cliona celata* Grant, 1826.

Geographic distribution: This species is presently known from Massachusetts (Morse in Eyster, 1980); Maryland (Marcus & Marcus, 1972); Virginia (Vogel in Eyster & Stancyk, 1981); North Carolina (Marcus, 1961, Eyster, 1980); South Carolina (Shoemaker et al., 1978); Georgia (Marcus & Marcus, 1967c); and Florida (Eyster, 1980). The present paper constitutes the first record from Cuba.

Remarks: Marcus (1961) described *Doriopsilla leia* and *Doriopsilla pharpa* from North Carolina based on preserved specimens. Both species show very similar features, and they were separated (Marcus, 1961) by the presence of dorsal tubercles and the contiguous pedal ganglia in *D. pharpa*. We have observed the type material of both nominal species and we have not found consistent differences between *D. leia* and *D. pharpa*. Specimens of *D. leia* have dorsal tubercles as in *D. pharpa*, but the spicules have been dissolved and tubercles are inconspicuous. Also, the reproductive systems of both nominal species, drawn by Marcus (1961, figs. 17, 21) are identical. All evidence indicates that *D. leia* and *D. pharpa* must be considered subjective synonyms. In Marcus' original description, *D. leia* is mentioned first, but we have chosen *D. pharpa* as the name for this species because it was better described and has been more used in the literature (see Marcus, 1967c; Marcus, 1972; Shoemaker et al., 1978; Eyster, 1980; Eyster & Stancyk, 1981). In selecting

the name *D. pharpa* over *D. leia*, we are acting as "first revisor" under the provisions of the Code.

Doriopsilla pharpa is distinguished from the other two Atlantic species mainly by the external coloration. It is the only species which has a yellow background color with numerous dark brown spots over the whole dorsum. *Doriopsilla areolata* also has a yellow background, but it is easily distinguished by the presence of white pigment on the dorsum. The long, fused oral tentacles and the numerous, minute tubercles (all of a similar size), which are present in the mantle margin edge, are also characteristic of *D. pharpa*. *D. areolata* also has the oral tentacles fused, but they are shorter than those of *D. pharpa*. *D. pelseneeri* can have a yellow color when juvenile, like *D. pharpa*, but the former always has a white ring in the branchial pocket and lacks dark brown spots. *D. pelseneeri* and *D. areolata* have larger tubercles than *D. pharpa* and they are not on the mantle margin edge. Internally, *D. pharpa* is very different from *D. areolata* and *D. pelseneeri*. The former has a tubular prostate, while the other two species both have a large and flat prostate. Another difference of *D. pharpa* is the disposition of the ducts from the gametolytic gland (three in *D. areolata* and *D. pelseneeri*, and two in *D. pharpa*).

Material examined: Cienfuegos, Cuba, 13 August 1988, 1 specimen 8–11 mm preserved length. Beaufort, North Carolina, USA, 20 July 1955, 1 specimen 8 mm preserved length, LECTOTYPE of *Doriopsilla leia* (USNM 575616); 2 specimens 7–8 mm preserved length, PARALLECTOTYPES of *Doriopsilla leia* (USNM 880115); date unknown, 1 specimen 15 mm preserved length, LECTOTYPE of *Doriopsilla pharpa* (USNM 575617); 5 specimens 5–9 mm preserved length, PARALLECTOTYPES of *Doriopsilla pharpa* (USNM 880116)

DISCUSSION

In the Pacific coast of North America there is a group of species of *Doriopsilla* with white rings around the tubercles of the dorsum: *Doriopsilla nigromaculata* (Cockerell in Cockerell & Eliot, 1905), *Doriopsilla rowena* Marcus & Marcus, 1967, and *Doriopsilla janaina* Marcus & Marcus, 1967. On the basis of their external features described by Cockerell & Eliot (1905) and Marcus & Marcus (1967a, b), these three nominal species could be synonyms of *D. areolata*. We have studied several specimens from the Galapagos very similar to the original description of *D. rowena* whose internal anatomy was identical to the Atlantic *D. areolata*. Only a full review of the genus *Doriopsilla* in the Indo-Pacific will clarify the status of northwest American species and their taxonomic relationships with *Doriopsilla areolata*.

Doriopsilla albopunctata (Cooper, 1863) [synonyms: *Doriopsilla reticulata* (Cockerell & Eliot, 1905), *Doriopsilla fulva* (MacFarland, 1905)] from the Pacific coast of North America has been described as having one white

spot in the center of each dorsal tubercle (Cooper, 1863; Cockerell & Eliot, 1905; MacFarland, 1905). It is easily differentiated from *Doriopsilla areolata*, because the latter never has white pigment on the tubercles.

Doriopsilla capensis was originally described from the Atlantic coast of South Africa (Bergh, 1907) as having a whitish background color with the nodules of the dorsum white. This pattern differs from that of *Doriopsilla areolata albolineata* (the West African subspecies of *D. areolata*), which have a background color yellow to pale grey with white lines on the dorsum, most of them transversal. Gosliner (1987) reported two other species of *Doriopsilla* from South Africa. One of them, reported as *Doriopsilla miniata*, has a color pattern very close to *Doriopsilla areolata*, and they are probably conspecific. However, the material from South Africa is distinguished from the subspecies *D. areolata albolineata* by the network of white lines, which is formed by transverse as well as longitudinal lines. This specimens could be included in a new subspecies of *D. areolata*. The other species, *Doriopsilla* sp. 1, is very different from other Atlantic species in the color pattern, which is white to brown with large black spots on the dorsum.

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Cross-Species Associations of *Octopus cyanea* Gray, 1849 (Mollusca: Cephalopoda)

by

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Abstract. Casual observation of several *Octopus* species suggested that the modification of the habitat involved in construction of sheltering dens might attract other animal species, sometimes called "den associates." A study comparing the presence of motile epibenthos in areas around dens of *Octopus cyanea* with nearby control areas quantified this assumption. One species group, juvenile *Scaerigus* parrotfish, was significantly less likely to be found around *O. cyanea* dens, possibly because den construction disrupted growth of algae on which the parrotfish fed. Two species, the wrasse *Thalassoma duperry* Quoy & Gaimard, 1824, and the hermit crab *Calcinus latens* Randall, 1839, were more likely to be found at dens of *O. cyanea*. Both species appeared to be scavenging on the remains of prey left by octopuses, and their presence thus appeared to indicate an opportunistic but loose association.

INTRODUCTION

Animal species from a variety of taxa physically modify their environment to provide shelter and, when occupying such areas, attract other species to these locations. Thus the ancestors of the domestic dog were attracted to the shelter of early hominids (Olsen, 1985) and starlings nest in abandoned woodpecker holes. An example in the marine environment is sea anemones which attach to empty gastropod shells used by hermit crabs (Ross, 1974). Octopuses build homes (also called dens), and Mather (1994) has described the modification of the rocky sea bottom that is involved. Does this physical modification of the environment lead to a symbiotic relationship (Smith & Douglas, 1987) between the octopus and other species? If so, is the attraction in the shelter of the space itself, or does some

other aspect of the octopus' presence attract other species, and is the association a flexible or an obligate one?

Although it has been little examined because of the lack of observations of octopuses in the ocean, some documentation of such association exists. Hartwick & Thorarinsson (1978) listed a variety of fish, echinoderm, crab, and snail species found within the sheltering dens of *Octopus dofleini* Wülker, 1910, and discussed whether they might be "den associates." Mather (1992) reported the frequent occurrence of scavenging wrasse and territorial damselfish around juvenile *O. vulgaris* Cuvier, 1797, in Bermuda. She found that fish were nearby significantly more often when octopuses were out of home foraging across the rocky bottom than when they were sheltering in the home. Animals could be attracted to octopus den sites not by shelter but by the remains of prey, including empty gastropod shells, which

octopuses leave both in the shelter and outside (Ambrose, 1983; Hartwick et al, 1978; Ambrose & Nelson, 1983; Mather, 1991). To find out whether any species is truly associated with octopus homes and why, a study must both quantify the number of sightings of such species and compare this with observations at areas without octopus dens. The opportunity to do such a study arose during observations of feeding and activity of *Octopus cyanea* Gray, 1849, in Hawai'i.

MATERIALS AND METHODS

During August, 1993, homes containing adult *O. cyanea* were monitored on the approximately 40 hectares of shallow (1–2 m) fringing reef surrounding Coconut Island in the reef-sheltered Kane'ohe Bay, O'ahu. The minimum distance between homes was 50 meters. In preparation for observation of associates, a circular area one meter in diameter was delineated with string around each of six dens occupied by an octopus and chosen for continuity of occupancy. A circle was marked out similarly around a control area 2 to 3 meters away, on the reef face and as close as possible in habitat type (coral, broken coral rubble, and sand) to the home area. Since octopuses chose potential home sites and modified them rather than selecting appropriate unmodified sites for homes (Mather, 1994), an approximate match was adequate for a control in this instance. Observers watched the home area and the control area for 20 minutes each, one right after the other, randomly choosing which to observe first, remaining as still as possible and moving as far away as possible, compatible with seeing the animals. While some observer effect is likely, there is no reason for any difference across sites. They recorded the number and duration of the presence of individuals of species which could be designated as motile epibenthos, found either on the surface of the coral or rubble or just above it and capable of moving into and out of the area, at control and den sites. Observations took place between 0630 and 1900; octopuses were usually present, as *O. cyanea* has a crepuscular activity pattern (Yarnall, 1969). This observation continued over a period of 10 days, until six sets of observations had been accumulated for each octopus home.

RESULTS

Seventeen species of animal were recorded as motile epibenthos within home or control areas (Table 1). Most were fish that swam in the shallow water immediately above the bottom, though some were crustaceans and mollusks walking or crawling on the reef surface. Only four species were sufficiently often observed that quantitative comparison of their presence could be made. Data about the number and duration of visits of these species were submitted to 2-way repeated-measures Analyses of Variance, with Octopus and Area as variables. Results were as follows:

Table 1

Motile epibenthic animals observed near homes of *Octopus cyanea* and in nearby control areas (N = 6)

	Number of sites observed at:	
	Home	Control
Fish Species:		
	Bluespotted goby— <i>Asterropteryx semipunctatus</i> Rüppell, 1830	6 6
**	Saddleback wrasse— <i>Thalassoma duperrey</i> Quoy & Gaimard, 1824	6 6
**	Juvenile parrotfish— <i>Scarus</i> sp.	4 6
	Zebra blenny— <i>Istiblennius zebra</i> Vailant & Sauvage, 1875	3 4
	Striped wrasse— <i>Coris flavovittata</i> Bennett, 1829	1 3
	Convict tang— <i>Acanthurus triostegus</i> Linnaeus, 1758	0 1
	Bird wrasse— <i>Gomphosus varius</i> Lacepède, 1801	2 3
	Sergeant— <i>Abudefduf sordidus</i> Forsskål, 1775	1 0
	Yellowstripe goatfish— <i>Mulloides flavolineatus</i> Lacepède, 1801	0 1
	Sergeantfish— <i>Abudefduf abdominalis</i> Quoy & Gaimard, 1824	1 1
	Whitespot puffer— <i>Arothron meleagris</i> Lacepède, 1798	0 1
	Cornetfish— <i>Festularia commersoni</i> Rüppell, 1838	0 1
Crustacean Species:		
**	Whitetip hermit crab— <i>Calcinus latens</i> Randall, 1839	5 2
	Hairy xanthid crab— <i>Phymodius monticulosus</i> Dana, 1852	4 3
	Smooth crab— <i>Leptodius exaratus</i> Edwards, 1869	0 2
	Portunid crab— <i>Thalamita integra</i> Dana, 1852	0 1
Mollusk Species:		
	Top snail— <i>Trochus intextus</i> Kiener, 1850	5 4

** Difference in occurrence ($P \approx 0.05$) between Home and Control areas.

- (1) The most reliably observed species was a small (3 cm long) fish, the bluespotted goby (*Asterropteryx semipunctatus* Rüppell, 1830). These territorial fish were resident within the crevices and gaps in the coral reef surface. On average, there were 2.9 resident within home areas and 2.4 within control areas, not a significant difference by *t*-test ($P > 0.05$). Gobies were not attracted to homes, but they did not avoid the much larger octopuses, and sometimes carried on territorial fights and chases right over top of the arms of a resting octopus.
- (2) A second common fish was the saddleback wrasse,

Thalassoma duperry, which moved actively in the shallow water over the reef face. Observations of the presence of wrasse were converted into a percentage of time a fish was present. They were more likely to be present in the home area (11% of the time) than in the control area (3%); the significance is marginal, $F(1,5) = 6.01$, $P = 0.058$, despite the large mean difference because of the variable duration of the fishes' presence. Wrasse were common on the reef face, patrolling for food to scavenge, and patrols were more frequent and longer in the home areas.

- (3) A common crustacean species was the small (2 cm long) whitetip hermit crab, *Calcinus latens*, which forages in reef crevices. Crabs were significantly more often found in den areas (70% of the time versus 10% for control areas), $F(1,5) = 15.97$, $P = 0.01$. As with the wrasse, the hermit crabs were observed using the octopus dens as a location for periods of scavenging. As empty gastropod shells were almost never a component of prey remains (Mather, 1993; Van Heukelem, 1966), snails were not normally captured by the octopuses. Hermit crabs appeared to be ignored; during observation one fell off the vertical side of a den onto the arm of a resting octopus, which picked it up with a sucker and pushed it back onto the wall.
- (4) A very common group of species in the water above the reef surface was the herbivorous juvenile parrotfishes, *Scarus* sp., (individuals can only be identified to genus as juveniles). They foraged on the algae growing on the reef face in large schools of varying number, up to 50. They were significantly more likely to be found in the control than home areas, 12% versus 24% of the time, $F(1,5) = 9.32$, $P = 0.028$. Algae might grow more densely on the undisturbed surface of the control areas; octopuses were never seen to interact with parrotfish.

DISCUSSION

The results of these observations indicate that the modification of their physical environment by octopuses attracted other species. The two species commonly attracted were scavengers. Most of the time that they were under observation, hermit crabs in the octopus homes were picking at the substrate with their chelae. Wrasse moved into and out of octopus homes, and once, four wrasse surrounded a den area after an octopus pushed out remains of crab prey, spending 10 minutes picking at food remaining on the exoskeletons. Losey (personal communication) reported that individual wrasse on the reef around Coconut Island learn to specialize in utilizing the opportunities for scavenging around specific target species, though we were not able to confirm this because fish were never captured and marked. Hartwick & Thorarinsson (1978) noted the presence of scavengers, including sculpin fish, the echinoderm *Pycnopodia*, the spider crab *Hyas*, and the snail *Amphissa*, near the dens of *O. dofleini*. Mather (1992)

observed that the wrasse *Halichoeres* not only followed foraging *O. vulgaris* for the opportunity of capturing escaping potential prey, but also attended octopuses in their dens to consume pieces of prey remains.

What do octopuses do about the attendance of these scavengers? No reports were given on *O. dofleini* (Hartwick & Thorarinsson, 1978). *O. cyanea* were never observed reacting to hermit crab and wrasse scavengers. Hermit crabs were captured and eaten by smaller octopus species such as *O. vulgaris* and *O. joubini* Robson, 1929 (see Mather, 1980) but not by these *O. cyanea* (Mather, 1993; Van Heukelem, 1966), possibly because of the great size difference. *O. vulgaris* (Mather, 1992) occasionally blew jets of water or aimed a "slap" of an arm or two at scavenging wrasse, but generally ignored them also. Sometimes scavengers are at danger from the predators they attend (Barnard, 1984), but this seemed only occasionally true for these species.

This study confirms and extends Hartwick & Thorarinsson's (1978) suspicion that when octopuses modify their environment, they produce a microhabitat that might provide food or shelter and attract other species. Nevertheless, the pairing is not obligate for the species attracted, and the cause is probably not the modification itself but the food that octopuses bring home to consume. *O. vulgaris* consumes 2/3 of its food within the home (Mather, 1991), and preliminary observation confirm this also for *O. cyanea* (Mather, 1993) and octopuses can live in the same shelter for months (Hartwick et al, 1984; Mather, 1994). Thus this is probably an adaptive food-getting strategy for the scavenger. While the association appears opportunistic and fits only the most liberal definition of symbiosis (Smith & Douglas, 1987), it must be remembered that the association between early hominid shelter and the ancestors of the domestic dog probably began as a similar scavenging relationship, with ensuing physical (Olsen, 1985) and behavioral (Fentress, 1992) changes. Over time, the association between octopuses and scavengers may also become tighter.

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Quantitative Karyotype of *Choromytilus chorus* (Mollusca: Bivalvia: Mytilidae)

by

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Abstract. Chromosomes of the mussel *Choromytilus chorus* were studied using mitotic metaphase plates from early embryos. The diploid chromosome number was $2n = 30$, and the karyotype showed metacentric and submetacentric chromosomes. Heteromorphic pairs and the nucleolar organizer region (NOR) were not observed clearly. The karyotype of this species differs from those of other species of Mytilidae in chromosome number and chromosome morphology of metacentric and submetacentric chromosomes, and absence of subtelo-centric chromosomes.

INTRODUCTION

Chromosome numbers are known for most bivalve mollusks currently cultured. The species belonging to the family Mytilidae that have been studied cytogenetically are *Mytilus edulis* Linnaeus (Lubet, 1959; Menzel, 1968; Moynihan & Mahon, 1983; Dixon & Flavell, 1986), *M. californianus* Conrad (Ahmed & Sparks, 1970), *M. coruscus* Gould (Ieyama & Inaba, 1974), and *M. desolationis* Lamy, and *M. galloprovincialis* Lamarck (Thiriot-Quievreux, 1984). The diploid chromosome number is constant for all species with $2n = 28$. However, karyotypic differences were found in different populations of *M. galloprovincialis* (Martinez-Lage et al., 1992; Pasantés et al., 1990). The chromosome number found in *Perumytilus purpuratus* La-

marck (Alvarez-Sarret et al., 1991) is the largest found in a species of the family Mytilidae with $2n = 34$. For *Brachidontes recurvus* Rafinesque a mitotic chromosome number of 15 was found, and the chromosomes could not be arranged in pairs because of their differences in length (Diupotex-Chong et al., 1978).

Another species of the family Mytilidae, *Choromytilus chorus* Molina, 1782, shows a discontinuous distribution along the Chilean and Peruvian coast, from Callao (Perú) to the Magallanes Strait, at the southernmost tip of Chile (Osorio, 1979), but there is no record of occurrence of this species between Los Vilos (31°55'S, 71°30'W) and Arauco (37°25'S, 73°30'W). This separation into northern and southern populations perhaps took place in the early Quaternary (Viviani, 1979).



Figure 1

Metaphase plate from cleavaged eggs (Feulgen reaction stain).

Basic biological studies of this species are rare, but attempts have been made to understand its fertilization and early larval development (Toledo et al., 1990). This species is much larger than other mussels, and it is a potential species for culture.

The present study describes the mean karyotype of *Choromytilus chorus* from samples collected from the northern population, and a comparison with the karyotypes from *Mytilus edulis* (Moynihan & Mahon, 1983) and *M. desolationis* (Thiriôt-Quévèreux, 1984).

MATERIALS AND METHODS

Adult specimens, larger than 14 cm shell length, were collected in Los Choros Bay (20°14'S, 71°30'W), Chile. Ten animals of each sex were chosen, and in vitro fertilization was performed using pooled male and female gametes, obtained by gonad stripping. The eggs from this species are in meiotic prophase with a germinal vesicle (Lozada et al., 1971; Cortés, 1978). The development of cleavages was observed, and after 3 hours, four samples of 100–200 embryos were incubated in 0.01% colchicine in seawater for 2 hours. Then they were hypotonized in 30% diluted seawater for 10 minutes (Beaumont & Gruffyd, 1974), and fixed in fresh Carnoy (methanol: acetic acid, 3:1) for at least 1 hour. The samples were washed several times in fixative to partially dissolve the yolk (Longwell & Stiles, 1968), and finally stored in acetic acid (50%) at 4°C. The fixed samples were stained using a modified Feulgen technique (Darlington & La Cour, 1976), and squashed with propionic-carmin. The chromosomes were counted in 170 metaphase plates, in four to eight cell embryos. The best 20 metaphase plates (without overlapping) were photographed, and the chromosomes measured and arranged according to length and shape. The measurements of the long arm (LA) and the short arm (SA) were expressed as a percentage of the total length of the haploid chromosome set. To obtain a detailed description of chromosome morphology to aid

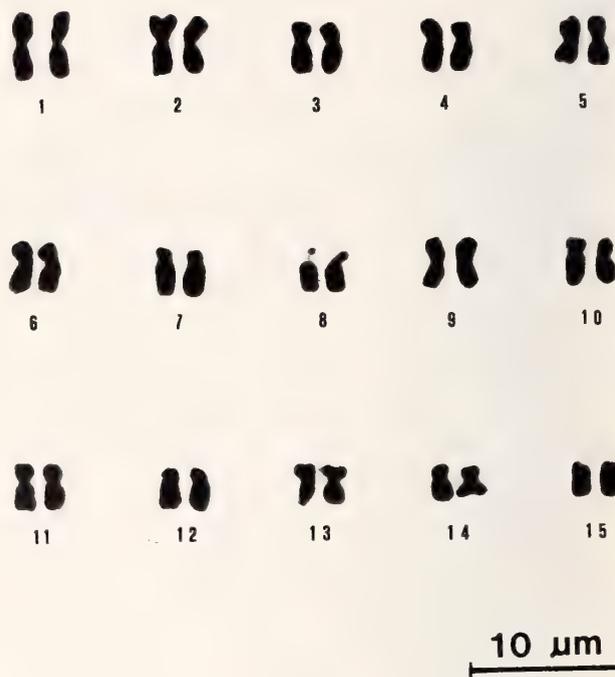


Figure 2

Karyotype of *Choromytilus chorus*.

future comparisons, means and confidence intervals of relative arm lengths of each chromosome pair were plotted in a karyo-idiogram (Spotorno, 1985), using the nomenclature of centromeric position proposed by Levan et al. (1964).

RESULTS

A diploid complement of $2n = 30$ was found in 170 metaphases from cleavaged eggs (Figure 1). The karyotype of *C. chorus* can be observed in Figure 2. There are no visible secondary constrictions or other conspicuous features in the karyotype. Table 1 shows the mean relative arm length of each chromosome pair with the confidence interval and standard deviation. The karyo-idiogram (Figure 3) shows that *C. chorus* has an almost symmetric karyotype with 10 chromosome pairs located at the metacentric area (M), while the remaining five pairs are in the submetacentric region (SM). In the same figure, the 14 chromosome pairs of *Mytilus edulis* described by Moynihan & Mahon (1983) and those described for *M. desolationis* by Thiriôt-Quévèreux (1984) were included as comparison.

DISCUSSION

The karyotype of *Choromytilus chorus* shows significant differences in number as well as in chromosome morphology with those described for *Mytilus edulis*, *M. de-*

Table 1

C. chorus chromosome, mean relative length, 95% confidence interval (CI), and standard deviation (SD) of the long arm (LA) and short arm (SA).

Chrom. pair	SA +	CI	SD	LA +	CI	SD
1	4.48	0.22	0.39	4.83	0.25	0.44
2	3.76	0.22	0.38	4.55	0.23	0.40
3	3.29	0.25	0.43	4.43	0.23	0.40
4	2.86	0.28	0.49	4.73	0.22	0.38
5	2.57	0.26	0.46	4.67	0.17	0.29
6	2.64	0.26	0.46	4.43	0.17	0.29
7	2.54	0.28	0.49	4.46	0.28	0.48
8	2.67	0.38	0.66	3.94	0.28	0.49
9	2.43	0.24	0.41	4.11	0.3	0.52
10	2.00	0.2	0.36	4.24	0.21	0.37
11	2.13	0.19	0.34	3.81	0.27	0.47
12	2.23	0.19	0.34	3.48	0.32	0.56
13	1.76	0.21	0.37	3.66	0.26	0.46
14	1.96	0.15	0.25	2.99	0.21	0.37
15	1.78	0.08	0.13	2.65	0.22	0.38

solationis, and other mussels. From the 10 metacentric chromosome pairs of *C. chorus*, the pairs 1, 4, 6, 8, 9, 14, and 15 have no morphological similarity with any of the metacentric pairs belonging to the other species (Figure 3). In case of the submetacentric pairs, *M. edulis* shows eight pairs, *C. chorus* has only five and has no subtelocentric pairs like those present in *M. desolationis*.

The resemblance between the karyotypes is the size of the chromosomes observed in the three species, and the pairs 2, 3, 10, and 13 of *C. chorus* show a reasonable degree of superimposition with the pairs 3, 4, 13, and 14 of *M. edulis* (Figure 3), reason to consider them morphologically similar (Spotorno, 1985). The same situation can be observed between the chromosome pairs 7 and 12 of *C. chorus* with the pairs 9 and 12 of *M. desolationis*. This analysis suggests that the karyotype of *C. chorus* is more similar to that of *M. edulis* than to *M. desolationis*. However, these similarities could change because the data of *M. edulis* and *M. desolationis* are unique values without standard deviation or confidence interval. On the other hand, the existence of chromosomes similar in size, but with the centromere in a different position, could imply that during evolution or differentiation of these karyotypes, pericentric inversions could have occurred, like those proposed to explain the differences found in other species of Mytilidae (Ahmed & Sparks, 1970; Thiriot-Quievreux & Ayraud, 1982; Thiriot-Quievreux, 1984).

The symmetric tendency of the *C. chorus* karyotype has been described in other mussels (Thiriot-Quievreux & Ayraud, 1982; Thiriot-Quievreux, 1984; Moynihan & Mahon, 1983; Dixon & Flavell, 1986) and in oysters (Ahmed & Sparks, 1967; Ahmed, 1973; Ladrón de Guevara et al., 1994), where also only metacentric and submeta-

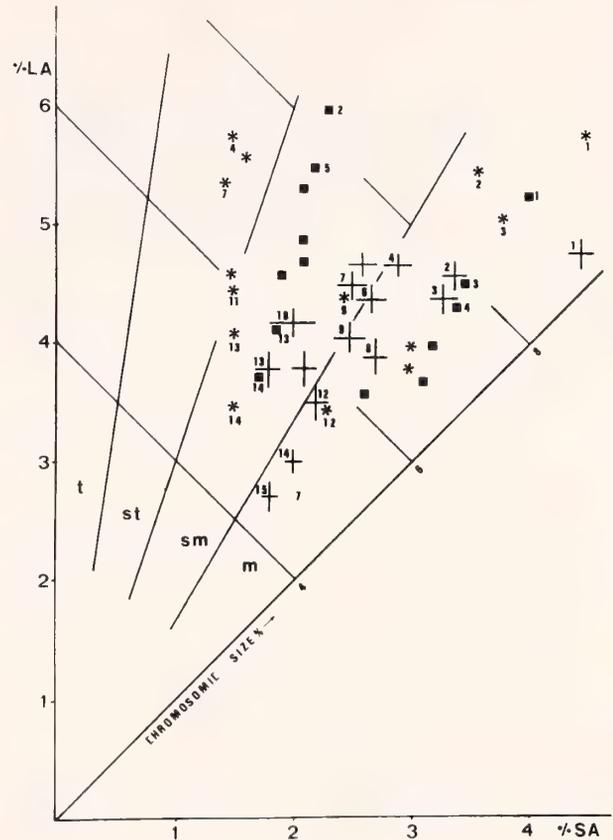


Figure 3

Mean karyo-idiogram of *Choromytilus chorus*. The symbols represent: + = means and confidence intervals (95%) for each chromosome pair, \blacksquare = chromosomes of *Mytilus edulis*, and * = those of *Mytilus desolationis* t = telocentric; st = subtelocentric; sm = submetacentric; m = metacentric LA = long arm, SA = short arm.

centric chromosomes were observed. Furthermore, other cytogenetic characteristics such as C-bands and the position of active nucleolar organizer region (NOR) within the karyotype of *C. chorus* must be determined to improve its karyotype description. Finally, Knowing the karyotype and the phylogenetic relationships of *C. chorus*, a species considered to have potential for commercial culture like *M. edulis* (Newkirk et al., 1980), within the group, opens up the possibility of hybridization and triploid induction, as has already been successfully achieved in *M. edulis* (Yamamoto & Sugawara, 1988; Desrosiers et al., 1993) and *M. galloprovincialis* (Scarpa et al., 1994).

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Growth and Production of an Intertidal Population of the Chiton *Plaxiphora aurata* (Spalowski, 1795)

by

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Abstract. A population of *Plaxiphora aurata* was studied by non-destructive sampling from March 1994 to March 1995 at Quequén (Argentina). Chitons occurred in hollows on shaded vertical walls, but were absent on horizontal substrata. Density fluctuated between 7.3 and 11.8 ind. m⁻² (mean: 9.5 ind. m⁻²). Recruitment occurred during early summer. Recruits were patchily distributed on the substratum during the early phases of benthic life, occurring in areas where larger chitons were rare or absent. A Von Bertalanffy growth model was fitted by simultaneous analysis of five size-frequency distributions. This method gave an estimation of $K = 0.359$ and $L_{\infty} = 53.0$ mm. Growth rate decreased in winter during the second year of benthic life, but not during the first year. The longevity of this species was estimated at 6–7 y. A survey of museum collections showed that maximum size was significantly correlated with latitude, reaching 95 mm in Tierra del Fuego. Annual production amounted to 3.51 g.m⁻².y⁻¹ (dry weight). Cohorts recruited in 1994, 1993, and 1992, accounted for 58%, 28%, and 12% of this total, respectively. Cohorts recruited in 1991 or before accounted for only 2% of the total production. Mean annual biomass amounted to 3.44 g.m⁻². The production/biomass ratio was 1.02.

INTRODUCTION

Population ecology has been studied in only a relatively few species of chitons. Several studies have reported observations on growth rates and longevity (Heath, 1905; Crozier, 1918a, b; Arey & Crozier, 1919; Grave, 1932; Boolootian, 1964; MacGinitie & MacGinitie, 1968; Glynn, 1970; Palmer & Frank, 1974; Bode, 1989; Otway, 1994), or have estimated the parameters of a Von Bertalanffy growth model (Baxter & Jones, 1978; Horn, 1986; Emam et al., 1992). Data on recruitment (Bode, 1989; Otway, 1994), mortality (Glynn, 1970; Otway, 1994), production (Horn, 1986; Bode, 1989), turnover rate (Bode, 1989), and energy budget (Horn, 1986) were also reported for some species.

Plaxiphora aurata (Spalowsky, 1795) is very frequent and widely distributed in subantarctic waters (Kaas & Van Belle, 1994). In South America, it has been reported from Buenos Aires Province (Argentina) in the Atlantic Ocean, to central Chile (31–32 °S) in the Pacific Ocean.

The biology and ecology of *P. aurata* have been dealt with in just a few studies. Brandani et al. (1974) described the community growing on the shell-plates in an

intertidal population at Mar del Plata (Buenos Aires Province, Argentina). These authors also reported observations on sex ratio, feeding, activity rhythms, and homing behavior. Simpson (1976, 1977) has described the vertical distribution, density, feeding, predators, tolerance to physical factors, and reproductive cycle in a population from Macquarie Island.

The aim of this study was to assess growth, annual production, and turnover rate in an intertidal population of *P. aurata* at Quequén, Argentina. In addition, some observations on recruitment, spatial distribution of newly recruited chitons, and geographic variation in maximum size along the Argentine coast are reported.

MATERIALS AND METHODS

The study area was located at Punta Carballido, approx. 4 km eastward of Quequén Harbor (38°35'S, 58°42'W, Figure 1). The intertidal zone consists of mudstone platforms divided by a vertical wall. The chiton population occurred approximately at mid-tide level, 250 m west of the site where untreated sewage from the cities of Necochea and Quequén is discharged. The zone inhabited

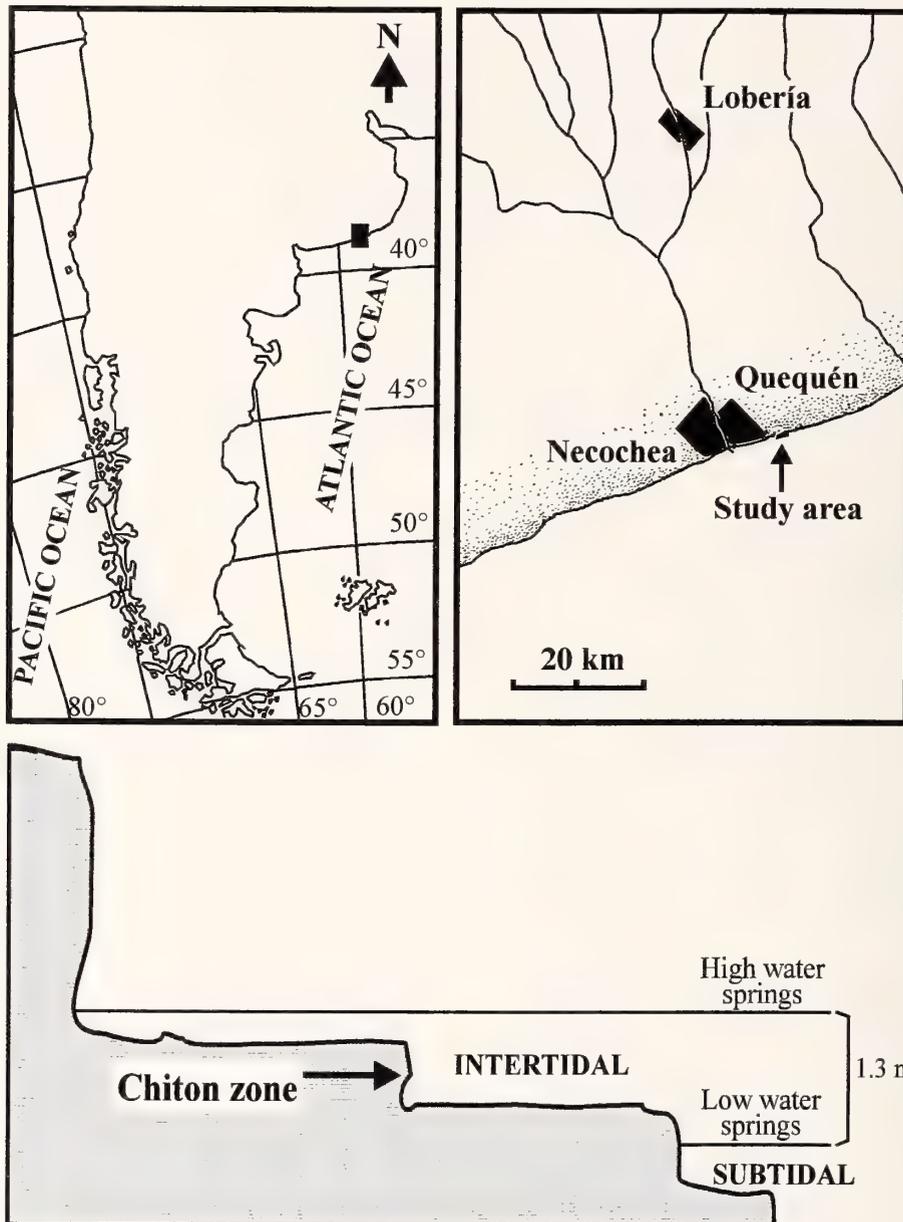


Figure 1

Study area and location of the *Plaxiphora aurata* population in the intertidal zone at Quequén, Argentina.

by the chitons was, however, outside the range strongly affected by the effluents due to the influence of a coastal current flowing eastward. Community structure, physical and chemical characteristics of the water, and seasonal weather changes have been extensively treated in previous papers (López Gappa et al., 1990, 1993). Briefly, mean monthly water temperatures vary between 9 and 22°C. Mean monthly air temperatures fluctuate between 8 and 23°C, although extreme values may exceed widely this range. Salinity varies between 24 and 32 g.l⁻¹, due

to the influence of the Quequén River. The area is completely exposed to storms and heavy wave action, which cause a rapid dilution of the effluents.

The chitons occurred only on vertical, southward facing, shaded walls of 30–60 cm height. The benthic community is dominated by two mytilid species, *Brachidontes rodriguezii* (d'Orbigny, 1846) and *Mytilus edulis* Linnaeus, 1758. The latter is abundant on vertical substrata but is extremely scarce or absent on adjacent horizontal platforms. The most frequent algae are *Gelidiella cf. ni-*

grescens (Feldm.) Feldm. et Hamel, *Corallina officinalis* Linnaeus, and *Ulva rigida* Agardh. The dominant herbivore is the pulmonate limpet *Siphonaria lessoni* (Blainville, 1824) (Tablado et al., 1994). The crab *Cyrtograpsus angulatus* Dana, 1851, is the most conspicuous mobile organism.

Hollows in the vertical substratum can be temporarily inhabited by large individuals. The external appearance of the chitons was often disguised by a variety of algae and invertebrates attached to the shell-plates (Brandani et al., 1974).

During diurnal low-tides, the chitons are inactive and firmly attached to the substratum. Foraging excursions occur during submersion, and homing behavior is absent (Brandani et al., 1974). They usually move their resting sites only a few cm away between consecutive low-tides. Thus, net displacement of the resting site seems to be horizontal and fairly restricted.

The population was censused during lowest low-tides, at intervals ranging from 2 to 4 months, from March 1994 to March 1995 (Table 1). Preliminary sampling and observations were done since March 1993. The sampling area was exactly the same throughout the study period. All the chitons present in two vertical areas totalling 28.5 m² (30–56 cm high, 31–32 m long), were censused. Since the area inhabited by this species was spatially isolated, it is very probable that the same individuals have been repeatedly censused.

The individuals were measured always along the same linear sequence, since *P. aurata* occurred along a very narrow vertical band of substratum. Therefore, the order in which data were obtained reflected the spatial distribution of the chitons. The hypothesis that the distribution of the newly recruited individuals was patchy was tested by means of a runs test (Sokal & Rohlf, 1981). In order to maintain the nominal Type I error rate in repeated tests, only probability values lower than 0.01 were regarded as significant. Maximum length of the youngest cohort was estimated from each size-frequency distribution.

Whenever possible, chitons were measured *in situ* to the nearest mm with dividers and Vernier callipers. Manipulation stress was completely avoided, since chitons were not removed from the substratum. Preliminary trials indicated that the mortality was high if the specimens were detached and resettled during each measurement. Sex was not determined in the present study, but Brandani et al. (1974) have reported that the sex proportion was 1:1 in an intertidal population at Mar del Plata, located some 100 km away from Quequén. The length of contracted individuals was estimated by linear regression, by measuring the width of the fourth shell-plate.

Chitons located within inaccessible pits or crevices were not measured. Their presence, however, was recorded in order to estimate population density.

The program MULTIFAN (Fournier et al., 1990) was used for the simultaneous analysis of all size-frequency

distributions, in order to estimate the parameters K and L_∞ of a Von Bertalanffy growth model. MULTIFAN utilizes a robust likelihood-based estimation protocol that provides an objective criterion for hypothesis testing.

On September 1994, 100 chitons measuring 17–41 mm were tagged with 6 × 3 mm plastic pennants (Floy Tag FTF-69) attached with cyanoacrylate glue. Fifteen chitons were recovered in December, and only six of the originally tagged chitons were found in March 1995. These data were used for an independent estimation of the growth constant K by means of a Ford-Walford plot.

All *P. aurata* specimens deposited in the mollusk collection of the Argentine Museum of Natural Sciences "Bernardino Rivadavia" were examined in order to study the latitudinal change in maximum size. A list of localities and catalogue numbers of these museum specimens can be found in Castellanos (1951). Since museum collections are probably biased toward larger specimens, they cannot be used to obtain representative estimates of mean sizes at different latitudes. They can be usefully employed, however, to compare maximum sizes along the coast of Argentina.

A sample of 113 chitons obtained on 13 March 1995 in an immediately adjacent vertical wall showing similar physical features as that chosen for length measurements, was used to estimate the length-dry weight relationship. After scraping off the biota attached to the shell-plates, the chitons were measured, oven-dried at 60°C for 72 h, and individually weighed to the nearest mg in an analytical balance.

Production was estimated by growth increments (Method 1 in Crisp, 1984). Each cohort was analyzed separately, according to the polymodal decomposition performed by the program MULTIFAN.

RESULTS

Density

Population density varied between 7.3 and 11.8 ind.m⁻² (Table 1). As has already been reported in previous studies (Glynn, 1970; Otway, 1994), the small size of the newly recruited chitons, together with the presence of algae, mytilids, crevices, and pits on the substratum, biased the density estimations. Therefore, density values must have been underestimated in March and May 1994 and March 1995. Maximum density was reached in September, when the youngest cohort was easily distinguishable (approx 15 mm in length).

Recruitment

The arrival of a new cohort to the population occurred once a year, during the summer. Recruits had a size of 5–11 mm (mean: 7.7 mm) in early March 1994. The new cohort recruited in the next summer had a size of at least

Table 1

Number of individuals in each cohort (N) estimated by the MULTIFAN software, number of chitons measured, and total number of chitons censused at each date.

Date	05/ Mar/94	22/ May/94	09/ Sep/94	07/ Dec/94	13/ Mar/95
N cohort 1995	—	—	—	—	16
N cohort 1994	38	168	196	161	209
N cohort 1993	98	72	70	31	42
N cohort 1992	30	32	24	21	7
N cohort 1991	2	6	1	1	1
N cohort 1990	1	1	1	1	1
N cohort 1989	3	1	1	1	—
N measured	172	280	293	216	276
N total	207	296	337	323	311
Density (ind.m ⁻²)	7.26	10.39	11.82	11.33	10.91
Biomass (g.m ⁻²)	2.93	2.78	3.39	4.06	4.06

6 mm (mean: 8.0 mm) during the second week of March (Figure 2).

The cohort first observed in March 1995 was absent in the first week of December 1994 (Figure 2). No recruits were found while examining different algae growing on vertical walls under stereomicroscope. Chitons smaller than 7 mm were also absent in preliminary samples collected on 11 December 1993. Thus, recruitment of new individuals to the benthic stage probably occurred in the second half of December or in January (i.e., early summer).

Recruit number was twice as high in 1994 as in the next year (Table 2).

The spatial distribution of the youngest cohort was patchy when it was first observed a few months after recruitment (runs test, March 1994 and March 1995, $P < 0.001$; May 1994, $P < 0.01$). Recruits were mostly distributed on patches of substratum where adults were rare. On the contrary, juveniles were already randomly interspersed among larger chitons in September and December ($P > 0.05$), when they were approaching their first year of benthic life (Table 2).

Growth

The following equation was used to estimate the length of contracted individuals measuring the width of the fourth shell-plate:

$$\text{Length} = \text{width } 4^{\text{th}} \text{ shell-plate} \cdot 2.445 - 1.602$$

(n = 54; r² = 0.92)

Size-frequency distribution analysis with MULTIFAN produced an estimation of $K = 0.359$ and $L_{\infty} = 53.0$ mm. The estimations obtained including four, five, or six cohorts to the model were roughly the same. The six cohort model was chosen (Figure 2) to accommodate several iso-

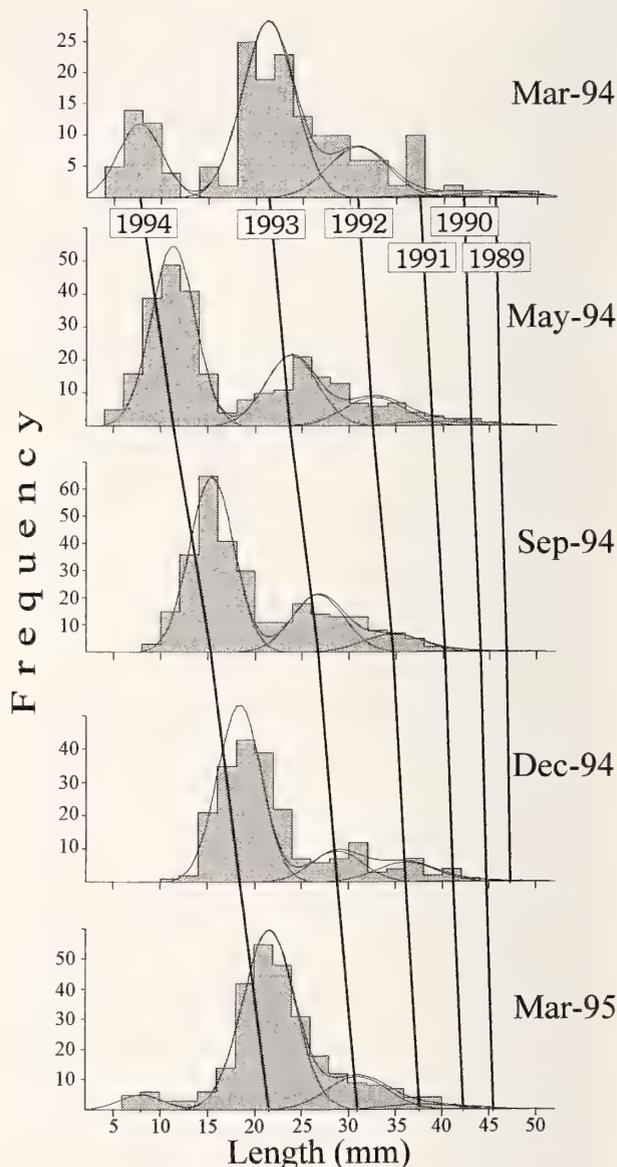


Figure 2

Size-frequency distributions obtained at quarterly intervals during the study period. Curves were fitted by the program MULTIFAN. Lines connecting distributions indicate modal displacement of six cohorts, according to a Von Bertalanffy growth model.

lated large individuals (45–49 mm), representing the older cohorts.

During the first year of benthic life, the chitons attained 19 mm, which represents 36% of L_{∞} . Most of the population consisted always of young individuals. The first two cohorts comprised between 79 and 91% of the population. According to the equation fitted, the age to attain

Table 2

Results of runs tests of the spatial distribution of the youngest cohort during their first year of benthic life. t_s : value of the Student's t statistic.

Date	N° young-est cohort	Ind. size (mm) young-est cohort	N° large chitons	N° runs	t_s	P
05/Mar/94	35	≤11	137	31	-6.10	<0.001
22/May/94	168	≤16	112	111	-3.04	<0.01
09/Sep/94	195	≤20	98	127	-0.58	>0.05
07/Dec/94	163	≤23	53	87	1.11	>0.05
13/Mar/95	15	≤12	261	20	-5.58	<0.001

95% of L_{∞} (50.35 mm) is around 8.3 y. The largest chiton observed in the field had a size of 49 mm.

A decrease in the growth rate was not observed in the youngest cohort. On the contrary, growth decreased or stopped from May to September (i.e., late autumn and winter) during the second year of benthic life (Figure 2), while the modal size remained around 25 mm. Due to this contrast, the magnitude of the seasonal component of the growth rate (Pauly & Gaschütz, 1979) was not adequately estimated by the MULTIFAN software.

A low proportion of tagged chitons was recovered (Table 3). The growth constant estimated by this method for the spring-summer semester ($K = 0.373$) was similar to that obtained by the analysis of size-frequency distributions. Nevertheless, growth rate almost doubled during spring ($K = 0.691$).

Latitudinal Variation in Size

A total of 422 individuals belonging to 37 samples from the Argentine coast deposited in the mollusk collection was measured.

Maximum length and latitude were significantly correlated ($r = 0.89$, $P < 0.01$, Figure 3). Chiton maximum lengths did not exceed 45 mm in museum specimens from Buenos Aires Province (37° S), the northern distribution limit in the Atlantic Ocean, to Chubut (45° S). Length began to increase at Puerto Deseado (47° S), reaching a maximum of 95 mm in Tierra del Fuego (54° S).

Production

The following equation estimates the length-dry weight relationship:

$$\text{Weight} = 7.66 \cdot 10^{-5} \cdot \text{Length}^{2.667} \quad (r^2 = 0.97)$$

Total annual production amounted to $3.51 \text{ g.m}^{-2}\text{.y}^{-1}$ (Table 4). Cohorts recruited in 1994, 1993, and 1992, accounted for 58%, 28%, and 12% of this total, respec-

Table 3

Parameters of the regression equation from a Ford-Walford plot of mark-recapture data of *P. aurata* during spring and summer. N: number of recovered specimens.

K: Von Bertalanffy growth constant.

Period	Time (d)	N	Intercept	Slope	K (y^{-1})
10/Sep/94-05/Dec/94	86	15	6.164	0.850	0.691
10/Sep/94-13/Mar/95	184	6	7.963	0.829	0.373

tively. Cohorts recruited in 1991, or before, accounted for only 2% of the total production. Mean annual biomass amounted to 3.44 g.m^{-2} . The production/biomass (P/B) ratio was 1.02.

DISCUSSION

The density of *P. aurata* in the Quequén study site is slightly higher than in the intertidal zone of Mar del Plata (Brandani et al., 1974) and subtidal areas of Macquarie Island (Simpson, 1976). On the other hand, mean density may be one or two orders of magnitude higher in the European intertidal chiton *Acanthochitona crinita* (Pennant, 1777) (Bode, 1989) and in the Chilean species *Chiton granosus* Fremby, 1827 (Otaíza & Santelices, 1985). Results obtained in this study indicate that spatial distribution of the recruits was patchy during the first months of benthic life. Some areas were mostly inhabited by large chitons, whereas other areas were occupied by members of the youngest cohort. This spatial pattern, however, vanished with time. The causal mechanism producing this patchy distribution may be one (or several) of the following: (a) selective larval settlement in areas where large chitons were absent; (b) random settlement followed by juvenile migration toward areas not occupied by larger chitons; (c) random settlement and differential post-settlement mortality due to the foraging activity of larger individuals. The elucidation of this point is beyond the scope of the present paper, and would only be possible by performing more frequent sampling during the recruitment period and experimental field studies manipulating the density of adults. We believe, however, that the last hypothesis is the most probable, since several authors have documented the presence of small benthic invertebrates in the diet of different chiton species (Barnawell, 1960; Langer, 1983; Piercy, 1987). The diet of *P. aurata* in Mar del Plata included diatoms, green and blue-green algae, and sponges (Brandani et al., 1974).

Recruitment of *P. aurata* may take place during late December or January in Quequén. The reproductive cycle could probably be coincident with that reported for Macquarie Island populations, in which spawning occurred between December and March, with a peak in January (Simpson, 1977). The length of the planktonic stage is

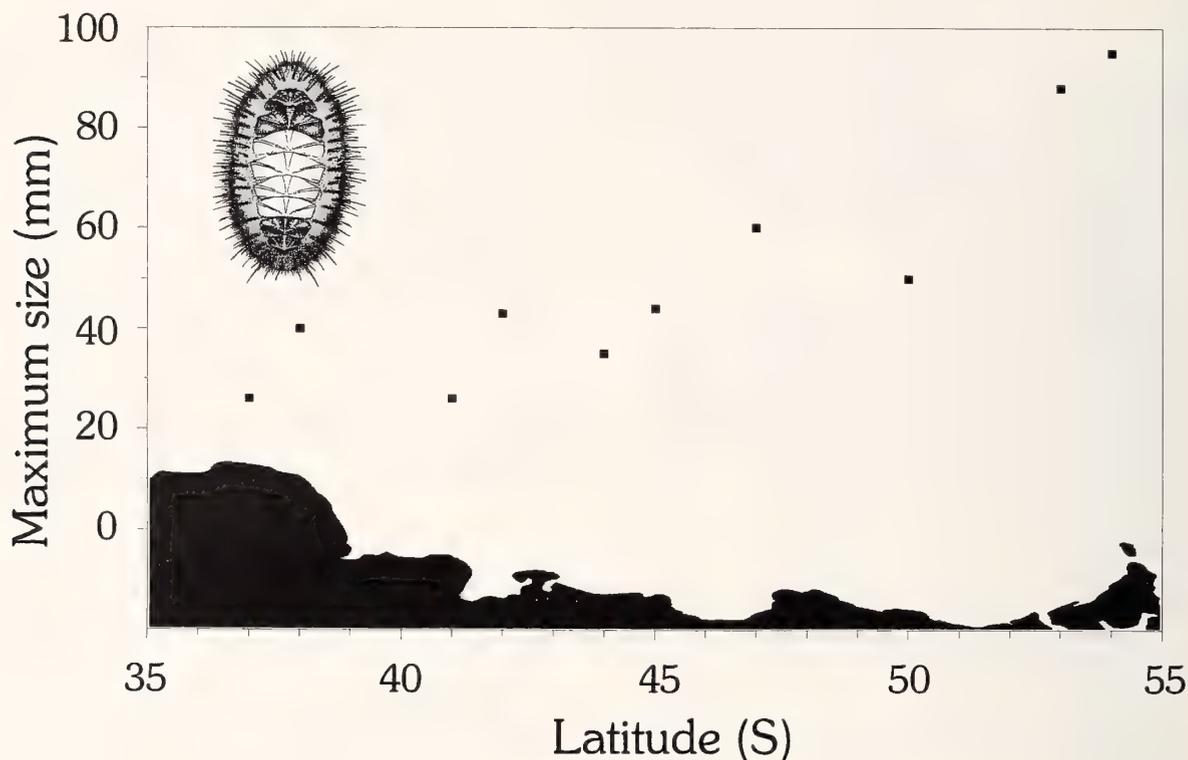


Figure 3

Relationship between maximum length of *Plaxiphora aurata* and latitude along the Argentine coast. Data obtained from samples deposited in the mollusk collection of the Argentine Museum of Natural Sciences "Bernardino Rivadavia."

not known in this chiton, but it is supposed to be short, since it lasts just a few days in other species (e.g., 6–10 d in *Chaetopleura apiculata* [Say, 1834]; Grave, 1932).

According to the Von Bertalanffy equation fitted in this study, the estimated date of zero length would be near the end of September (i.e., early spring). However, as has been pointed out by Yamaguchi (1975), the extrapolation of this equation toward early life stages in marine invertebrates requires an independent investigation. Newly settled chitons were absent in the study area during the first half of December 1993 and 1994. The growth rate of *P. aurata* during the early post-settlement stages may have been underestimated, since Grave (1932) found that the growth rate of *Chaetopleura apiculata* was 4 times higher during the first 2 months of benthic life than in the remaining months of the first year.

The interannual fluctuations in the magnitude of recruitment observed in the present study are common among many benthic invertebrates with planktonic larval stages, and were also reported for *Lepidochitona cinerea* (Linnaeus, 1766) by Baxter & Jones (1978). The reasons for such variations are poorly understood, and may be related to coastal oceanographic processes and mortality during early post-settlement stages.

P. aurata and *Plaxiphora albida* (Blainville, 1825) ($K = 0.274$, $L_{\infty} = 61.4$ mm; parameters estimated by us from data in table 6 of Otway, 1994) have similar growth patterns. The growth constant in *Acanthopleura spiniger* (Sowerby, 1840) ($K = 0.324$) is very close to the value estimated for *P. aurata* in the present study, but the former attains a length of approx. 90 mm (Emam et al., 1992). *Chiton pelliserpentis* (Quoy & Gaimard, 1835) is a slightly smaller species and grows at a lower rate ($K = 0.197$ – 0.245 ; Horn, 1986).

A higher growth rate during spring was measured both in the tagged chitons and in the size frequency distributions, where a remarkable modal displacement from 25 to 31 mm can be seen between September and December in the cohort recruited in 1993 (second year of benthic life) (Figure 2). The analysis of size-frequency distributions indicates, however, that growth is decreased or interrupted during autumn and winter in the second year of life. This strongly suggests that sexual maturity could be attained during the second year of benthic existence, as has been reported for *P. albida* and *Onithochiton quercinus* (Gould, 1846) (Otway, 1994). The growth of *Mopalia muscosa* (Gould, 1846) also decreases or stops completely during winter (Booolootian, 1964). A seasonal

Table 4

Estimation of annual production by growth increments (Crisp, 1984). Cohort data (mean size and density of each cohort at each date) were estimated from the growth model fitted by the MULTIFAN program. ΔP : production increment.

Date	Time (y)	Mean size (mm)	Mean weight (g)	Density (ind.m ⁻²)	ΔP (g.m ⁻²)
05/Mar/94	0.00	7.74	0.018	1.605	—
22/May/94	0.21	11.30	0.049	6.232	0.195
09/Sep/94	0.52	15.41	0.113	7.910	0.501
07/Dec/94	0.76	18.42	0.181	8.448	0.580
13/Mar/95	1.02	21.62	0.278	8.263	0.798
Annual production 1994 cohort					2.034
05/Mar/94	0.00	21.34	0.268	4.138	—
22/May/94	0.21	23.81	0.359	2.671	0.243
09/Sep/94	0.52	26.73	0.489	2.825	0.367
07/Dec/94	0.76	28.83	0.599	1.627	0.178
13/Mar/95	1.02	31.02	0.728	1.661	0.214
Annual production 1993 cohort					0.983
05/Mar/94	0.00	30.83	0.716	1.267	—
22/May/94	0.21	32.57	0.829	1.187	0.134
09/Sep/94	0.52	34.67	0.979	0.969	0.146
07/Dec/94	0.76	36.04	1.086	1.102	0.117
13/Mar/95	1.02	37.59	1.215	0.287	0.037
Annual production 1992 cohort					0.426
05/Mar/94	0.00	37.50	1.207	0.084	—
22/May/94	0.21	38.77	1.319	0.223	0.025
09/Sep/94	0.52	40.14	1.447	0.040	0.005
07/Dec/94	0.76	41.15	1.546	0.052	0.005
13/Mar/95	1.02	42.24	1.658	0.041	0.005
Annual production 1991 cohort					0.039
05/Mar/94	0.00	42.15	1.648	0.042	—
22/May/94	0.21	42.97	1.735	0.037	0.003
09/Sep/94	0.52	43.98	1.846	0.040	0.004
07/Dec/94	0.76	44.71	1.929	0.052	0.004
13/Mar/95	1.02	45.44	2.014	0.041	0.003
Annual production 1990 cohort					0.015
05/Mar/94	0.00	45.44	2.014	0.127	—
22/May/94	0.21	45.98	2.079	0.037	0.002
09/Sep/94	0.52	46.71	2.168	0.040	0.004
07/Dec/94	0.76	47.17	2.225	0.052	0.003
Annual production 1989 cohort					0.012
Total annual production					3.508

decrease of the growth rate associated to the reproductive effort in individuals older than 1 year has also been reported in *Chiton tuberculatus* Linnaeus, 1758 (Glynn, 1970).

Field observations indicate that *P. aurata* lives for at least 4 y. The maximum life span of this species, however, could not be established with certainty, but can be estimated using empirical equations relating turnover rates with longevity. For a P/B ratio of 1.02, the life span

should be around 10 y using the equation obtained by Robertson (1979) for gastropods, 6.7 y using Branch's (1981) equation based on 13 limpet species, and 6.8 y according to Hawkins & Hartnoll's (1983) equation based on 26 herbivorous gastropods. Moreover, according to the Von Bertalanffy equation fitted in the present study, the largest chiton observed in the field (49 mm) should be around 7.2 y, and the age to attain 95% of infinite length should be around 8.3 y. Therefore, the longevity of *P. aurata* in the study area can be conservatively estimated in 6–7 y.

Studies on growth rates and longevity of chitons were reviewed by Boyle (1977). *Plaxiphora albida* and *Onithochiton quercinus* from Australia (Otway, 1994), and *Acanthopleura spiniger* from the Red Sea (Emam et al., 1992) live 6 y or more. *Lepidochitona cinerea* survives for a maximum of five winters (Baxter & Jones, 1978), and *Chaetopleura apiculata* may live for at least 4 y (Grave, 1932). *Chiton tuberculatus* from Bermuda has a life span of 8–9 y (Crozier, 1918a, Arey & Crozier, 1919). *Cryptochiton stelleri* (Middendorff, 1846), the largest chiton in the world, may live more than 16 y (Palmer & Frank, 1974). *Acanthochitona crinita*, which has a completely different life history, lives less than 1 year and has a very high turnover rate (4.52) (Bode, 1989).

The increase in size of *P. aurata* in the southern Patagonian coast and Tierra del Fuego is remarkable. Fuegian subtidal specimens attain twice the length and almost 6 times the weight as those growing in the intertidal zone at Quequén. A similar latitudinal change in size along the Argentine coast has been reported for the crab *Haliscarcinus planatus* (Fabricius, 1775) (Boschi, 1964). Populations of *P. aurata* from Macquarie Island attain a maximum size even larger (115 mm, Simpson, 1977) than that recorded in Tierra del Fuego.

The intertidal zone appears to be a marginal habitat for *P. aurata* (Simpson, 1976). Therefore, it is to be expected that for the same locality, subtidal chitons reach higher sizes than intertidal ones. The growth curve fitted in this study may be probably valid for intertidal populations in Buenos Aires Province or northern Patagonia, but it should not be used for more southern localities.

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Caecum eliezeri sp. nov. (Prosobranchia: Mesogastropoda): A New Species from Brazil

by

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Abstract. A new species of *Caecum* previously known as *Caecum aff. condylum* is described. *Caecum (Caecum) eliezeri* sp. nov. is diagnosed by its small length, regular curvature, light varix at aperture, and the presence of 52-90 axial rings with expanded upper part. Many longitudinal microscopic sulci cross rings and interspaces.

INTRODUCTION

In 1979, the Brazilian Navy performed the operation GEOMAR XII in order to collect sediment samples of continental shelf off Rio de Janeiro. Some of this material was preserved without suffering the usual process of decalcification that precedes sedimentological analysis. It contained many micromollusks, among them, the family Caecidae, distinguished by its high diversity, and the new taxon herein described.

The Western Atlantic Caecidae still require a great deal of research, and a global review would be in order. Since Folin (1867), many taxonomic mistakes have been made. Some of the descriptions were imprecise and/or poorly illustrated, and often the geographic variability of species was not considered in their original descriptions. Many synonymies were established in a subjective way. However, while a full review is not made in this paper, I intend to study the Brazilian caecids like this unnamed taxon.

Taxonomic treatment follows Moore (1969, 1972), Abbott (1974), Keeler (1981), Leal (1991), Lightfoot (1992a,b), and Rios (1994). The subgeneric assignments are based on teleoconch ornamentation and on septum and mucro morphology.

MATERIAL EXAMINED

In addition to the type material of the new species cited below, two lots of *Caecum condylum* (Moore, 1969) were examined, one from Aruba with three specimens (Zoological Museum, Amsterdam, The Netherlands 2445), and another from St. Croix, Virgin Islands collected and identified by D.R. Moore (University of Miami Marine Laboratories, USA 308427).

Abbreviations used: BMNH, British Museum of Natural History (London), England; IBUFRJ, Instituto de Biologia da Universidade Federal do Rio de Janeiro (Brazil); MNHN, Muséum d'Histoire Naturelle (Paris), France; MNRJ, Museu Nacional do Rio de Janeiro (Brazil); MORG, Museu Oceanográfico Eliézer de Carvalho Rios da Fundação Universidade do Rio Grande (Brazil); MZUSP, Museu de Zoologia da Universidade de São Paulo (Brazil); UMML, University of Miami Marine Laboratories, USA. USNM, National Museum of Natural History (Washington), USA. ZMA, Zoological Museum, Amsterdam, The Netherlands.

SYSTEMATIC DESCRIPTION

CAECIDAE Gray, 1850

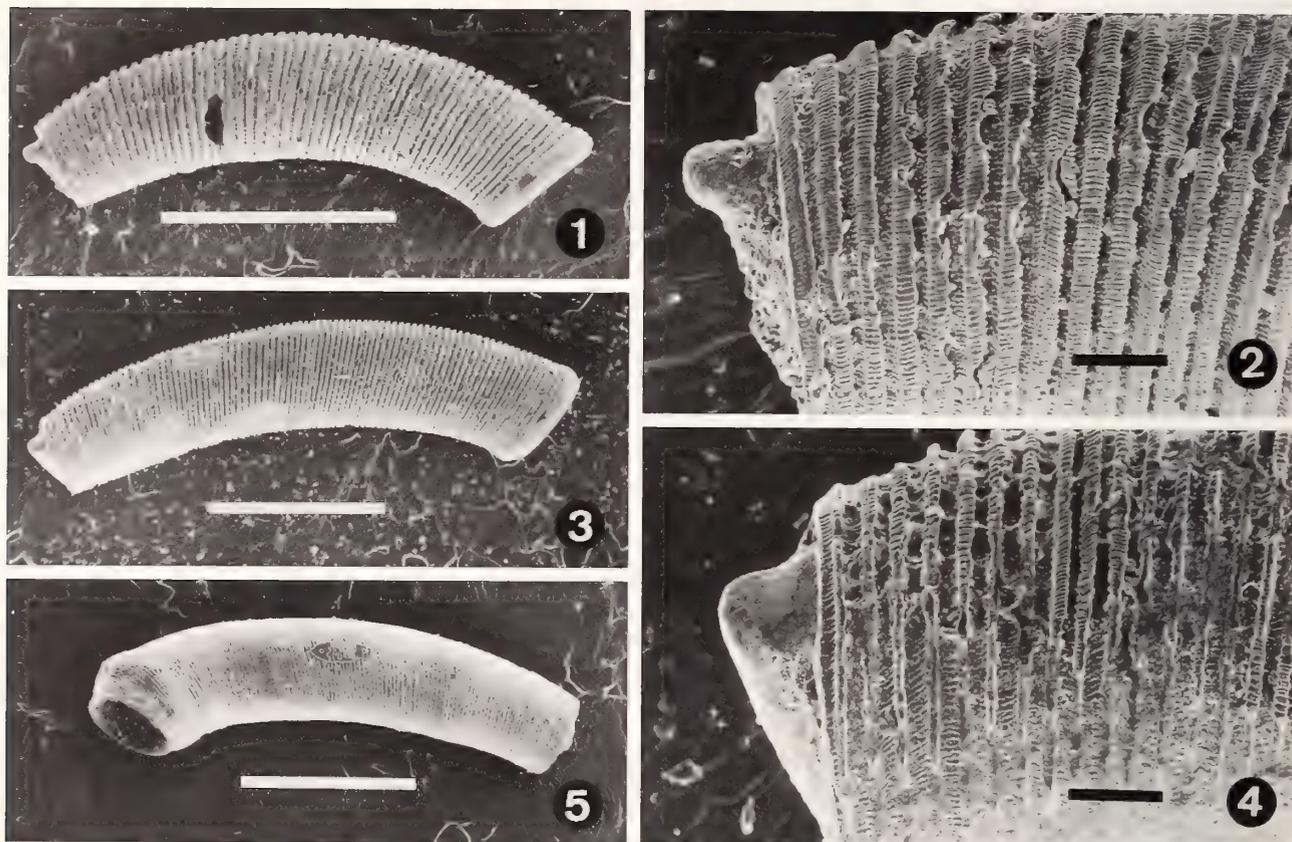
Caecum Fleming, 1813

Caecum (Caecum) eliezeri Absalão, sp. nov.

(Figures 1-4)

Diagnosis: Shell small, moderately and regularly curved, with a light varix at aperture; 52-90 rings with laminar horizontal expansion on the tops; abundant incised microscopic longitudinal striations crossing rings and interspaces.

Description: Teleoconch small, solid, and moderately curved on all extensions. Adults with a terminal varix that slightly increases the shell diameter at aperture. Presenting 52 to 90 ($x = 64$) axial rings, including two or three on the varix. Tops of rings showing a laminar horizontal expansion that is broader toward the anterior end. About



Explanation of Figures 1 to 5

Figures 1–4. *Caecum eliezeri* Absalão, sp. nov. 1. Holotype, MORG 32884, entire shell. 2. Holotype, detail of the septum, mucro, and ornamentation. 3. Paratype 1, IBUFRJ 6505, entire shell. 4. Paratype 1, detail of the septum, mucro, and ornamentation. 5. *Caecum condylum* Moore, 1969 UMML 308427. Scale bar, Figures 1, 3 and 5 = 1 mm; Figures 2 and 4 = 0.1 mm.

200 closely packed microscopic longitudinal striations crossing ring and interspaces. The ornamentation is the same over all the shell. Septum rounded, moderately high with a blunt dorsal mucro turned to the left when seen dorsally. Ground color cream to withish, but never translucent. Protoconch, second stage, and operculum unknown.

Type and type locality: Holotype MORG 32884, 21°31.7'S × 40°19.0'W, GEOMAR XII station 58, depth 41 m, 28 August 1979, 56 axial rings, 2.16 mm long, 0.51 mm aperture diameter, 0.35 mm posterior diameter. Paratype 1 IBUFRJ 6505, 21°15.3'S × 40°20.4', GEOMAR XII station 34, depth 45.7 m, 27 August 1979, 90 axial rings, 2.80 mm long, 0.55 mm aperture diameter, 0.41 mm posterior diameter. Paratype 2 IBUFRJ 6504, 21°09.7'S × 40°26.0', GEOMAR XII station 32, depth 18.3 m, 27 August 1979, 58 axial rings, 2.21 mm long, 0.51 mm aperture diameter, 0.35 mm posterior diameter. Paratype 3 USNM XXXXX, 22°21.4'S × 40°44.0', GEOMAR XII station 112, depth 59.5 m, 29 August 1979, 75 axial rings, 2.64 mm long, 0.58 mm aperture

diameter, 0.55 mm posterior diameter. Paratype 4 MNHN, 22°22.4'S × 40°56.5', GEOMAR XII station 124, depth 47.2 m, 29 August 1979, 73 axial rings, 2.67 mm long, 0.57 mm aperture diameter, 0.40 mm posterior diameter. Paratype 5 BMNH 1995190, 22°22.4'S × 40°56.5', GEOMAR XII station 124, depth 47.2 m, 29 August 1979, 73 axial rings, 2.67 mm long, 0.55 mm aperture diameter, 0.43 mm posterior diameter. Paratype 6 MNRJ 7158, 22°17.2'S × 40°49.6', GEOMAR XII station 111, depth 51.8 m, 29 August 1979, 52 axial rings, 2.49 mm long, 0.55 mm aperture diameter, 0.38 mm posterior diameter. Paratype 7 MZUSP 28102, 22°16.2'S × 41°04.5', GEOMAR XII station 127, depth 27.4 m, 29 August 1979, 52 axial rings, 2.67 mm long, 0.58 mm aperture diameter, 0.35 mm posterior diameter. Paratype 8 ZMA 395010, 21°15.3'S × 40°20.4', GEOMAR XII station 34, depth 45.7 m, August 27 1979, 79 axial rings, 2.87 mm long, 0.58 mm aperture diameter, 0.44 mm posterior diameter. Paratype 9 IBUFRJ 6506, 21°57.6'S × 40°51.0', GEOMAR XII station 76, depth 15.2 m, 28 August 1979, 85

axial rings, 2.70 mm long, 0.57 mm aperture diameter, 0.39 mm posterior diameter.

Range: *Caecum eliezeri* sp. nov. seems to be restricted to the southern regions of Brazil, since Mello & Maestrati (1986) did not obtain it from northern Brazil.

Etymology: This species is dedicated to Prof. Eliézer de Carvalho Rios, my friend and first malacology professor, in acknowledgment of his pioneering work on Brazilian marine mollusks.

DISCUSSION

Rios (1994: pl. 18, fig. 200) recorded *C. eliezeri* from the Brazilian seashore as *Caecum aff. condylum*. He stressed that the individuals examined by him had about 75 and not the 100 annular rings seen in *C. condylum* Moore, 1969. Furthermore, the material examined by Rios consisted of immature individuals, without the varix of *C. eliezeri* or the swelling of *C. condylum*.

C. condylum (Figure 5) can be distinguished from *C. eliezeri* by the following aspects:

The sculpture of *C. condylum* consists of approximately 100 rings; I counted 110 in the individuals that I examined (Figure 3), whereas *C. eliezeri* exhibits approximately 64 (52–90) rings. The rings in *C. condylum* are always much wider than the interspaces, whereas in *C. eliezeri*, the rings can be as wide or wider than the interspaces, but never as wide as in *C. condylum*. In addition, the rings in *C. condylum* have a simple distal edge, different from the horizontal expansion of *C. eliezeri*.

Caecum condylum has a broad, rounded swelling just before the anterior part, whereas *C. eliezeri* has a slight terminal varix. *C. condylum* does not present any axial sculpture, whereas *C. eliezeri* has more than 200 microscopic longitudinal striations crossing the shell. The septum of *C. condylum* is slightly depressed. On *C. eliezeri* the septum is moderately elevated. *C. condylum* is slightly curved with the anterior part more strongly curved. This differs from *C. eliezeri*, which is regularly curved over all its extension.

Another species that is similar to *C. eliezeri* is *C. strangulatum* Folin, 1867. This similarity is due to the similarity of their rings, longitudinal striations, and varix at aperture. On the other hand, they can be distinguished by the num-

ber of rings because *C. strangulatum* has 30 rings, whereas in *C. eliezeri* the number of rings varies between 52 and 90. The septum of *C. strangulatum* is retracted and the mucro is a rounded projection, whereas *C. eliezeri* has a mammilated septum with a blunt dorsal mucro. Finally, *C. strangulatum* is proportionally broader than *C. eliezeri*.

Apart from *C. condylum* and *C. strangulatum*, *C. eliezeri* does not resemble any Western Atlantic species.

ACKNOWLEDGMENTS

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NOTES, INFORMATION & NEWS

**Metallic Ions in Snail-Conditioned Water
from Two Strains of *Helisoma trivolvis* and
*Biomphalaria glabrata***

by

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Introduction

Planorbid snails release substances into water that serve as chemoattractants for larval trematodes and conspecific snails (Chernin, 1970; Marcopoulos & Fried, 1994). Water containing these substances has been referred to as snail-conditioned water (SCW). Recent studies in our laboratory have been concerned with the chemical analysis of SCW. Thus, Chaffee et al. (1996) used high performance thin layer chromatography (HPTLC) to examine neutral lipids in the M-line or albino Puerto Rican strain of *Biomphalaria glabrata* (Say, 1818), and Rivas et al. (1997) used HPTLC to quantify neutral lipids in the SCW of a Colorado (CO) and a Pennsylvania (PA) strain of *Helisoma trivolvis* (Say, 1816). Gennaro et al. (1997) extended the HPTLC studies to observations on individual phospholipids in SCW from the above snails.

Workers have suggested that inorganic ions are involved in chemical communication of larval trematodes to their snail hosts (see review in Haas et al., 1995) and that the concentration of Mg^{+2} ions or the ratio of Mg^{+2}/Ca^{+2} ion concentrations in the water may influence the attraction of miracidia to their snail hosts. However, quantitative analyses of metallic ions in SCW are not available, and the purpose of this study was to accumulate such information for SCW from the CO and PA strains of *H. trivolvis* and the M-line strain of *B. glabrata*.

Materials and Methods

Stock cultures of both strains of *H. trivolvis* and *B. glabrata* were maintained in aquaria containing chemically defined spring water (Higgs et al., 1990). Snails were maintained under diffuse overhead fluorescent light for 12 hr/day at 22–24°C and fed boiled leaf lettuce supplemented with Tetramin fish food.

An initial survey of 24 metallic ions in SCW was performed using inductively coupled plasma-atomic emission spectrometry (ICP-AES) as previously described (Layman et al., 1996). The ICP analyses were performed on six 2 hr and six 5 hr SCW samples from each of the *H. trivolvis* CO and PA strains, which were prepared as

follows. Ten snails having shell diameters of 8–10 mm (CO strain) or 10–14 mm (PA strain) were removed from the aquaria and were blotted dry using a paper towel. Each snail was then placed in a 1.8 cm diameter well of a multiple well chamber containing 2.0 ml of Milli-Q water for either 2 or 5 hr. After the specified time period, the snails were removed from the cell well and rinsed with a drop of Milli-Q water. The rinse water, as well as SCW in the cell wells for the 10 snails, were combined in a centrifuge tube, 0.5 ml of conc. nitric acid was added, and the sample was stored in a refrigerator until analysis. The ICP-AES data revealed that the following metallic ions were present in measurable quantities in both snail strains: Ca^{+2} , Mg^{+2} , Na^{+1} . A measurable quantity is defined as a concentration greater than 10 times the detection limit of the method. Once these elements had been selected, flame atomic absorption spectrometry (FAAS) was used for quantitative analyses of the metallic ions in SCW.

To prepare SCW samples from the CO strain of *H. trivolvis* for FAAS, 10 snails of shell diameter 5–8 mm were removed from an aquarium and blotted dry with a paper towel. The snails were then placed in approximately 500 ml of Milli-Q water in a beaker for 2 hr to rinse the snails of any metals that might have been contained in the aquarium water. After 2 hr, the snails were removed from the water and blotted dry with paper towels. The snails were then rinsed in ca. 500 ml of Milli-Q water for 15 min. After this second rinse, the snails were blotted dry and each snail was placed in 2.5 ml of Milli-Q water contained in a cell well. The preparation procedures and number of samples of SCW from the PA strain of *H. trivolvis* and from *B. glabrata* were the same as described above, except that the shell diameters were 10–12 mm and 7–12 mm, respectively.

To measure the metal ions by FAAS, 0.50 ml aliquots were taken from each of 10 cell wells at three different times. The first aliquot was taken immediately after placing the snail in the water (0 hr). The second aliquot was taken at 2 hr post-incubation, and the last aliquot was taken at 5 hr post-incubation. The 0.50 ml aliquots obtained at each sampling time were combined, yielding a sample of 5.00 ml for each of the three times. The samples were stored in a refrigerator until analysis. The procedure was repeated four times, for a total of four samples for each time period, with each sample consisting of the SCW from 10 cell wells; each well contained one snail. In total, SCW from 40 snails was analyzed.

Stock standard solutions (1000 ppm) of calcium, magnesium, and sodium were prepared by dissolving reagent

Table 1

Net masses of the metallic ions released per snail in two time periods by two strains of *Helisoma trivolvis* (Colorado and Pennsylvania) and *Biomphalaria glabrata*. All values are given in μg of the metal ion released per snail.

Metal ion	<i>H. trivolvis</i> (CO)		<i>H. trivolvis</i> (PA)		<i>B. glabrata</i>	
	2 hr (μg)	5 hr (μg)	2 hr (μg)	5 hr (μg)	2 hr (μg)	5 hr (μg)
Ca ⁺²	10 \pm 2	19 \pm 5	8 \pm 2	9.5 \pm 0.7	11 \pm 1	21 \pm 1
Mg ⁺²	0.3 \pm 0.1	0.8 \pm 0.3	0.36 \pm 0.05	0.8 \pm 0.2	0.54 \pm 0.04	1.81 \pm 0.08
Na ⁺¹	2 \pm 1	3.1 \pm 0.9	2 \pm 1	2 \pm 1	1.6 \pm 0.6	2.4 \pm 0.6

grade CaCO₃, MgCl₂, and Na₂CO₃, respectively, in 2% HNO₃. Analytical standard solutions for FAAS containing 0.00 (blank), 2.00, 4.00, 10.00, and 20.00 ppm of Ca⁺² were prepared by appropriate dilution of the stock standard solution with 2% HNO₃. Similarly, 0.00 (blank), 0.10, 0.50, and 1.00 ppm Mg⁺² and 0.00 (blank), 0.41, 1.00, and 2.00 ppm Na⁺¹ analytical standard solutions were prepared by dilution from the respective 1000 ppm stock standard solutions.

Solutions were analyzed for Ca⁺², Mg⁺², and Na⁺¹ using a Varian SpectrAA-10 computer-controlled atomic absorption spectrometer as described by Layman et al. (1996). The following parameters were similar for the three metals analyzed: slit, 0.5 nm; stoichiometric flame; air—11 L/min; sample flow rate, 6 ml/min; 1 integration of 5 sec for each absorbance reading. A different single-element hollow cathode lamp was used for each element with the following wavelengths: Ca⁺², 422.7 nm; Mg⁺², 285.2 nm; and Na⁺¹, 589.0 nm. The ppm readings for the aspirated sample solutions were converted by calculation to micrograms (μg) of metal released per snail into the SCW.

Results and Discussion

The metallic ion present in the highest level in the SCW samples from all three snail strains was Ca⁺². Sodium and magnesium ions were present in much lower quantities, and in all cases, Na⁺¹ was more abundant than Mg⁺². The values obtained at time 0 (immediately after the snails were placed in the water) were subtracted from the values obtained at 2 and 5 hr, in order to account for the metallic ions on the snails that had not been removed by the rinsing procedure. The quantitative results for the three ions obtained in this study are summarized in Table 1.

Based on Student's t-test, (with $P < 0.05$ being considered significant), a significant increase in the Ca⁺² concentration of SCW from 2 to 5 hr was seen in *H. trivolvis* (CO strain) and *B. glabrata*. The SCW samples obtained from *H. trivolvis* (PA strain) showed no significant increase in Ca⁺² from 2 to 5 hr. At 5 hr, the Ca⁺² content in SCW from the PA strain of *H. trivolvis* was significantly different than that of the CO strain of *H. trivolvis*. No significant differences in the Ca⁺² content of SCW

among the three snail strains were observed at 2 hr. A significant increase in the Mg⁺² content of SCW from 2 to 5 hr was seen in the SCW from both the PA strain of *H. trivolvis* and *B. glabrata*. No significant changes in the Mg⁺² content between the 2 to 5 hr samples of SCW from the CO strain of *H. trivolvis* were observed. The Mg⁺² content of the SCW from the *B. glabrata* snails and both strains of *H. trivolvis* were significantly different at 5 hr, but no significant differences among strains were observed at 2 hr. There was no significant increase in the Na⁺¹ content in the SCW of the CO and PA strains of *H. trivolvis* and that of the *B. glabrata* SCW samples from 2 to 5 hr; there were no significant differences in Na⁺¹ content among the three snails at 2 hr and at 5 hr.

The quantitative data presented herein on Ca⁺², Mg⁺², and Na⁺¹ may be useful to workers who desire to prepare test solutions with metallic ions for use in bioassays that examine the attractivity of larval trematodes. Moreover, if the ratio of Mg⁺²/Ca⁺² ion concentrations are important in the attraction of miracidia to planorbid snails (see review in Haas et al., 1995), it is interesting to note that these ratios are quite variable, ranging from 0.03 to 0.05 at 2 hr and 0.04 to 0.09 at 5 hr (see Table 1). Preparation of bioassay media to test the hypothesis of the ratio of Mg⁺²/Ca⁺² ion concentration as a presumptive larval chemoattractant should occur with consideration of the data reported herein.

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**Increasing Effective Malacological Communication:
A Commentary on Descriptions of Molluscan
Development**

by

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Descriptive studies of molluscan reproduction and development provide important and useful information for ecologists, evolutionary biologists, and embryologists. However, the omission of one or a few key facts, such as temperature or egg size, has caused some published studies of molluscan development to fall short of their potential. In many cases, such key information is known to the authors but its importance is underestimated or overlooked. This commentary outlines some of the facts that readers from different disciplines look for in descriptions of development and lists some suggestions of basic information that could profitably be included in descriptions of molluscan development.

Ecologists and conservation and fisheries biologists are interested primarily in descriptions of development as a way to obtain information on life-histories, dispersal capability, larval ecology, and factors affecting recruitment. Therefore, data concerning seasonality and periodicity of reproduction, egg size, number, and energy content, the duration of planktonic and benthic stages, and stage at hatching are particularly useful. Additionally, observations of larval feeding, settlement site preferences, and ability to delay metamorphosis provide important information for many studies. Because developmental progress is extraordinarily temperature-dependent, useful developmental timetables explicitly state the temperature or range of temperatures for which development was observed. Finally, an illustrated description of larval morphology that is sufficiently detailed to identify veligers caught in plankton tows is helpful.

Evolutionary biologists use developmental data for

systematics and to investigate mechanisms of morphological evolution. In order to help identify characters useful for systematics, descriptions of development should be as detailed as possible and place the reported observations in a comparative context. How was the observed development similar to and different from other related taxa? How much variation was there among individuals? Features such as polar lobes, cleavage type, nurse eggs, extraembryonic layers, larval kidneys, protoconchs, and developmental stage at hatching, which all vary among molluscan groups, are relatively easy to observe and have the potential to be useful for systematics. The importance of explicitly stating what characters are absent, as well as describing those characters that are present, cannot be overemphasized. Special attention should be paid to characters known to be of systematic importance in order to examine hypotheses of character homology and the polarity of character state changes.

Embryologists may read descriptive accounts of molluscan development to seek support for scenarios of the evolution of development. For example, recent papers proposing evolutionary scenarios for molluscan cleavage and mesentoblast formation (Freeman & Lundelius, 1992; van den Biggelaar, 1996) have relied heavily on published accounts of molluscan cleavage. Embryologists may also look to descriptive accounts of molluscan development to identify species that may be particularly amenable to experimental study. For example, patellogastropods are preferable to trochids for cell ablation studies because the embryos are not encased in a capsule within the jelly coat. Nudibranchs and freshwater pulmonates are ideal for studies that require a continuous supply of newly laid eggs, and embryos of opisthobranchs in the genus *Phyllaplysia* have natural markers of cytoplasmic segregation that make them a good choice for fate mapping studies. Descriptions of unusual culture conditions necessary to rear larvae are also useful.

Unfortunately, it is often not possible to produce exhaustive studies of development. Many observations may be based on fortuitous spawning events that cannot be repeated; some stages or events may be obscured by extra-embryonic structures or large amounts of opaque yolk, and long-lived larvae may be difficult to raise to metamorphosis. However, many important details of development like early cleavage patterns, extra-embryonic coverings, and larval morphology can be observed with simple light microscopy. Transparent jelly coats that often evade observation can be visualized with particles added to the water, such as Sumi ink (Strathmann, 1987). Opaque embryos can be cleared, and calcium carbonate structures can be visualized with polarized light (Strathmann, 1987). Developmental timetables can be based on daily or hourly microscopic observations.

As with all scientific studies, certain omissions may reduce the usefulness and interpretability of developmental studies. For example, if information on larval feeding

is not included in a study, it cannot be used by researchers working in such areas of current interest as the effects of egg size on larval type (planktotrophic vs. lecithotrophic) and correlations between latitude, adult body size, and larval type. Growth rates and larval mortality in cultures may also often be linked to larval diet. Explicitly stating if the larvae were fed and what food they were offered gives the reader some indication if they were nutritionally stressed. Clear descriptions of embryonic and larval morphology also give a reader who has experience working with molluscan development the ability to assess whether development was normal.

Our current understanding of mollusk development is based on a long and rich history of descriptive studies. However, recent technical advances in larval culture (e.g., sterile cultures and better algal diets for planktotrophic larvae) and microscopy (e.g., epifluorescence microscopy and SEM), combined with a renewed interest from ecologists and evolutionary biologists, give detailed descriptive studies of molluscan development the potential to contribute more than ever to the field of malacology.

SUGGESTED CONTENT OF DESCRIPTIONS OF DEVELOPMENT (appropriate information varies somewhat with species):

General:

Species (source and means of identification), location of vouchers, collection site, temperature, and time of year.

Spawning:

Method used to induce spawning, seasonal or periodic spawning, internal or external fertilization, mating sys-

tem, brooding or egg guarding behavior, type of egg mass or capsules, description of extraembryonic structures, egg size, egg number, arrangement of eggs within the extraembryonic coverings, egg color, and sperm morphology.

Early Development:

Description of nurse eggs, polar bodies, polar lobes for the first few divisions, equal or unequal cleavage, cytoplasmic markers that segregate during cleavage, gastrulation (by invagination, epiboly, or both), and relative timing of cleavages within and among embryos.

Later Development:

Stage at hatching, size at hatching, hatching behavior, larval type (feeding or non-feeding, planktonic or benthic), protoconch morphology, specialized larval or embryonic organs (pigmented mantle organ, larval kidneys, head vesicle etc.), velar morphology and pigmentation, larval behavior, planktonic period, settlement cues, size at settlement, and juvenile morphology.

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BOOKS, PERIODICALS & PAMPHLETS

Freshwater Mussels of Texas

by ROBERT G. HOWELLS, RAYMOND W. NECK & HAROLD D. MURRAY. 1996. Texas Parks and Wildlife Department, Inland Fisheries Division. Distributed by University of Texas Press, P.O. Box 7819, Austin, Texas 78713-7819 USA, \$29.95 + 3.50 shipping & handling (domestic). Web site: <http://www.utexas.edu/utpress>; telephone: (512) 471-7233.

This new monographic publication on Texas freshwater unionid clams provides an excellent summary of unionids in this state. The report provides thorough coverage of the 51 named species found in Texas (as of 1994), with descriptions and photo illustrations (black & white and color), descriptions of shell characters (and some soft part characters), habitat discussion, spawning characteristics, glochidia and hosts (where known), a short commentary for each, and mention of economic importance. Common names and short synonymies are also presented. The descriptions are presented in an outline format, with subsections for size, shell form and ornamentation, dentition, external and internal color, and major soft tissue characters (but no anatomical dissections). This format, and long (32 pages) introductory discussions, illustrations, and maps provide an easy-to-use monograph for field biologists, naturalists, ecologists, and environmentalists as well as malacologists. An important component of this monograph is the compilation and presentation of information on reproductive biology, concerning spawning, glochidia, and host fish species. Considerable detail about habitat and environmental tolerances of the species is integrated with data from other areas of occurrence. The results of biomolecular comparisons are presented for a few species whose relationships are not readily apparent.

Another excellent feature is the lead-off citation of previous reports providing a description of each species, supplemented by the authors in many cases. Distribution maps are provided for all unionid species within Texas, with collection sites marked. Following the unionids is a short section on other freshwater bivalves, including invader species (*Corbicula*, *Dreissena*), native brackish and estuarine species, and native sphaeriid bivalves. These are described and illustrated, except for the sphaeriids, which were not detailed in this study because they were not found to be common anywhere in the state. Black and white photos and a distribution map are placed with each species description, all printed on heavy stock, high quality paper. There are 141 color photographs of unionids on 16 color plates at the end of the report, but these are a disappointment because the magnifications should have

been larger. Half of the space on these plates remains empty of photo or text, and the photos could have been trimmed better, enabling higher magnifications to be used without increasing printing costs.

Freshwater biotas in Texas occur along a strong climatic gradient, ranging from wet, warm climates in east Texas to arid climates in south and west Texas, and this can be seen in the distribution patterns of unionids. A few species are distributed in all major river systems across the state, but most have restricted distribution. About 20% have distributions limited to central or southern Texas, including a few that range into Mexico. A large majority (80%) occur in the east and northeast portions of Texas, which contain the southwestern edge of the Mississippi Valley unionid assemblage. Many of these species range westward to the Trinity or Brazos river systems. Four named species are shown as endemic to central Texas outside the Rio Grande drainage and four are shown as endemic to the Rio Grande drainage, based on historical collections as well as current collecting data. The number of endemics in central Texas is appropriate for the degree of isolation (short river systems) and semi-arid climates with major flash flooding, but nearly all are reported as threatened or endangered species.

This monograph contains work up to 1994—data reported at the American Malacological Union annual meeting in Houston, 1994. Results of more recent surveys have modified some of the distribution results, and major field surveys in the Brazos River and Rio Grande drainage basins have filled in the undersampled coverage summarized in the monograph. The newer survey data is available only in agency yearly summary reports or in the agency unionid newsletter. As reported by Dr. Howells (personal communication, 1997), one additional species is now known, host species for many more unionid glochidia are now known, and a new compilation of unionid species has been made. Biomolecular work has reinforced earlier conclusions that many species are polymorphic, having different morphs in separated river systems.

The authors report that the impetus for this monograph came from the need for information on unionids at the Texas Parks and Wildlife, at a time of sharp increase in commercial harvesting of Texas unionids in the late 1980s. There even was a small fishery for pearls, active until the mid 1980s. A biological survey and program of documentation were undertaken to allow for the development of regulations concerning harvest. The survey started with a base collection made by Neck at Parks and Wildlife and by Murray at Trinity University, supplemented by the Strecker collection at Baylor University.

At the time the monograph was produced, Dr. Neck had joined the Houston Museum of Natural Science.

This is a superb report for working with Texas unionids. Until this report appeared, the works of Strecker (1931) and Burch (1973) were the primary statewide reference sources of information, but the Strecker reference is very hard to obtain and the Burch reference contains primarily drawings of exteriors of species. Few other reports are available on Texas unionids and most of those reports come from censusing emptied reservoirs. Anyone interested in unionids and all groups involved in environmental impact studies should get a copy of this report soon. A limited number of copies were printed and it may not stay in stock very long. For this reason, I strongly recommend that people in educational institutions make sure their libraries get a copy.

Thomas E. Yancey

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1996 IUCN Red List of Threatened Animals

International Union for Conservation of Nature and Natural Resources (J. BAILLIE & B. GROOMBRIDGE, compilers and editors). 1996. Co-published by IUCN, Gland, Switzerland, and Cambridge, UK, and Conservation International, Washington, D.C., USA. lxx + 368 + x pp. ISBN 2-8317-0335-2.

The fifth and latest edition of the IUCN Red List of Threatened Animals is available in book form, as above. The essential data file ("Threatened animals of the world") is accessible through the webserver of the World Conservation Monitoring Centre (<http://www.wcmc.org.uk>) and searchable by taxon, country, and survival category. The book contains valuable introductory essays, tables, and graphs concerning the sources and nature of the information contained in the list, the criteria for categories of threat, and analyses of the data (e.g., which bird orders are the most threatened? what countries have the largest number of threatened species?).

Molluscan records were contributed by the Mollusc Specialist Group of the IUCN Species Survival Commission (SSC) under the leadership of Dr. Mary Seddon.

About 10,000 species of animals are now on the list. Over 1700 of these are mollusks; an additional 239 mollusk species are considered extinct (that is, having gone extinct less than 400 years ago) or extinct in the wild. A

rather large number (545) of the mollusk species are in the category "data deficient," which means that the SSC lacks the data needed to make an assessment of risk in their cases. Numerically, the Unionoida stand out among the bivalves and the Stylommatophora among the gastropods. These are, of course, freshwater mussels and land snails, respectively. Mesogastropods, buoyed by numerous freshwater snails of the Hydrobiidae and Pleuroceridae, also show prominently.

As remarked by J. Baillie in the introduction, while the 5205 species listed in this document as threatened is alarmingly high, less than 10% of the 1.7 million documented species have been evaluated for their survival status. And that 1.7 million documented species represents only a fraction of the number of species believed to exist. Thus, "it is reasonable to believe that the 5,205 threatened species is a small indicator of a much larger global phenomenon of biodiversity loss" (introduction, p. 41).

The Red List is fundamentally a tool—one of many sources of data necessary for the conservation of species. It is made more valuable by the recent decision of the United States Fish and Wildlife Service to discontinue the practice of maintaining a list of "Category 2" candidate species (*Federal Register* 61:64481–64485, 1996). (Category 2 candidates are, or were, those for which "information now in the possession of the Service indicates that proposing to list the species as endangered or threatened is possibly appropriate, but for which conclusive data on biological vulnerability and threat(s) are not currently available . . ."; *Federal Register* 49:21664, 1984.) Although Category 2 candidate species received no substantive or procedural protection under the Endangered Species Act, the Fish and Wildlife Service encouraged Federal agencies and other planners to take such taxa into account in environmental planning under the National Environmental Policy Act and similar statutes; the Service also encouraged research on vulnerability and potential threats to those taxa. It now has abandoned that advocacy role. A high percentage of former Category 2 species appear on the Red List, including many in the "Endangered," "Critically Endangered," and "Vulnerable" classes.

Some errors are known to have crept into the Red List molluscan listings—at least a few during the electronic transfer of data from the Mollusc Specialist Group—but need not be belabored here. The Group solicits information on omissions or corrections; this is best sent to Dr. Mary Seddon, Curator (Terrestrial Mollusca), National Museum and Gallery of Wales, Cathays Park, Cardiff, UK, CF1 3NP. The Red List book itself is available from IUCN Publications Services Unit, 219c Huntingdon Road, Cambridge, CB3 0DL, United Kingdom.

B. Roth

When Are Characters Not Homologies and Patterns Not Evolutionary?

An Atlas of Cowrie Radulae (Mollusca: Gastropoda: Cypraeoidea: Cypraeidae) by HUGH BRADNER and E. ALISON KAY. 1996. *The Festivus*, vol. 28, Supplement. 179 pp., 238 figures. Published by San Diego Shell Club, 3883 Mt. Blackburn Avenue, San Diego, CA 92111, USA.

The study of evolution concerns itself with change of form through time. In order to understand diversity of form, therefore, one must first collect and document the existing range of morphology. Bradner and Kay's *Atlas of Cowrie Radulae* does just that; it is a tremendous compendium of radular forms that exist among 202 species of cypraeid gastropods. Cowries are known predominantly for their diversity of shell form and color pattern. With this collection of radular images, Bradner and Kay provide a valuable, additional morphological data set. The breadth and completeness of taxonomic sampling, which must have taken hours of preparation, mounting, and photography, are commendable. Three electron micrographs and one optical photograph of the radula are presented for each species. Occlusal and oblique views permit a full appreciation of the morphology. In its presentation of radular diversity and as a tool for the recognition of species, this atlas is an unqualified success; and it should have ended there.

We believe, however, that this volume is intended to be more than simply the description of the radulae of 202 species of cowries. Instead, some implicit but important statements about character-states and evolutionary patterns are presented. The authors classify the 202 species into 13 "patterns" based on radular morphology, and state that those features are to be used later in "a monograph of systematics and phylogeny" (p. 7). But there is a difference between classification and systematics; the former is the process of grouping, by some chosen set of criteria; the latter is the activity of determining evolutionary relationships based upon special similarity (synapomorphy). To phylogeneticists, synapomorphy implies taxic homology (although plesiomorphic character-states can also be homologies). If the radular features used in this compendium are later to be used in a phylogenetic

analysis as characters and thus putative homologies, then by establishing 13 groups, the authors are doing a crude, preemptive form of non-cladistic phylogenetics based on a single character set. We argue that the only reason to put species into larger groupings is that we have evidence, based on character sorting, that those groups are monophyletic. Thus we are compelled to ask the ultimate question: Are the 13 groups monophyletic lineages? If so, then the radular features can be used to recognize evolutionary pattern (i.e., monophyletic lineages). If not, the groupings based solely on radular features will obscure the true evolutionary relationships.

We do believe that careful assessment of the characters of the radula may provide important information for use in the estimation of phylogeny. However, the criteria used to assess putative homologies must be explicit. Bradner and Kay use shape and positional information, but this is merely the first cut. Assessment of similarity must be tested by other means. Parallelism and convergence in structural form are to be expected among closely related species, particularly in a complex structure such as the radula that must be under some selection. In addition to these initial criteria, ontogenetic information can be used. Are the structures generated by the same secretory cells, or at the same time in the advancement along the radular ribbon? Are the structures composed of the same material? Even if these criteria are fulfilled, then there must be a test of congruence. How do these radular features fall out when a phylogeny is constructed based on other independent character sets, or using a total evidence approach? Only then would we be confident that any character, radular or otherwise, is phylogenetically informative.

Many of Bradner and Kay's 13 groups will undoubtedly turn out to be paraphyletic. The challenge will be to pull apart these paraphyletic groups and construct a hypothesis of relationship based on sister groups rather than basal clouds. This atlas is a first step in assembling the data of radular form, but falls short in the use of that information for interpreting evolutionary patterns.

Christopher Meyer
Robert Guralnick

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Manuscripts must be typed, one side only, on A4 or equivalent (e.g., 8½" × 11") white paper, and double-spaced throughout, including references, figure legends, footnotes, and tables. All margins should be at least 25 mm wide. Text should be ragged right (i.e., not full justified). Avoid hyphenating words at the right margin. Manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics; no other manipulation of type faces is necessary on the manuscript. Metric and Celsius units are to be used. For aspects of style not addressed here, please see a recent issue of the journal.

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In most cases, the parts of a manuscript should be as follows: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, footnotes, tables, and figures. The title page should be a separate sheet and should include the title, authors' names, and addresses. The abstract should be less than 200 words long and should describe concisely the scope, main results, and conclusions of the paper. It should not include references.

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

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c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

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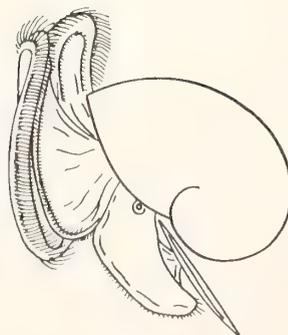
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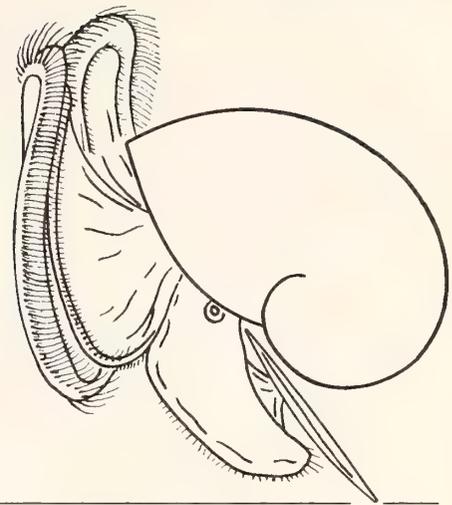
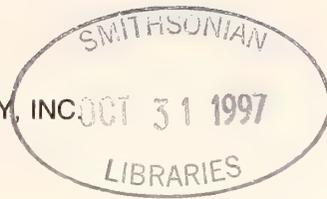
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THE VELIGER

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Haminaea elegans (Gray, 1825)
(Opisthobranchia: Cephalaspidea), a Truly
Amphiatlantic Species

by

EUGENIA MARTÍNEZ AND JESÚS ORTEA

Departamento de Biología de Organismos y Sistemas,
Laboratorio de Zoología, Universidad de Oviedo,
33007-Oviedo, Spain

Abstract. *Haminaea elegans* (Gray, 1825), a tropical species considered as amphiatlantic by some authors solely on the basis of the shell, is recorded for the first time in West African equatorial waters. New data on the shell microsculpture, radula, jaws, gizzard plates, and soft parts are provided. Anatomical comparison with western Atlantic specimens confirms the amphiatlantic status of this species. A review of the type material of *Haminaea taylorae* Petuch, 1987, allows us to include this taxon as a junior synonym of *Haminaea elegans*.

INTRODUCTION

The original description of *Haminaea elegans* (Gray, 1825) is brief and refers only to the shell, described as "dense spiraliter striata" and with an apical perforation; as the type locality Gray (1825:408) recorded "Mare Britannicum et Mediterraneum." A later record is found in Leach (1852:42), who pointed out that Gray received this species from Devon, but, at the same time, described the shell as "longitudinaliter striata." There seems to be a problem with the type locality, because there is no European species with a "dense spiraliter striata" shell; furthermore, the name *elegans* has been subsequently used for a tropical species (see for example Pilsbry, 1895; Marcus, 1957; Thompson, 1977). After searching for the type material of *Bulla elegans* Gray, 1825, we have concluded that it is untraceable. Nevertheless, Pilsbry (1895) did not consider *Haminaea elegans* a controversial species, its shell, in his opinion, being one of the most distinct.

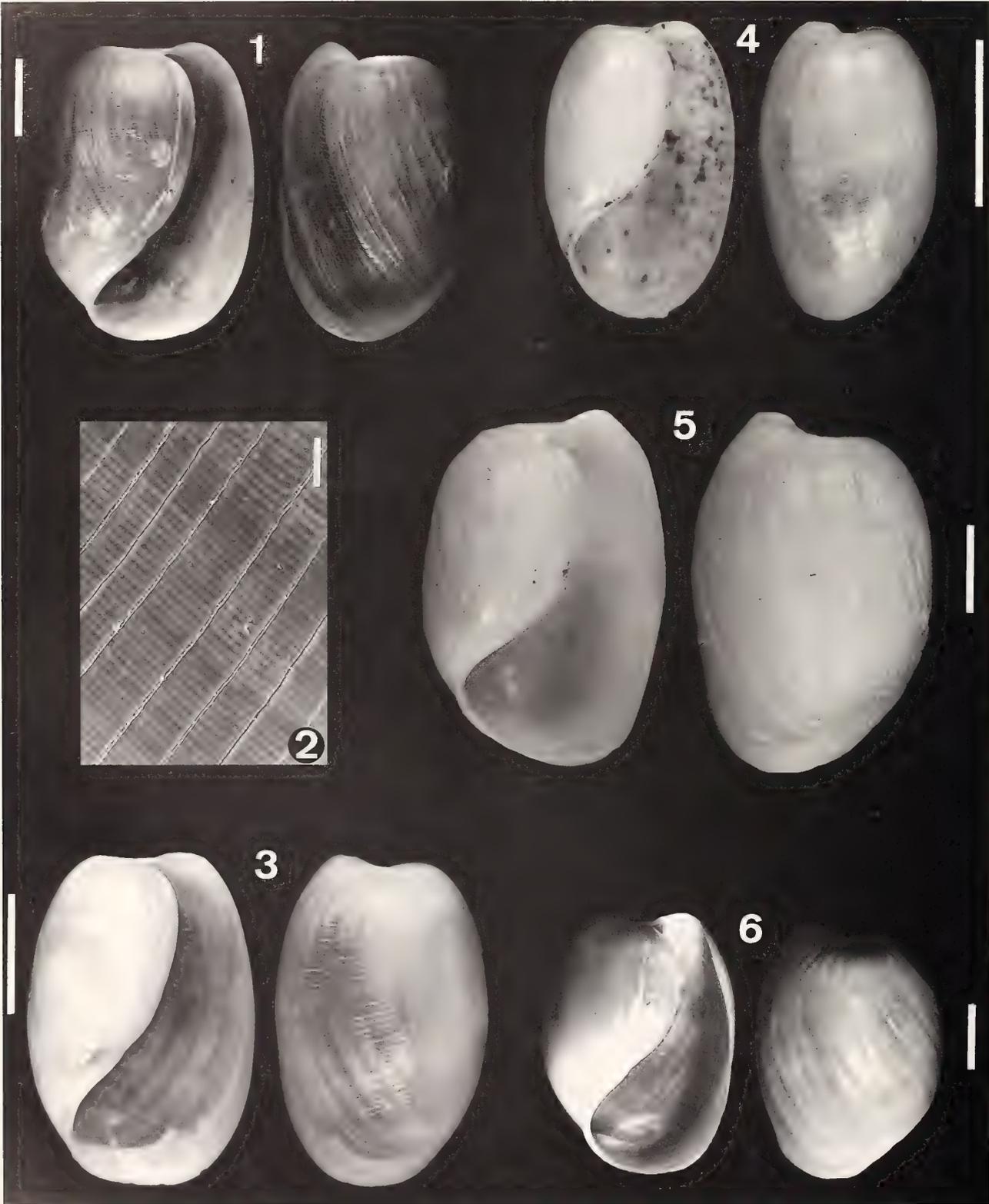
The internal anatomy of *Haminaea elegans* was studied by Marcus (1958) in 12 mature living animals collected near Ubatuba (São Paulo State, Brazil). This same author (Marcus, 1957) had previously described the hard parts of the digestive tract (radula, jaws, and gizzard plates) in about 100 snails collected at São Sebastiao Island, some of them containing the dried bodies. In his first paper, Marcus (1957) identified his material as *Bulla diaphana*

Gould, 1852, originally described from Rio de Janeiro, and which Pilsbry (1895) considered synonymous with *Bulla elegans*.

Haminaea elegans has been considered amphiatlantic by several authors, after an original reference given by Nicklès (1947) from the East Atlantic, off Mauritania. In later papers, Nicklès (1950) figured the shell, and Marche-Marchad (1958) repeated this Mauritanian record. Some years later, Nordsieck & García-Talavera (1979) recorded it from Tenerife (Canary Islands), and Sabelli et al. (1990) from the Mediterranean Sea. García-Talavera (1981) included this species in a checklist of amphiatlantic marine gastropods, and Bernard (1984) recorded it from Gabon. However, all these previous records must be considered as doubtful, because the species was identified solely on the basis of the shell morphology, and the soft parts of animals were not taken into account. Using this reasoning, Thompson (1977) pointed out that the Marche-Marchad record of *H. elegans* on Mauritanian shores was doubtful and needed confirmation.

Examination of some *Haminaea* material from West African shores, as well as an anatomical comparison with western Atlantic specimens, confirms the presence of this species in the eastern Atlantic Ocean. This material includes both preserved animals and empty shells.

In addition, examination of the type material of *Haminaea taylorae* Petuch, 1987, recently described



off Florida only on the basis of shell characters, allows us to include this taxon as a junior synonym of *Haminaea elegans*.

The following abbreviations are used: FSBC, Florida Department of Natural Resources, Florida Marine Research Institute, St. Petersburg, Florida; LZUO, Laboratorio de Zoología, Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo; MNHN, Muséum National d' Histoire Naturelle, Paris; USNM, National Museum of Natural History, Washington.

SYSTEMATICS

Order Cephalaspidea Fischer, 1883

Genus *Haminaea* Leach, [1820]

Haminaea elegans (Gray, 1825)

Material examined: The studied material was collected during several scientific expeditions (and now conserved in the LZUO) or provided by various institutions and private collections.

CONGO: Pointe Noire (North of the lighthouse and Plage Mondaine), three specimens collected between 1.5–2 m (MNHN, R. V. Cosel coll., 1985). The shell of the largest specimen measured 19×7.5 mm.

GABON: Libreville and Port Gentil, nine empty shells, all about 15×10 mm, collected between 2–5 m (MNHN, P. Bernard coll., 1982).

SÃO TOMÉ ISLAND: Esprinha, four specimens from the intertidal zone, whose shells measured about 14×8.5 mm (LZUO, E. Rolán coll., 1990); Praia Milha, one empty shell (MNHN, R. V. Cosel coll., 1983).

PRÍNCIPE ISLAND: San Antonio, one small 9×5.5 mm empty shell (LZUO, E. Rolán coll., 1990).

CUBA: La Broa inlet, Batabanó Gulf (NW of island), two specimens (LZUO, O. Gómez coll., 1993), the shell of the largest one measuring 20×13.2 mm.

MEXICO: Puerto Morelos, Quintana Roo (Yucatan Peninsula), 16 specimens (LZUO, J. Ortea coll., 1994), the largest shell measuring 8.5×4.5 mm

FLORIDA: Indian River, Martin County, six specimens (P. M. Mikkelsen private collection, P. & P. M. Mikkelsen coll., 1983), the largest shell measuring 20×15 mm; Marco Island, Collier County ($25^{\circ}54'36''N$,

$81^{\circ}42'33''W$), two specimens collected at 5 m (FSBC I 11375, C. M. Courtney coll., 1974). Type material of *Haminaea taylorae* Petuch, 1987: Florida Bay, Joe Kem Key, Everglades National Park, Florida (USNM 859898); four paratypes (empty shells) examined, one of them (measuring 12.2×8.5 mm) with dried specimen inside, from which radula and gizzard plates were obtained.

Description: The shell is globular, transversely sculptured (Figures 1–6). These transverse lines, together with the growth lines give the shell a reticulate appearance. With the scanning electron microscope, the transverse lines look like “grooves,” with a more complex microsculpture among them (Figure 2). The apex is concave, with an apical perforation. Young animals have a fragile shell, with a pale yellow periostracum; the shell in larger animals is thicker and reddish-orange.

Material from Gabon, Príncipe and Praia Milha (São Tomé) consisted solely of shells, but we have identified them on the basis of their shape and sculpture, which are identical to those of the whole young specimens examined from São Tomé (compare Figures 3 and 4).

The soft parts present a narrow cephalic shield, rounded at the front and entire, not bilobed, at the end, and short parapodial lobes. Living specimens from Mexico showed a light ground color, with scattered opaque white spots as well as brown spots on the cephalic shield and the parapodia. Marcus & Marcus (1967:24–25) described some specimens from Florida as follows: “the body is pepper and salt, with numerous white elements; larger individuals have a dark greenish cast on the parapodia and head shield.”

The radula possesses a wide rachidian tooth, with a central cusp and one smaller denticle on each side, and with a shape typical for the genus (Figures 7, 10, 13). Lateral teeth, including the innermost one, have a single long, narrow cusp, not denticulate (Figures 8, 9). This cusp was slightly broader in all the western Atlantic examined specimens (Figures 10–15), and in all cases, the entire cusp is bordered by a thin rim. Radular formulae for specimens from various localities are recorded in Table 1.

The jaws are two symmetrical bow-shaped plates which have long and flattened uncini, the latter bearing small denticles on their free edge (Figures 23, 24).

Figures 1–6

Haminaea elegans (Gray, 1825)

Figure 1. Shell of specimen from Pointe Noire, Congo (MNHN).

Figure 2. The same, detail of the microsculpture under SEM.

Figure 3. Shell of specimen from São Tomé (LZUO).

Figure 4. Shell of specimen from Príncipe Island (LZUO).

Figure 5. Shell of specimen from Cuba (LZUO).

Figure 6. Shell of specimen from Florida (P. M. Mikkelsen private collection).

(Figures 1, 3, 4, 5, 6, scale = 5 mm; Figure 2, scale = 100 μ m).

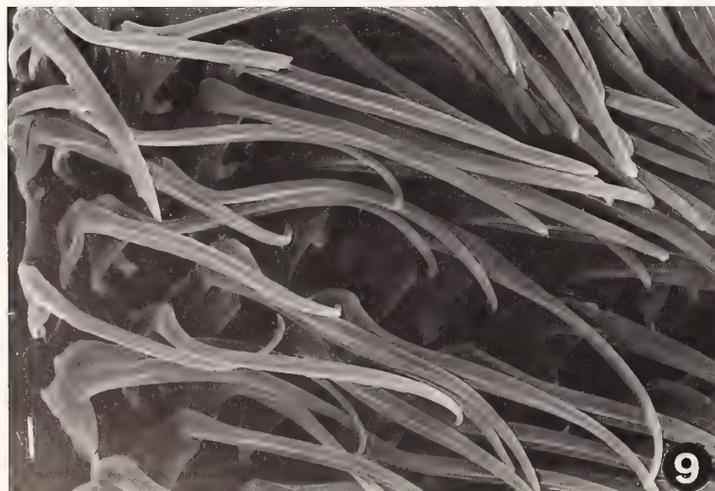
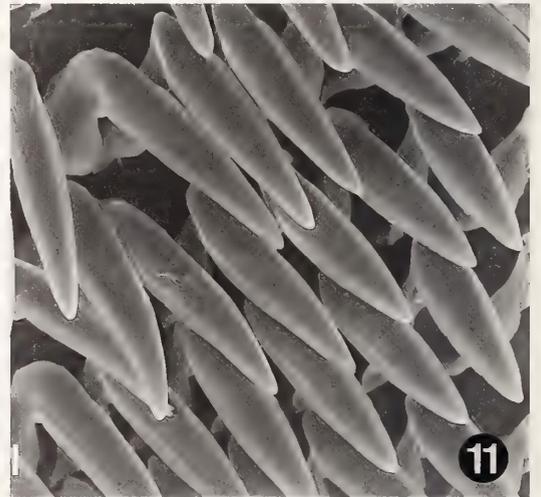
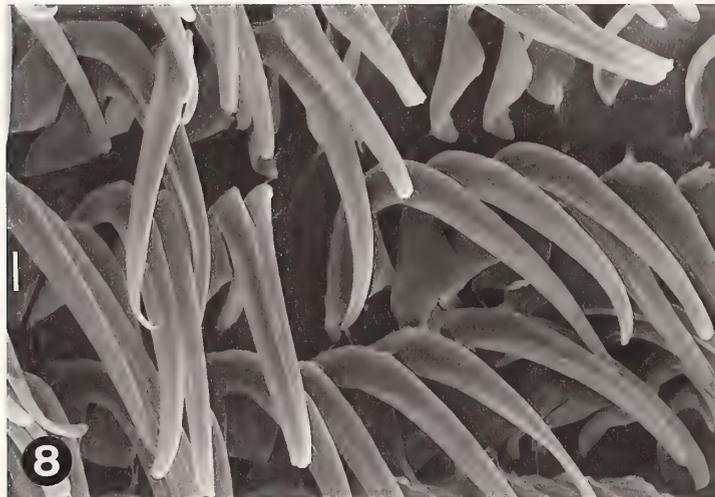


Table 1
Comparative table for specimens of *Haminaea elegans* from different localities
(* data belonging to the dried paratype of *Haminaea taylorae* Petuch).

Locality	Radular formula	Length of gizzard plates (mm)	Number of transverse ridges	Shell length (mm)	Reference
Congo	41 × 33.1.33	3	25–26	19	present paper
São Tomé	21 × 20.1.20	0.97	21–22	14	present paper
Cuba	29 × 26.1.26	2.8	25	20	present paper
Florida (Indian River)	32 × 26.1.26	2.5	20	20	present paper
Florida (Marco Island)	27 × 23.1.23	2	23	15	present paper
Florida * (Everglades N. P.)	25 × 19.1.19	1.6	16	12.2	present paper
Mexico	29 × 14.1.14	1.14	16	7	present paper
Brazil	35–39 × 20.1.20	?	24	20	Marcus (1957)

Each of the three identical gizzard plates has several transverse ridges, forming an inverted “V” at the center (Figures 19, 22). Under SEM examination a large number of minute papillae covering these ridges are visible (Figures 20, 21). The number of ridges varies from 16 to 26, the larger specimens having the most (Table 1).

In the prostate gland, the proximal lobe is twice the size of the distal one (Figure 25A). The penis is long and

rounded near the tip (Figure 25B) and has more than 20 transverse folds, each one bearing a row of minute pegs (Figures 20–25); on one side the folds are interrupted by a wide groove, which guides the sperm to the tip. This description is in accordance with that of Marcus (1958), both in the text and figures 17 and 18. In the penial base there is a small flap, which Marcus (1958:37) described as “a myo-epithelial organ which constitutes the entrance

←

Figures 7–12

Haminaea elegans (Gray, 1825)

Figure 7. Radula from a specimen from Congo (MNHN); rachidian and first lateral teeth.

Figure 8. The same, inner lateral teeth.

Figure 9. The same, outer lateral teeth.

Figure 10. Radula from a specimen from Cuba (LZUO); rachidian and first lateral teeth.

Figure 11. The same, inner lateral teeth.

Figure 12. The same, outer lateral teeth.

(All scales = 10 μm).

→

Figures 13–18

Haminaea elegans (Gray, 1825)

Figure 13. Radula from a specimen from Mexico (LZUO); rachidian and first lateral teeth.

Figure 14. The same, outer lateral teeth.

Figure 15. Radula from a specimen from Florida (P. M. Mikkelsen private collection); rachidian and first lateral teeth.

Haminaea taylorae Petuch, 1987

Figure 16. Paratype (USNM 859898), rachidian and first lateral teeth.

Figure 17. Paratype (USNM 859898), outer lateral teeth.

Figure 18. Paratype (USNM 859898), gizzard plate.

(Figures 15, 18, scale = 100 μm; Figures 13, 14, 16, 17, scale = 10 μm)

Figures 19–24

Haminaea elegans (Gray, 1825)

Figure 19. Gizzard plate from a specimen from Congo (MNHN); general view.

Figures 20, 21. Details of the same.

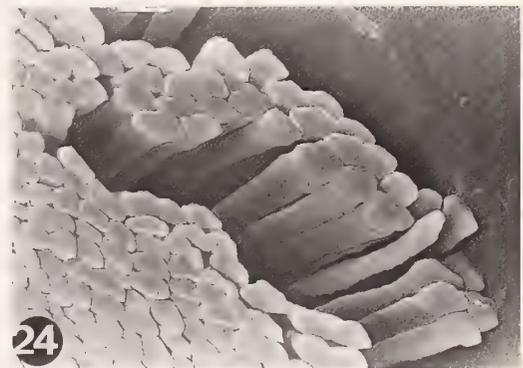
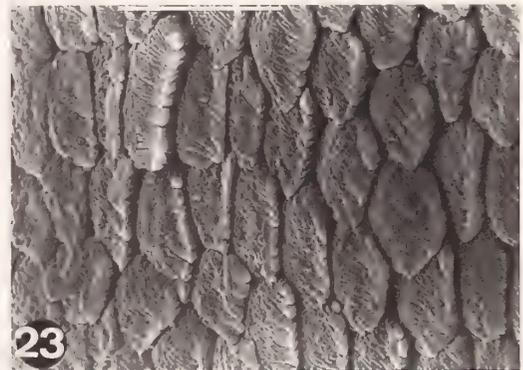
Figure 22. Gizzard plate from a specimen from Florida (FSBC I 11375).

Figure 23. Elements of the jaws from a specimen from Cuba (LZUO).

Figure 24. The same, near the masticatory edge.

(Figures 19, 20, 22, scale = 100 μm; Figures 21, 23, 24, scale = 10 μm).





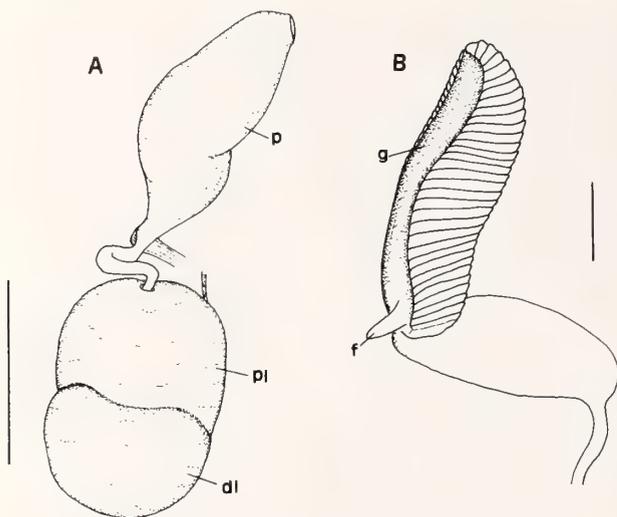


Figure 25

Haminaea elegans (Gray, 1825), A: Male genital apparatus from a specimen from São Tomé (LZUO), scale = 1 mm; B: Scheme of the penis, scale = 0.5 mm. Abbreviations: dl, distal lobe of prostate; f, flap on penial base; g, sperm groove; p, penial sac; pl, proximal lobe of prostate.

of the prostatic duct." The general shape of the penis is identical in all the examined specimens from opposite Atlantic shores (Figures 26–31); the penial pegs measure about 10 μm in length.

We have examined the four paratypes of the Floridian species *Haminaea taylorae* Petuch, whose shells were fragile and globular, provided with well-defined transverse grooves. From a dried paratype of this species we obtained radula and gizzard plates, examining both under SEM (Figures 16–18), and found that they showed a general morphology identical to the examined western Atlantic specimens of *H. elegans*. Unfortunately, the penial morphology of the types of *H. taylorae* was not available for examination.

Distribution: Off western Atlantic coasts, *Haminaea elegans* is currently known to inhabit the area between the Caribbean and Brazil (Pilsbry, 1895); Marcus (1957, 1958) recorded it in Brazil; Marcus & Marcus (1963) in the Lesser Antilles (Curaçao and Bonaire) and in Florida

(Marcus & Marcus, 1967); and Thompson (1977) in Jamaica. In Cuba, the species was first recorded by Arango y Molina (1878–1880) as very common, although only the shell was described. Bandel (1976) described the egg masses in specimens from Santa Marta, Colombia.

In the present paper, this species is recorded for the first time from the following East Atlantic localities: Congo, São Tomé and Príncipe Islands, and also from the Caribbean coast of Yucatan, Mexico, in West Atlantic shores.

In eastern Atlantic waters, the species was previously recorded off Gabon (Bernard, 1984), Mauritania (Nicklès, 1947, 1950; Marche-Marchad, 1958), the Canary Islands (Nordsieck & García-Talavera, 1979), and in the Mediterranean Sea (Sabelli et al., 1990), but all these records remain unverified.

DISCUSSION

Shell features are not reliably diagnostic in the genus *Haminaea* as far as identifying species is concerned. Despite this, the shell of *H. elegans* is one of the most distinct; Pilsbry (1895:356) referred to "the engraved spirals clearly visible without a lens," and also to "the apical perforation and the mode of insertion of the upper end of the lip" as very reliable characters for identification of *H. elegans*.

As previously stated, all earlier records of *H. elegans* in eastern Atlantic waters are doubtful and unproven. For instance, Talavera et al. (1987:61), in their description of the species *Haminaea ortei*, pointed out that the shell described and figured by Nordsieck & García-Talavera (1979) as *H. elegans* Gray "is quite similar to the one of *H. ortei* and it could belong to this species"; this hypothesis is supported by the fact that we have found *H. ortei* in Tenerife, Canary Islands (unpublished data).

On the other hand, Nicklès (1950:fig. 281) figured a transversely sculptured shell that has the same shape as our specimens. However, this illustration is undetailed and nothing is said about the presence of an apical perforation. Sabelli et al. (1990) included the species in a catalogue without any description or reference. Only Bernard (1984:pl. 53, fig. 217) included quite good photographs of five empty shells from Gabon (Banié, Komo estuary, and Port Gentil).

Figures 26–31

Haminaea elegans (Gray, 1825)

Figure 26. Apical view of penis from a Congo specimen (MNHN).

Figure 27. The same, detail of folds and penial groove.

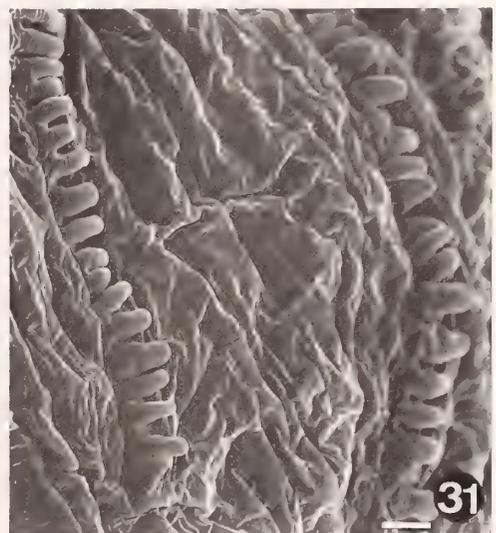
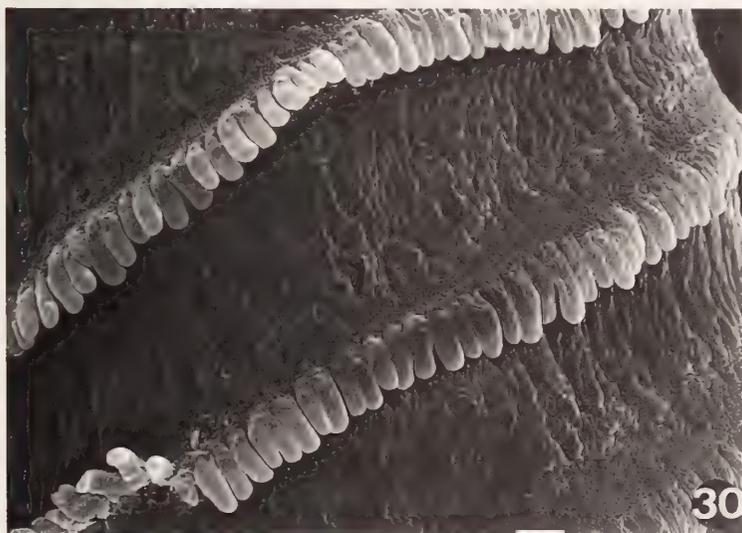
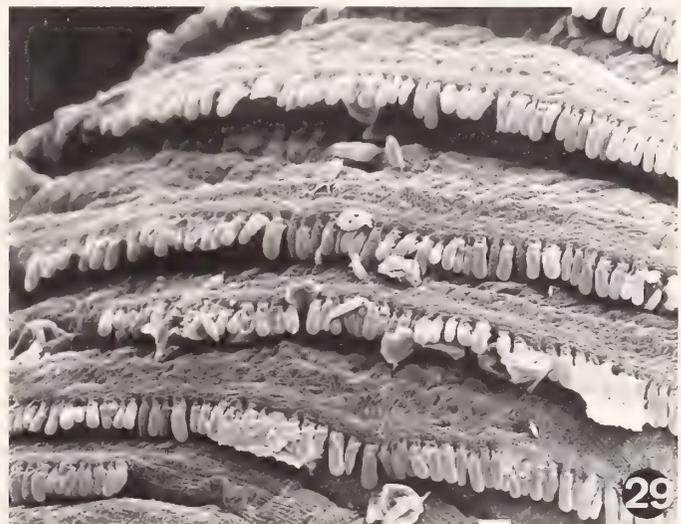
Figure 28. The same, detail of penial pegs.

Figure 29. Detail of pegs from a Cuban specimen (LZUO).

Figure 30. Detail of pegs from a Mexican specimen (LZUO).

Figure 31. The same, from a Florida specimen (P. M. Mikkelsen private collection).

(Figures 26, 27, scale = 100 μm ; Figures 28, 29, 30, 31, scale = 10 μm).



The present material allows us to place this species with certainty around the equatorial area off West African coasts, and also confirms the amphiatlantic character of *H. elegans*. As far as its internal anatomy is concerned, radular morphology, the general shape of the gizzard plates, and particularly the penial morphology are all very reliable diagnostic features.

As Schaefer (1992) pointed out, the male copulatory apparatus is of very great value for recognizing species of *Haminaea*. Thus, the penial morphology of *H. elegans* is clearly different from that of several East Atlantic species: penis with a sharpened tip in *H. hydatis* (Linnaeus, 1758), *H. orbignyana* (Férussac, 1822), and *H. fusari* Álvarez, García & Villani, 1993; with an apical crest in *H. ortei* Talavera, Murillo & Templado, 1987, *H. templadoi* García, Pérez-Hurtado & García-Gómez, 1991, and *H. exiqua* Schaefer, 1992; or cylindrical with a spiculate apex in *H. navicula* (Da Costa, 1778).

After examination of radula and gizzard plate morphology, we can conclude that the taxon *Haminaea taylorae*, recently described from Florida by Petuch (1987) only on the basis of the shell morphology, is a synonym of *H. elegans* (Gray). In his description, Petuch (1987: 32) considered *H. taylorae* as "very similar to the widespread Caribbean *H. elegans*," but he found some differences in the general shape of shell (more cylindrical and with a much more recurved columella in *H. taylorae*) and also in shell color (*H. taylorae* being pink instead of yellowish-white). These facts show how necessary it is to study the soft parts of the body in Cephalaspideans.

There is disagreement about the correct spelling of the generic name, which can be found both as *Haminaea* Leach, [1820], and *Haminoea* Turton & Kingston, 1830, in the literature. In the most recent papers (García et al., 1991; Schaefer, 1992; Álvarez et al., 1993) *Haminaea* is used, following a proposal for conservation made by Giannuzzi-Savelli & Gentry (1990) (Case 2588). But there is a previous version of this same case proposing the conservation of *Haminoea* (Giannuzzi-Savelli, 1987). As both names are of common current usage and no decision has been made by the International Commission on Zoological Nomenclature after 5 and 8 years respectively, either generic name could be used.

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Opisthobranch Mollusks and the Pulmonate Limpet *Trimusculus reticulatus* (Sowerby, 1835) from the Outer Washington Coast

by

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Abstract. Forty-two species of opisthobranchs were found at nine sites on the outer Washington coast, including 39 species intertidally at Kayostla Beach in Olympic National Park. The ranges of *Cuthona cocoachroma*, *C. flavovulta*, *C. fulgens*, *Diaphana californica*, and the pulmonate limpet *Trimusculus reticulatus* are extended northward from Oregon to Kayostla Beach. These records bring to 46 the number of species of opisthobranchs known from the Pacific coast of Washington and the south shore of the Strait of Juan de Fuca.

INTRODUCTION

Few records of opisthobranch mollusks exist for the outer Washington coast, representing a gap in our knowledge of the geographic distribution of northeastern Pacific species. Bergh (1904) described *Melibe pellucida* (a synonym of *M. leonina* [Gould, 1852]) based on specimens collected off the mouth of the Columbia River. To our knowledge, this is the first record from the Pacific coast of Washington. More recently, Robilliard (1971) reported *Archidoris odhneri* (MacFarland, 1966) and *Cuthona abronia* (MacFarland, 1966) from sites near Cape Flattery; Robilliard & Baba (1972) described *Aldisa cooperi* based in part on specimens collected subtidally off the Olympic Peninsula; and Robilliard (1974:991) noted the

abundance of *Tochuina tetraquetra* (Pallas, 1778) off the outer coast.

Additional records can be found in Smith (1976:table 1 and figs. 32, 33, 69-72, 122, and 145) who recorded the following species from the Pacific coast of Washington and/or the south shore of the Strait of Juan de Fuca: *Anisodoris nobilis* MacFarland, 1905 (misidentified as *Archidoris montereyensis* [Cooper, 1863]); *Cadlina luteo-marginata* MacFarland, 1966; *Dendronotus iris* Cooper, 1863 (identified to genus only); *Dialula sandiegensis* (Cooper, 1863); *Flabellina trilineata* (O'Donoghue, 1921) (misidentified as *Hermisenda crassicornis* [Eschscholtz, 1831]); *Phyllaplysia taylora* Dall, 1900; *Rostanga pulchra* MacFarland, 1905; and *Triopha catalinae* (Cooper, 1863) (as *Triopha carpenteri* [Stearns, 1873]).

Smith's figure 5 also shows a specimen of *Hallaxa chani* Gosliner & Williams, 1975 next to its sponge prey *Halisarca* sp. underneath an intertidal boulder from an undisclosed outer coast locality. In the text referring to this figure, Smith pointed out a variety of taxa including the "tan sponge" but did not mention any nudibranchs. Finally, Wertheim (1984) pictured *Flabellina trilineata*, *Hermisenda crassicornis*, and *Rostanga pulchra* from Tatoosh Island, just off Cape Flattery (see her plates 47, 55a, and 81, and the photographic sites listed on pp. 153–154).

Based on the above records, 15 species of opisthobranchs have been reported from the Pacific coast of Washington and the south shore of the Strait of Juan de Fuca. Many more species may be expected to occur in this region based on the number of species known to range from Alaska or British Columbia to California (see range summaries in McDonald, 1983, and Behrens, 1991).

We report herein on observations of opisthobranchs from the outer coast of Washington, including sites just inside the Strait of Juan de Fuca. We also document the occurrence on the outer coast of *Trimusculus reticulatus* (Sowerby, 1835), a pulmonate limpet previously known as far north as southern Oregon (Beeman & Williams, 1980).

STUDY SITES AND METHODS

During July and August 1995, we examined four rocky intertidal sites and floating docks in four bays (Figure 1). With the exception of Kayostla Beach, which we sampled during five consecutive minus tides in mid-July, each of the intertidal sites was examined once. Previous visits by two of us (TAW and KRW) to Olympic National Park had indicated that Kayostla Beach has some of the most diverse intertidal biota on the Olympic coast; we therefore decided to focus our efforts there.

Specimens were identified in the field with the aid of hand lenses and McDonald & Nybakken (1980), McDonald (1983), and Behrens (1991). Many specimens collected at Kayostla Beach were identified in base camp and returned alive to the field the following day. The senior author confirmed the identity of all specimens collected by the junior authors.

Voucher specimens have been deposited in the Invertebrate Zoology collection at the California Academy of Sciences or are in the personal collection of the senior author; these are listed with their catalogue numbers in the Appendix.

Intertidal Sites:

1. Kayostla Beach, Olympic National Park (48°02'N, 124°41'W). We examined a 900 m long section of low intertidal in front of the small unnamed stream flowing onto Kayostla Beach. The intertidal zone is gently

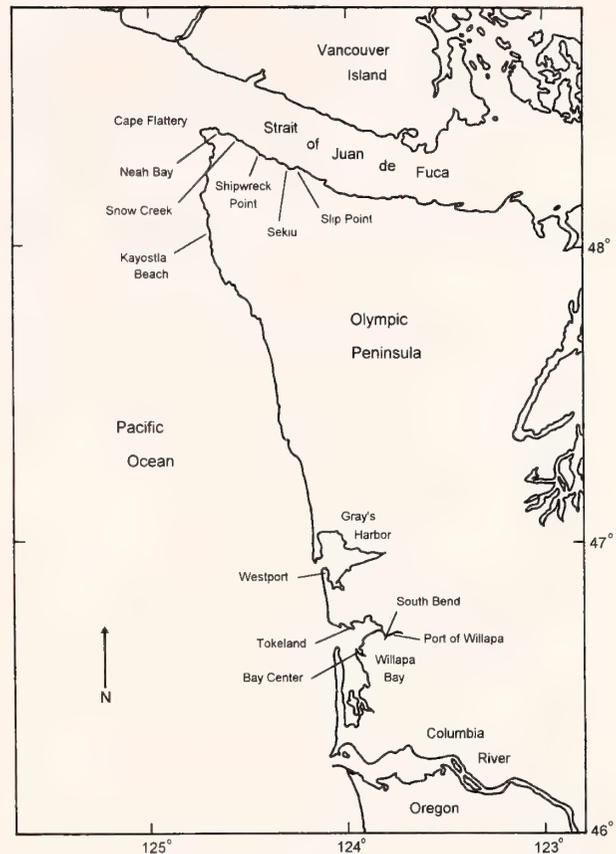


Figure 1

Map of the outer Washington coast, showing location of the study sites.

sloping, 400–500 m wide, and consists of cobbles and boulders interspersed with patches of sand. This site is protected outer coast as defined by Ricketts et al. (1985:5).

2. Snow Creek (48°21'N, 124°33'W). We examined the boulders and low bedrock ridges immediately west of the Snow Creek resort. The intertidal zone is about 30 m wide and drops off steeply at its seaward edge. Wave action is so reduced here and at the next site, at least during the summer, that both sites can be classified as transitional between protected outer coast and bay and estuary (Ricketts et al., 1985; Kozloff 1983: 117).
3. Shipwreck Point (48°19'N, 124°27'W). Cobbles and small boulders make up a gently sloping intertidal zone about 100 m wide.
4. Slip Point (48°16'N, 124°15'W). This point is more wave-exposed than the previous two sites and has a rock bench approximately 75 m wide with scattered tidepools, ridges, and boulders. This site is probably best classified as protected outer coast as defined by Ricketts et al. (1985).

Table 1

Opisthobranchs found at four rocky intertidal sites on the outer Washington coast, July and August 1995. ●●●● = abundant (20 or more individuals sighted); ●● = moderate (20 > n > 2); ● = rare (n ≤ 2); x = present, but abundance not recorded.

Species	Site			
	Kayos-tla Beach	Snow Creek	Shipwreck Point	Slip Point
Cephalaspidea				
<i>Diaphana californica</i> Dall, 1919	●			
Notaspidea				
<i>Berthella californica</i> (Dall, 1900)	●			
Nudibranchia, Doridacea				
<i>Acanthodoris nanaimoensis</i> O'Donoghue, 1921	●			x
<i>Adalaria</i> sp. 1 of Behrens (1991)	●●			
<i>Aldisa cooperi</i> Robilliard & Baba, 1972	●			
<i>Ancula pacifica</i> MacFarland, 1905	●			
<i>Anisodoris nobilis</i> (MacFarland, 1905)	●●			x
<i>Archidoris montereyensis</i> (Cooper, 1863)	●●	●●	x	
<i>Archidoris odhneri</i> (MacFarland, 1966)	●●			
<i>Cadlina luteomarginata</i> MacFarland, 1966	●●	●●●		x
<i>Cadlina modesta</i> MacFarland, 1966	●●●●	●		
<i>Diaulula sandiegensis</i> (Cooper, 1863)	●●	x	x	
<i>Geitodoris heathi</i> (MacFarland, 1905)	●			
<i>Hallaxa chani</i> Gosliner & Williams, 1975	●●	●●●		x
<i>Laila cockerelli</i> MacFarland, 1905	●●			x
<i>Onchidoris muricata</i> (Müller, 1776)	●●			
<i>Rostanga pulchra</i> MacFarland, 1905	●●●●	●●●●	●●	●●●●
<i>Triopha catalinae</i> (Cooper, 1863)	●●			x
Nudibranchia, Dendronotacea				
<i>Dendronotus frondosus</i> (Ascanius, 1774)	●●			
<i>Dendronotus subramosus</i> MacFarland, 1966	●●			
<i>Doto amyra</i> Marcus, 1961	●●●●	●●		●●
<i>Doto kya</i> Marcus, 1961	●			
<i>Doto</i> form B of Goddard (1996)		●●		

Table 1

Continued.

Species	Site			
	Kayos-tla Beach	Snow Creek	Shipwreck Point	Slip Point
<i>Tritonia festiva</i> (Stearns, 1873)	●●	●		
Nudibranchia, Arminacea				
<i>Dirona albolineata</i> Eliot in Cockerell & Eliot, 1905	●●			
<i>Janolus fuscus</i> O'Donoghue, 1924	●●	x		x
Nudibranchia, Aeolidacea				
<i>Aeolidia papillosa</i> (Linnaeus, 1761)	●			
<i>Cátriona columbiana</i> (O'Donoghue, 1922)	●			
<i>Cuthona abronia</i> (MacFarland, 1966)	●●			
<i>Cuthona cocoachroma</i> Williams & Gosliner, 1979	●●			
<i>Cuthona divae</i> (Marcus, 1961)	●●			
<i>Cuthona flavovulta</i> (MacFarland, 1966)	●●			
<i>Cuthona fulgens</i> (MacFarland, 1966)	●			
<i>Eubranchus olivaceus</i> (O'Donoghue, 1922)	●●		x	x
<i>Eubranchus rustys</i> (Marcus, 1961)	●●	●●	x	
<i>Flabellina trilineata</i> (O'Donoghue, 1921)	●●	x		x
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	●●			x
Sacoglossa				
<i>Aplysiopsis enteromorphae</i> (Cockerell & Eliot, 1905)	●●			
<i>Hermaea vancouverensis</i> O'Donoghue, 1924	●			
<i>Placida dendritica</i> (Alder & Hancock, 1843)	●●	x		x
Total number of species per site	39	13	6	12

Bays

Floating docks were examined for opisthobranchs at five sites in two bays on the Pacific coast and at two sites in two bays on the outer Strait of Juan de Fuca (Figure 1). Docks in Neah Bay were examined on 15 July 1995; the other six sites from 8 August to 10 August 1995. We sampled the docks in Westport on 2 consecutive days; otherwise, each of these sites was examined only once.

Table 2

Opisthobranchs found on floating docks in bays on the outer Washington coast, July and August 1995. ●●● = abundant (20 or more individuals sighted); ●● = moderate (20 > n > 2); ● = rare (n ≤ 2); x = present, but abundance not recorded.

Species	Location				
	South Bend	Tokenland	Westport	Neah Bay	Sekiu
<i>Cuthona albocrusta</i>	●●●				
<i>Archidoris montereyensis</i>		●	●		
<i>Dendronotus frondosus</i>		●	●	●	
<i>Dirona albolineata</i>			●		
<i>Janolus fuscus</i>			●●		x
<i>Eubranchus olivaceus</i>				●●●	●●
<i>Triopha catalinae</i>					x
<i>Hermisenda crassicornis</i>					x
<i>Diaulula sandiegensis</i>					x
<i>Doridella steinbergae</i>					●●●
Number of species per site	1	2	4	2	6

RESULTS

We found 42 species of opisthobranchs, 40 in the rocky intertidal zone and 10 on docks in bays (Tables 1, 2). *Cuthona albocrusta* (MacFarland, 1966) and *Doridella steinbergae* (Lance, 1962) were the only species found on docks which did not also occur intertidally. *Aplysiopsis enteromorphae* (Cockerell & Eliot, 1905) was found on the green algae *Chaetomorpha* sp. and *Cladophora* sp. in high intertidal pools; the rest of the species observed intertidally were found in the low intertidal zone.

The aeolid nudibranchs *Cuthona cocoachroma* Williams & Gosliner, 1979, *C. flavovulta* (MacFarland, 1966), and *C. fulgens* (MacFarland, 1966), and the cephalaspidean *Diaphana californica* Dall, 1919, were all found at Kayostla Beach, extending their known ranges northward from Oregon (Goddard, 1984 and unpublished observations).

Cuthona cocoachroma from Kayostla Beach was found only on *Thuiaria* sp., a hydroid with which this aeolid is consistently associated from northern California to northern Oregon (Goddard, 1985 and unpublished observations).

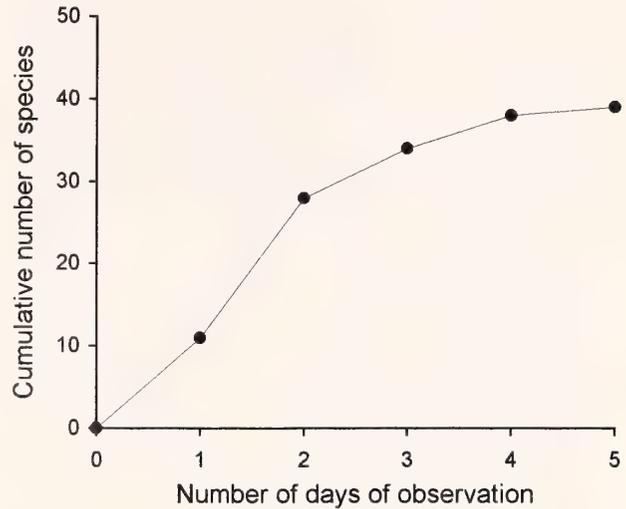


Figure 2

Cumulative number of species of opisthobranchs found at Kayostla Beach, Washington as a function of the number of days of observation. Except for day 1, each day of observation consisted of two or three observers searching the low intertidal zone for approximately 3 hours. On day 1, two observers searched for 1 hour.

Thirty-nine species of opisthobranchs were found at Kayostla Beach, many more than at the intertidal sites on the Strait of Juan de Fuca (Table 1). Although Kayostla Beach was examined over the course of 5 days, compared to only 1 day for each of the other sites, differences in sampling effort and conditions do not account for the observed differences in species richness. A mean of 23.5 species per day was found at Kayostla Beach, compared to a mean of 9.7 species per day for the intertidal sites on the Strait, and conditions for observation were good at all sites¹.

A plot of the cumulative number of species observed at Kayostla Beach as a function of the number of days of observation (Figure 2) begins to level off at 38 species, suggesting that we found most of the species present at that site.

Of the 10 species of opisthobranchs found on floating docks in bays (Table 2), three were abundant: *Cuthona albocrusta* on the basal stolons of the hydroid *Bimeria* sp. on the docks at South Bend in Willapa Bay; *Eubranchus olivaceus* (O'Donoghue, 1921) and its egg masses on *Obelia* sp. in Neah Bay; and *Doridella steinbergae* and its egg masses on *Membranipora membranacea* (Linnaeus, 1767) growing on *Laminaria* sp. on the docks at Sekiu. Opisthobranchs were not found on the docks at

¹ Means were calculated using the daily totals of the one of us (JHRG) who sampled every day at all of the sites. The first day at Kayostla Beach was omitted from this analysis because our observations that day were cut short by the early flooding tide.

either Bay City or the Port of Willapa, both in Willapa Bay.

Cuthona albocrusta from South Bend had little encrusting white pigment on its cerata and thus differed somewhat from the descriptions for this species given by MacFarland (1966), McDonald (1983), and Behrens (1991). Six specimens of *Cuthona albocrusta* from South Bend have been deposited in the California Academy of Sciences (CASIZ 105926).

While searching for opisthobranchs at Kayostla Beach, we found several clusters of the pulmonate limpet *Trimusculus reticulatus* on the ceiling of an intertidal cave. Specimens measured up to 19 mm in diameter and were surrounded by their translucent, petal-shaped, gelatinous egg masses. Three specimens of *T. reticulatus* from Kayostla Beach have been deposited in the California Academy of Sciences (CASIZ 105924).

DISCUSSION

Our records, combined with those from previous reports, bring to 46 the number of opisthobranch species known from the Pacific coast of Washington and the south shore of the Strait of Juan de Fuca. This total should increase substantially as more records are obtained from less studied subtidal and estuarine habitats.

Kayostla Beach appears to be as rich in species of opisthobranchs as any of the better intertidal sites in northern California or Oregon (Goddard, 1984, 1987, 1990, and unpublished observations). Features shared by these sites include large area, complex topography with an abundance of pools and shaded microhabitats, and at least some protection from waves (personal observations). Our results at Kayostla Beach and some of these other sites suggest that a sampling effort of two experienced observers searching for 2 to 3 hours per low tide for 4 or 5 days is needed to accurately determine the number of species of opisthobranchs present in the low intertidal zone.

With some exceptions mentioned above, we found few species and individuals of opisthobranchs on floating docks. This was especially surprising at Westport, where the docks had luxuriant growths of *Obelia* sp., *Bugula* sp., and other fouling species eaten by a wide variety of nudibranchs. We expect further observation in these habitats to yield more species.

ACKNOWLEDGMENTS

We thank the Makah Tribal Council, especially agent Steve Davis, for permission to examine floating docks in Neah Bay, and Dr. Barry Roth and two anonymous reviewers for their suggestions on the manuscript. This research was funded in part by a grant (to JHRG) from Conchologists of America, Inc.

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APPENDIX: LOCATION AND CATALOGUE NUMBERS OF VOUCHER SPECIMENS

We generally limited our collection of voucher specimens to: (1) specimens representing range extensions; (2) spe-

cies we have not frequently encountered in the Pacific Northwest; (3) species of uncertain taxonomic status (e.g., *Doto* spp.); and (4) specimens which were identified in camp and could not be returned to the wild.

Catalogue numbers preceded by CASIZ indicate specimens deposited in the Invertebrate Zoology collection at the California Academy of Sciences in San Francisco; those beginning with a G indicate specimens in the personal collection of the senior author. Data concerning each species are listed in the following order: catalogue number, collection site, date of collection, and number of specimens.

Adalaria sp. 1 of Behrens (1991): G7-13-95-2, Kayostla Beach, 13 July 1995, 2 specimens; G7-13-95-3, Kayostla Beach, 13 July 1995, 2 specimens. *Aldisa cooperi*: G7-11-95-2, Kayostla Beach, 11 July 1995, 1 specimen. *Cadlina modesta*: G7-11-95-4, Kayostla Beach, 11 July 1995, 1 specimen. *Catriona columbiana*: G7-12-95-2, Kayostla Beach, 12 July 1995, 2 specimens. *Cuthona albocrusta*: CASIZ 105926, South Bend, 8 August 1995, 6 specimens. *Cuthona flavovulva*: CASIZ 105927, Kayostla Beach, 11 and 13 July 1995, 3 specimens. *Cuthona fulgens*: CASIZ 105928, Kayostla Beach, 11 July 1995, 1 specimen. *Diaphana californica*: CASIZ 105925, Kayostla Beach, 12 and

14 July 1995, 2 specimens. *Doridella steinbergae*: G8-10-95-3, Sekiu, 10 August 1995, 4 specimens. *Doto amyra*: G7-12-95-3, Kayostla Beach, 12 July 1995, 12 specimens; G7-15-95-3, Snow Creek, 15 July 1995, 6 specimens; G8-11-95-1, Slip Point, 11 August 1995, 3 specimens in 2 lots. *Doto kya*: G7-10-95-1, Kayostla Beach, 10 July 1995, 1 specimen. *Doto* form B of Goddard (1996): G7-15-95-1, Snow Creek, 15 July 1995, 3 specimens. *Eubranchius olivaceus*: G7-11-95-1, Kayostla Beach, 11 July 1995, 1 specimen; G7-15-95-2, Neah Bay, 15 July 1995, 4 specimens; G8-10-95-2, Shipwreck Point, 2 specimens; G8-10-95-4, Sekiu, 10 August 1995, 8 specimens; G8-11-95-2, Slip Point, 11 August 1995, 1 specimen. *Eubranchius rustyus*: G7-10-95-2, Kayostla Beach, 10 July 1995, 2 specimens; G7-15-95-4, Snow Creek, 15 July 1995, 2 specimens; G8-10-95-1, Shipwreck Point, 10 August 1995, 1 specimen. *Hermaea vancouverensis*: G7-12-95-1, Kayostla Beach, 12 July 1995, 1 specimen. *Onchidoris muricata*: G7-11-95-3, Kayostla Beach, 11 July 1995, 3 specimens; G7-14-95-2, Kayostla Beach, 1 specimen. *Placida dendritica*: G7-14-95-1, Kayostla Beach, 14 July 1995, 1 specimen. *Triopha catalinae*: G7-13-95-1, Kayostla Beach, 13 July 1995, 1 specimen. *Trimusculus reticulatus*: CASIZ 105924, Kayostla Beach, 13 July 1995, 3 specimens.

Recent Species of the Genus *Petricola* in the Eastern Pacific (Bivalvia: Veneroidea)

by

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Abstract. The taxonomy of 16 Recent eastern Pacific species that have been allocated to the bivalve genus *Petricola* is discussed. Two new species, *Petricola hertzana* and *P. scotti* are described. Fifteen lectotype designations are made. One species is placed in the genus *Choristodon*, two in the genus *Petricolaria*, four species in *Petricola* (*Petricola*), and five in *Petricola* (*Petricolirus*); four species remain in *Petricola*, *s.l.* A list is provided of species-level taxa excluded from the family (and *nomina dubia*).

INTRODUCTION

About 2 years ago, during preparation of a volume on the bivalves of the northeastern Pacific (Coan et al., in preparation), I noted several nomenclatural problems involving eastern Pacific species that have been allocated to the bivalve genus *Petricola*. The present study addresses these problems. There is by no means a consensus on the arrangement of the genera within the Petricolidae, or even which genera are members of that family, or indeed on the arrangement of the families and subfamilies in the Veneroidea as a whole. I hope that improving the understanding of the eastern Pacific petricolids will be useful to workers addressing these broader topics.

This group was more difficult to understand than I anticipated. In part, this is because unlike the California *Petricola* (*Petricola*) *carditoides* (Conrad, 1837), one of the most common marine bivalves on the West Coast with an extremely variable morphology depending on its nesting site, many other taxa seem to be very uncommon, making it difficult to understand the limits of their variability. A second reason for the difficulty in working out the eastern Pacific species is the high proportion of missing type material, compounded by early, cryptic descriptions unaccompanied by illustrations.

Key treatments on the systematics of the Petricolidae

in general are those of Deshayes (1853, 1855), G. B. Sowerby II (1854b, 1874a), Tryon (1872), Dall (1900c), Jukes-Browne (1910), Lamy (1921, 1923b), Habe (1951, 1951–1952, 1977), and Keen (1969). A short account of the present study has appeared in a newsletter (Coan, 1996).

FORMAT

In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and type localities, notes on distribution and habitat, and an additional discussion.

The synonymies include all major accounts about the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes given in brackets.

The distributional information is based on specimens I have examined, except as noted. For many species, the available habitat information is sparse. I have summarized the data available. Most occurrences in the fossil record are taken from the literature.

References are provided in the Literature Cited for all works and taxa mentioned.

The following abbreviations for institutions and collections are used in the text: AMNH, American Museum of Natural History, New York, New York, USA; ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; BM(NH), British Museum (Natural History)

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collection in The Natural History Museum, London, England; CAS, California Academy of Sciences, San Francisco, California, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; LACM, Natural History Museum of Los Angeles County, California, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MHNG, Muséum d'Histoire Naturelle, Geneva, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNH-U, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; PRI, Paleontological Research Institution, Ithaca, New York, USA; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; SDNHM, San Diego Natural History Museum, San Diego, California, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM, United States National Museum collection, National Museum Natural History, Smithsonian Institution, Washington, DC, USA; PMYU, Peabody Museum, Yale University, New Haven, Connecticut, USA; UMML, University of Miami Marine Laboratory [Rosensteil School of Marine and Atmospheric Sciences], Miami, Florida, USA; ZISP, Zoologisches Institut, St. Petersburg, Russia; Hertz Collection, collection of Carol and Jules Hertz, San Diego, California USA; Redfern Collection, collection of Colin Redfern of Boca Raton, Florida, USA; Skoglund Collection, collection of Carol C. Skoglund, Phoenix, Arizona, USA.

DIFFERENTIATING CHARACTERS

Shape: Many species have a characteristic shape. For example, *Petricolaria cognata*, which penetrates soft substrata, is always elongate (Figures 49, 50, 69), and *Choristodon robustum*, which inhabits and can enlarge cavities in coral and other calcareous substrata, is always ovate (Figures 42–48, 68). However, other species, such as *Petricola carditoides*, which nestles in existing cavities and has only limited capacity to enlarge its home, can vary enormously in shape (Figures 3–12). I have here given the most characteristic shape, including the relative position and prominence of the beaks, degree of inflation, shell thickness, and prominence of the beaks, while noting the potential for variability.

The term **ovate** means a length/height ratio of 1.0 to 1.5; **ovate-elongate**, a l/h ratio of 1.5 to 2.0; **elongate**, a l/h ratio of 2.0 to 3.0; **very elongate**, a l/h ratio of greater than 3.0. **Anterior end shortest** means that the anterior end is from 40% to 30% of shell length; **anterior end short**, from 30% to 20%; **anterior end very short**, less than 20%. The term **inflated** means having a thickness/height ratio of 0.5 to 1.0; adult specimens of only two taxa may be **flattened**, with a ratio of less than 0.5.

Sculpture: As with many bivalves, the external sculpture is often diagnostic. Radial sculpture predominates in most members of the Petricolidae, and may be characterized

by the number of ribs and where the most prominent ribs occur. Commarginal elements may also be present, from mere growth checks to conspicuous lamellae.

Pallial sinus/pallial line: The shape of the pallial sinus is an important differentiating character, particularly its depth, whether it is rounded or pointed anteriorly, and the extent to which it is horizontal or is directed dorsally. The pallial sinuses of most species are of **moderate depth**, being from about 50% to 60% of the shell length (Figures 55, 56, 58, 60–68, 70); **deep sinuses** are greater than 60% of shell length (Figures 57, 59, 69); in some specimens of one species, the sinus may be **shallow** and close to 40%. The pallial sinuses of some taxa are **pointed** anteriorly (Figures 61, 69, 70), but most are **rounded**. A **broad** pallial sinus has a ratio between the vertical dimension at its posterior end to its length of from 2.5 to 1.1; a **moderate** sinus of 1.0 to 0.8; a **narrow** sinus of 0.7 to 0.3. The pallial line anteroventral to the pallial sinus is also important, being **slightly confluent** (Figures 56, 64, 65, 67), **substantially confluent** (Figures 57, 66), **closely paralleling** (Figure 59) or entirely **separate** from the sinus (Figures 60–63), and it may be **bowed** dorsally to a greater (Figures 57, 64–66) or lesser (Figures 59, 67) extent.

Hinge: Whereas nearly all the species treated have two cardinal teeth in the right valve and three in the left, the anterior cardinal in the left valve may disappear in the adult, or be absent entirely. The hinge and teeth vary in robustness and in such details as their length and which of them are bifid. Two species have a low posterior lateral-ridge in the right valve.

Ligament: The ligament on all species is external, but a portion of it may be sunken onto the hinge, and this is particularly important in differentiating the species. A partly sunken ligament occurs in members of *Petricola* (*Petricola*) (Figures 55–58) and in *Choristodon* (Figure 68); in the rest, it is not sunken.

Color: Although many species are drab, being white or tinged with brown, in some cases color pattern can provide important clues, and overall color is characteristic of two species.

Lunule/escutcheon: Most species have neither, but each puts in a token appearance among these taxa.

SYSTEMATIC ACCOUNT

Family PETRICOLIDAE d'Orbigny, 1840

[Deshayes, 1830:Table on classification of the bivalves, as Family "Pétricolées," but not accepted as of this date by later authors; dated as first Latinized by d'Orbigny, 1840:109; ICZN Code Art. 11f(iii)]

Genus *Petricola* Lamarck, 1801

Petricola Lamarck, 1801:121 [Type species: *Petricola costata* Lamarck, 1801:121, = *Venus lapicida* Gmelin,

1791:3269, which is based on Chemnitz, 1788: 356–357, pl. 172, figs. 1664, 1665; subsequent designation of Schmidt, 1818:55, 176]. Recent, western Atlantic, IndoPacific.

Naranio Gray, 1853:38 [Type species: *Petricola costata* Lamarck, 1801, = *Venus lapicida* Gmelin, 1791; subsequent designation of Lamy, 1923b:318].

Pseudoirus Habe, 1951:98; 1952:187 [Type species (original designation): “*Petricola mirabilis* Deshayes, 1853,” *auctt., non* Deshayes, 1853]. Recent, Japan. (See Discussion under *Petricola carditoides*.)

Members of this genus are ovate to elongate, with fine to heavy radial sculpture; sculpture divaricate or zig-zag in some taxa. Ligament superficial to partially sunken below hinge margin.

Up to the 1940s, when Winckworth (1944:24) pointed out Schmidt’s (1818) type designation for the genus *Petricola*, the type species was generally taken to be *Venus lithophaga* Retzius, 1788. As a result, Gray (1853) established the genus *Naranio* for *Petricola costata*, and *Ruppellaria* Fleury de Bellevue, 1802, of which *Venus lithophaga*, is the type species, was considered to be a synonym of *Petricola*.

No original specimen from the Chemnitz material that formed the basis of Gmelin’s *Venus lapicida* is now present in the Universitetets Zoologisk Museum in Copenhagen (T. Schiøtte, e-mail, 22 May 1995), but there is little doubt as to its identity.

Habe’s genus *Pseudoirus* was established for a Japanese species identified as “*Petricola mirabilis* Deshayes, 1853,” chiefly on the basis that it does not occur in coral. The sculpture is otherwise similar. Until more is known about its morphology, *Pseudoirus* should be regarded as a synonym of *Petricola*, *s.s.* If the genus proves to be needed, this can be interpreted as case of a “misidentified type species” (ICZN Code Art. 70b), requiring a petition to the International Commission on Zoological Nomenclature to resolve.

Subdivision of this genus into meaningful subgenera or genera awaits more detailed morphological studies by other workers. Four eastern Pacific species are associated with *Petricola*, *s.s.* Five other species are tentatively placed in the subgenus *Petricolirus*, while four species remain in *Petricola*, *s.l.*

Subgenus *Petricola* Lamarck, 1801, *sensu stricto*

Members of this subgenus have fine, divaricating, sometimes zig-zag sculpture, an ovate shape, and a some-

what sunken ligament. At least the type species is thought to be able to use chemical secretions as an aid in enlarging its burrows in calcareous substrata.

Petricola (Petricola) botula Olsson, 1961

(Figures 1, 2, 55)

Petricola (Naranio) botula Olsson, 1961. Olsson, 1961:317, pl. 55, figs. 7, 7a [misabeled as 1, 1b in plate explanation], 8; Keen, 1971:197 [as a possible synonym of *P. exarata*]; Bernard, 1983:57 [as a synonym of *P. exarata*].

Type material & locality: *P. botula* ANSP 218908, left valve; length, 14.4 mm; height, 7.9 mm; thickness, 3.6 mm (Figure 1). Judging by the originally listed measurements, there were at least four paratypes (15.5 mm, 13.7 mm, 12.5 mm, 11.4 mm), but none of these are in the ANSP, as indicated by Olsson (1961), nor are they at the PRI or the UMML. However, the latter does have three paratypes (UMML 30.9601) of lengths 9.9 mm (right valve), 7.8 mm (right valve), and 7.6 mm (pair). [Punta] Guánico, Península de Azuero, Los Santos Province, Panamá (7.3°N).

Description: Shell ovate to ovate-elongate; anterior end short, rounded; posterior end rounded. Shell inflated, moderately heavy; beaks inflated. Without lunule or escutcheon. Sculpture of 90–100 very fine radial ribs that bifurcate in various places over entire surface. Pallial sinus of moderate depth, broad, not projecting dorsally, rounded, paralleling or confluent with pallial line for a very short distance; pallial line not significantly bowed dorsally (Figure 55). Hinge moderately heavy; right valve with a triangular anterior cardinal and a bifid posterior cardinal; left valve with a small anterior cardinal, a conspicuously bifid central cardinal (broad in the two northern lots), and an elongate posterior cardinal. Ligament of moderate length, deeply sunken; nymph heavy. Color white within and without. Length to 15.5 mm (a paratype listed by Olsson, 1961). A specimen from Mexico is also illustrated here (Figure 2).

Geographic distribution and habitat: Mazatlán, Sinaloa (23.3°N) [SBMNH 128884]; Tizate, Bahía Banderas, Nayarit (20.8°N) [Skoglund Collection] (Figure 2), Mexico, to Punta Guánico (7.3°N) [type locality] and Bahía Chame (8.6°N) [UMML 30,9602], Los Santos Province,

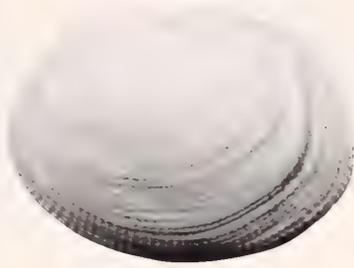
Explanation of Figures 1 to 7

Figures 1, 2. *Petricola (Petricola) botula* Olsson, 1961. Figure 1. Holotype; ANSP 218908; length, 14.4 mm. Figure 2. SBMNH 143211; Tizate, Bahía Banderas, Nayarit, Mexico; length, 15.0 mm. Figures 3–7. *Petricola (Petricola) carditoides* (Conrad, 1837). Figure 3. *Saxicava carditoides*; original figure; length, 38 mm. Figure 4. *S. californica* Conrad, 1837; original figure; length, 27 mm. Figure 5. *S. legumen* Deshayes, 1839; original figure; length, 37 mm. Figure 6. *Petricola arcuata* Deshayes, 1839; holotype; MNHN; length 38.2 mm. Figure 7. *P. cylindracea* Deshayes, 1839; original figure; length, 20 mm.

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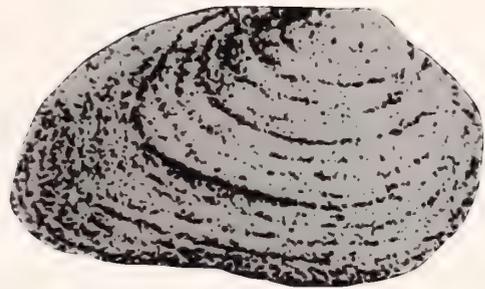
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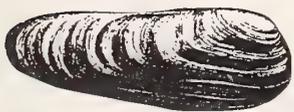
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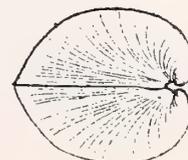
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6



7

Table 1

Relative frequency in collections: number of lots studied.

<i>Petricola carditoides</i>	516
<i>Petricola californiensis</i>	251
<i>Petricola denticulata</i>	181
<i>Petricolaria cognata</i>	91
<i>Choristodon robustum</i>	82*
<i>Petricola lucasana</i>	73
<i>Petricola hertzana</i>	55
<i>Petricola rugosa</i>	37
<i>Petricola exarata</i>	34
<i>Petricola dactylus</i>	32
<i>Petricolaria pholadiformis</i>	32*
<i>Petricola linguafelis</i>	23
<i>Petricola olssoni</i>	22
<i>Petricola scotti</i>	9
<i>Petricola concinna</i>	8
<i>Petricola botula</i>	5
Total lots examined	1,451

* Eastern Pacific lots only.

Panamá, boring into rock or clay. I have examined five lots.

Discussion: This species is very poorly known. With its bifurcating sculpture and deeply sunken ligament, it most closely resembles *P. lucasana*, from which it differs in being more inflated, in having finer, more even sculpture and a less sunken ligament, and in lacking red coloration. The right valve also lacks the posterior lateral ridge present in *P. lucasana*. It differs from *P. carditoides* in having coarser sculpture.

Petricola (Petricola) carditoides (Conrad, 1837)

(Figures 3–12, 56)

Saxicava carditoides Conrad, 1837. Conrad, 1837:255–256, pl. 20, fig. 8; [all the following as *Petricola*]; Conrad, 1849b:213; Carpenter, 1857a:214 [as a synonym of *P. californica*]; Carpenter, 1857b:196, 229, 232, 234, 284; Carpenter, 1864b:526, 528, 534, 536, 540, 590, 592, 602, 634, 641 [1872:12, 14, 20, 22, 26, 76, 78, 88, 120, 127] [with *P. californica* as both a junior or senior synonym]; Tryon, 1872:255, 257 [as a synonym of *P. nivea* "(Chemnitz, 1785)"]; Arnold, 1903:154 [*Petricola (Petricola)*]; Dall, 1921:44; Lamy, 1923b:334–337; I. S. Oldroyd, 1924:50, 214, pl. 42, fig. 6a, b; I. S. Oldroyd,

1925:163, pl. 34, fig. 6a, b; Grant & Gale, 1931:355, 906, pl. 13, figs. 14a, b; Burch, 1944:19 [*Petricola (Rupellaria)*]; Keen, 1966a:170; Addicott, 1966:4, pl. 4, figs. 2, 3; Hertlein & Grant, 1972:283–284, pl. 44, figs. 15, 16 [as *Petricola (Rupellaria)*]; Bernard, 1983:57 [*Petricola (Rupellaria)*].

Saxicava californica Conrad, 1837. Conrad, 1837:256, pl. 20, fig. 9; [the following all as *Petricola*]; Conrad, 1849b:213; Deshayes, 1853:208; Carpenter, 1857a:214; Carpenter, 1857b:196, 229, 299, 349, 351; Carpenter, 1864b:526, 559, 634, 641 [1872:12, 45, 120, 127] [as a junior synonym of *P. carditoides*]; Tryon, 1872:255, 257 [as a synonym of *P. nivea*]; Arnold, 1903:154 [as a synonym of *P. carditoides*]; Lamy, 1923b:334 [as a variety of *P. carditoides*]; Keen, 1966a:170 [as a synonym of *P. carditoides*]; Bernard, 1983:57 [as a synonym of *P. carditoides*].

Saxicava legumen Deshayes, 1839. Deshayes, 1839:358; Deshayes, 1841:1–2, pl. 29; Carpenter, 1857b:202, 203 [as a synonym of *Hiatella pholadis* (Linnaeus, 1771)]; Carpenter, 1864b:528, 529, 637 [1872:14, 15, 123] [as a synonym of *Hiatella pholadis*]; Dall, 1898:835 [as a possible synonym of *P. carditoides*]; Grant & Gale, 1931:355 [as a possible synonym of *P. carditoides*]; Bernard, 1983:59 [as a synonym of *Hiatella pholadis*].

Petricola arcuata Deshayes, 1839. Deshayes, 1839:358; Deshayes, 1840:2–3, pl. 19; [the following four references as a synonym of *P. californica*]; Conrad, 1849b:213; Deshayes, 1853:208; Carpenter, 1857a:214; Carpenter, 1857b:196, 203, 229; Carpenter, 1864b:526, 528, 559, 634, 641 [1872:12, 14, 45, 120, 127] [as a synonym of *P. carditoides*]; Tryon, 1872:255, 257 [as a synonym of *P. nivea*]; Lamy, 1923b:334 [as a synonym of *P. carditoides*]; Arnold, 1903:154 [as a synonym of *P. carditoides*]; Bernard, 1983:57 [as a synonym of *P. carditoides*].

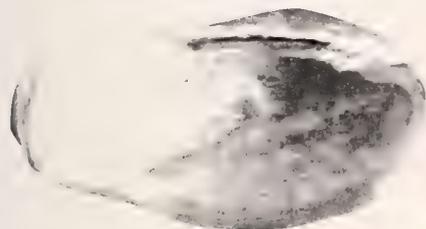
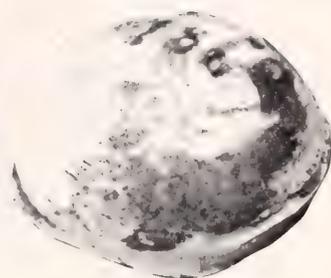
Petricola cylindracea Deshayes, 1839. Deshayes, 1839:358–359; Deshayes, 1840:3–4, pl. 20; Conrad, 1849b:213 [as a possible synonym of *P. carditoides*]; Deshayes, 1853:208 [as a possible synonym of *P. carditoides*]; G. B. Sowerby II, 1854a:769–770, pl. 165, figs. 36–38 [as *Venerupis*]; Carpenter, 1857a:214 [as a possible synonym of *P. carditoides*]; Carpenter, 1857b:196, 203, 219, 224, 229, 284, 299 [as a possible synonym of *P. carditoides*]; Carpenter, 1864b:526, 528, 534, 592, 634, 641 [1872:12, 14, 20, 78, 120, 127] [as a synonym of *P. carditoides*]; Tryon, 1872:255, 257 [as a synonym of *P. nivea*]; Lamy, 1923a:282 [as a synonym of *P. carditoides*].

Petricola gibba Middendorff, 1849. Middendorff, 1849:573–574 [1872:57–58], pl. 18, figs. 5–7; Deshayes, 1853:208; Carpenter, 1857b:196, 219, 223, 299 [as possible synonym of *P. carditoides*]; Carpenter, 1864b:534, 641 [1872:20, 127] [as a synonym of *P. carditoides*];

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Explanation of Figures 8 to 12

Figures 8–12 *Petricola (Petricola) carditoides* (Conrad, 1837). Figure 8. *P. gibba* Middendorff, 1849; holotype; ZISP; length, 37 mm [rough scanned image, courtesy ZISP]. Figure 9. *P. mirabilis* Deshayes, 1853; holotype; BM(NH) 1966555; length, 35.9 mm. Figure 10. *Saxicava abrupta* Conrad, 1855; lectotype; USNM 1869; length, 20.5 mm. Figure 11. *Petricola pedroana* Conrad, 1855; original figure; length, 31 mm. Figure 12. CAS 102584; Carmel, Monterey Co., California; length, 4.8 mm; SEM image.



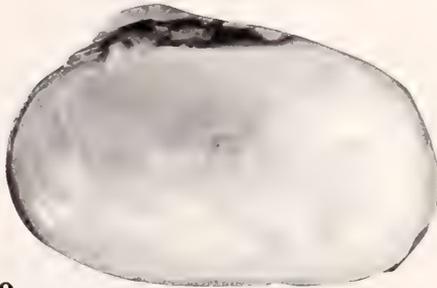
8



10



11



9



12

Table 2
Differentiating characters in Eastern Pacific petricolids.

	Ligament	Lunule/ escutcheon	Pallial sinus- depth/Rounding	Pallial line- lined dorsally	Pallial line- confluence with sinus	Radial sculpture	Commarginal sculpture	Hinge teeth- RV/LV	Maximum length, mm
<i>P. botula</i>	deeply sunken	neither	moderate, rounded	no	short distance	~ 90-100 fine, bifurcating	growth checks only	2/3	15.5
<i>P. carditoides</i>	deeply sunken	neither	moderate, rounded	no	short distance	~ 130 fine, bifurcating	growth checks only	2/3; LV ant. card. lost in many adults	63.3
<i>P. linguafelis</i>	deeply sunken	neither	deep, rounded	yes	substantially	network of beads	growth checks only	2/3; RV with elongate posterior lat- eral ridge	7.3
<i>P. lucasana</i>	deeply sunken	neither	moderate, rounded	no	short distance	~ 40-60 fine, bifurcating	growth checks only	2/3; LV ant. card. lost in many adults; RV with low posteri- or lateral ridge	43.5
<i>P. californiensis</i>	shallow	neither	deep, rounded	slightly	substantially confluent or parallel	~ 60; 12 anterior broadest	fine ribs	2/3; LV ant. card. not ev- ident in many adults	42.2
<i>P. concinna</i>	shallow	slight escut- cheon	moderate, rounded	no	no	~ 12; on anterior end; very fine posterodorsal ribs	lamellae	2/3	21.1
<i>P. dactylus</i>	shallow	neither	moderate, pointed	no	no	~ 27; 12 anterior broadest	narrow, lamel- lar anteriorly	2/3	57.5
<i>P. denticulata</i>	slightly sunken posteriorly	neither	shallow-mode- rate, rounded to pointed	no	no	~ 50; 13 anterior broadest	strong, dense	2/3; LV ant. card. lost in adults	42
<i>P. rugosa</i>	shallow	neither	moderate, rounded	slightly	no	~ 40, strongest on both ends	growth checks only	2/2; no LV ant. card. evident at all	50
<i>P. exarata</i>	shallow	long, narrow es- cutcheon	moderate, rounded	yes	short distance	~ 100 fine threads	growth checks only	2/3; LV ant. card. lost in adults; RV with posteri- or lateral ridge	15

Table 2
Continued.

	Ligament	Lunule/ escutcheon	Pallial sinus- depth/Rounding	Pallial line- bowed dorsally	Pallial line- confluence with sinus	Radial sculpture	Commarginal sculpture	Hinge teeth- RV/LV	Maximum length, mm
<i>P. hertzana</i>	shallow	neither	moderate, rounded	yes	short distance	low, obscure near ends in most	irregular striae	2/3; teeth very delicate, fre- quently bro- ken	7
<i>P. olssoni</i>	shallow	neither	moderate, rounded	yes	substantially	~ 50-60 fine, narrow	growth checks only	2/3	30
<i>P. scotti</i>	shallow	slight escutch- con	moderate, rounded	slightly	short distance	~ 50, finer posteriorly	lamellae	2/3	18.5
<i>C. robustum</i>	deeply sunken	neither	moderate, rounded	no	no	~ 50 heavy, heaviest posteriorly	fine threads	2/3; LV ant. car. lost in most adults; hinge often gerontic in adults	42.5
<i>P. cognata</i>	shallow	lunule	deep, pointed	no	no	~ 8 scaly ribs anteriorly, ~ 20 posterior threads	growth checks only	2/3	80
<i>P. pholadiformis</i>	shallow	neither	deep, pointed	no	no	~ 8 scaly ribs anteriorly, ~ 36 posterior threads	fine threads	2/3	60 in eastern Pac.; 71.3 in western Atl.

Tryon, 1872:256, 257 [as a synonym of *P. nivea*]; Arnold, 1903:154 [as a synonym of *P. carditoides*]; Lamy, 1923b:355 [as a variety of *P. carditoides*].

Petricola mirabilis Deshayes, 1853. Deshayes, 1853:207; G. B. Sowerby II, 1854a:766, pl. 165, fig. 24 [as *Venerupis*]; Carpenter, 1857b:281; Tryon, 1872:257; G. B. Sowerby II, 1874b:pl. 1, fig. 4a, b [as *Venerupis*]; Lamy, 1923a:284; Lamy, 1923b:341–342.

[*non P. mirabilis* Deshayes, *autt.*]. Lischke, 1871:122; Habe, 1951:98; Habe, 1952:187; Habe, 1977:275.

Saxicava abrupta Conrad, 1855. Conrad, 1855a:13; Conrad, 1857:824, pl. 3, figs. 25, 25a; Carpenter, 1864b:590 [1872:76] [as a probably synonym of *P. carditoides*]; Dall, 1898:835; [the following three references as a synonym of *P. carditoides*]; Dall, 1909a:124; Grant & Gale, 1931:355; Hertlein & Grant, 1972:283.

Petricola pedroana Conrad, 1855. Conrad, 1855a:13–14; Conrad, 1857:824, pl. 3, fig. 24 [not “fig. 26,” as implied by plate explanation; this figure is not even present on plate]; Carpenter, 1864b:590 [1872:76] [as similar to *P. ventricosa*]; [the next three references as a synonym of *P. carditoides*]; Grant & Gale, 1931:355; Woodring, 1938: 51; Hertlein & Grant, 1972:283.

Type material and localities: *S. carditoides*—Lost. The holotype, a right valve that measured 38 mm in length (Figure 3). Santa Barbara, Santa Barbara County, California (34.4°N); T. Nuttall, spring 1836. *S. californica*—Lost. The original figure measures 27 mm in length (Figure 4). Conrad had specimens from Santa Barbara, Santa Barbara County, California (34.4°N), and San Diego, San Diego County, California (32.7°N); both T. Nuttall, spring 1836. *S. legumen*—Lost. (P. Bouchet, e-mail, 3 January & 30 January 1996). The original figure measures 37 mm in length (Figure 5). California, from marine “marl.” *P. arcuata*—MNHN, holotype, paired valves; length, 38.2 mm; height, 19.8 mm; thickness, 18.6 mm (Figure 6). California, from marine “marl.” *P. cylindracea*—Lost. The holotype, paired valves, measured 20 mm in length, 22 mm in height, and 20 mm in thickness (Figure 7). California, from marine “marl.” *P. gibba*—ZISP, holotype, paired valves; length, 37 mm (original measurement) (Figure 8). Sitka Island, Alaska (about 57°N); the original text cites Eschscholtz as collector, but the label specifies Wosnessenski. *P. mirabilis*—BM(NH) 1966555, holotype, paired valves; length, 35.9 mm; height, 23.7 mm; thickness, 23.7 mm (Figure 9). California; the label adds “Monterey, in sandstone, deep water” (36.6°N). *S. abrupta*—USNM 1869, **lectotype here designated**, a sealed pair separate from matrix, probably the specimen figured in Conrad (1857:pl. 3, fig. 25a); length, 20.5 mm; height, 12.9 mm; thickness, 10.5 mm (Figure 10). Paralectotypes, a smaller pair inside lectotype, and three whole pairs, one broken pair, and two valves imbedded in holes in rock matrix. This matrix may also be that in which the next species was found. San Pedro, Los Angeles County, California (33.7°N); Pleistocene; in cavities in rock. *P. pedroana*—Lost. Holotype, right valve (Figure 11). No size was specified; the figure in Conrad (1857)

measures 31 mm in length. San Pedro, Los Angeles County, California (33.7°N); Pleistocene; in cavities in rock.

Description: Shell typically ovate, but variously shaped depending on nestling site, becoming elongate in some situations; anterior end short, rounded; posterior end subtruncate to rounded. Shell inflated, thick; beaks prominent. Without lunule or escutcheon. Surface completely covered with very fine (at least 130), somewhat divaricate radial ribs in uneroded specimens. Pallial sinus of moderate depth, broad, rounded, confluent with pallial line for a very short distance; pallial line not bowed dorsally (Figure 56). External and internal color white to tan; juveniles mottled with brown. Hinge heavy; right valve with a heavy anterior cardinal and a bifid posterior cardinal; left valve with a small anterior cardinal (lost in many adult specimens), a bifid central cardinal, and a narrow posterior cardinal. Ligament elongate, deeply sunken. Length to 63.3 mm [MNHN; Monterey, California]. A small pair showing fine sculpture is depicted with an SEM image in Figure 12.

Distribution and habitat: Sitka Island, Alaska (approximately 57°N) (type locality of *P. gibba*); Edna Bay, Kosciusko Island [CAS 105780] (55.9°N), and near Ratz Harbor, Prince of Wales Island [SBMNH 14224] (53.9°N), Alaska, to Punta Pequeña, Baja California Sur (26.2°N) [LACM 71-5, 71-6, 71-181], from the intertidal zone to 46 m, nestling in rocky areas. Orcutt (1919:40) and Dall (1921:44) reported this species from Bahía Magdalena, Baja California Sur, but I have been unable to find any material in collections from there. A single specimen in the CAS labeled as having come from Mazatlán, Sinaloa, Mexico [CAS 102501], requires additional verification, and a specimen labeled as having come from Kamchatka [MNHN] seems implausible. I have examined 516 lots.

There are many records of this species in the Pleistocene of central California (Woodring & Bramlette, 1951: 54; Valentine, 1958:690; Addicott, 1966:4), southern California (Santa Barbara—Valentine, 1961:389; Kennedy et al., 1993:347; northern Los Angeles—Woodring, in Hoots, 1931:120; Addicott, 1964:146; Playa del Rey—Willett, 1937:390; San Pedro—T. S. Oldroyd, 1914:82, 1925:6; Crickmay, 1929:631; DeLong, 1941:242, table at p. 244, Valentine, 1961:370, 372; Capistrano—Willett (1938:106); San Clemente—Valentine (1961:364); San Diego—Webb, 1937:345; Emerson & Addicott, 1953: 440; Valentine, 1960:163, 1961:360, 361; Valentine & Meade, 1961:10); San Nicolas Island—Vedder & Norris, 1963:46, 47), northern Baja California (Emerson, 1956: 339; Valentine, 1957:296, 1961:357; Emerson & Addicott, 1958:8; Addicott & Emerson, 1959:17; Emerson & Hertlein, 1960:3; Valentine & Meade, 1961:16; Valentine & Rowland, 1969:517), and central Baja California (Emerson, 1980:72).

There are also records in the late Pliocene of central California (Nomland, 1917:220; ?Woodring & Bramlette, 1951:90), Ventura (Waterfall, 1929: checklist col. 2; Woodring, in Winterer & Durham, 1962:304–305), the Los Angeles area (Moody, 1916:45; Soper & Grant, 1932:1060), Newport Bay (Zinsmeister, 1971:124), and San Diego (Hertlein & Grant, 1972:283–284).

Records of this species from the Miocene, such as Gale, in Preston (1931:15) and Woodring & Bramlette (1951:66, 90), are uncertain and may refer to *P. buwaldi* (see under *Choristodon robustum*).

Discussion: Conrad (1837) described this species twice in the same paper. Carpenter (1857a:214) acted as First Reviser in the sense of ICZN Code Art. 24 and made *P. carditoides* a synonym of *P. californica*. However, he later reversed his action and began using *P. carditoides* for the species, a course followed by all subsequent workers. Under the present Code, a petition to set aside his first action would be required. However, because use of *P. carditoides* has been universal for a century and because, in all likelihood, the next version of the Code will leave such questions entirely up to taxonomists working on particular groups (P. Tubbs, letter, 20 December 1995), a petition seems pointless. (This species is not to be confused with the Australian *Venerupis carditoides* Lamarck, 1818: 508, most recently placed in the venerid genus *Timoclea* [Lamprell & Whitehead, 1992:pl. 62].)

Petricola arcuata and *P. cylindracea* Deshayes, 1839, have long been regarded as synonyms. The type specimen of only one of these taxa survives. *Saxicava legumen* Deshayes, 1839, was suggested as a possible synonym by Dall (1898:835), but more recently it has been allocated to synonymy under *Hiatella* (Bernard, 1983:59). However, because Deshayes mentioned and illustrated a deep pallial sinus, it is far more likely to belong in synonymy here.

Petricola gibba is undoubtedly a synonym, and its holotype has been located. It remains the northern record by about 2° in latitude. Additional collecting in southeast Alaska may bring additional material from as far north as Sitka Island to light.

Petricola mirabilis, although described from California, was attributed to Japan by Lischke (1871), and subsequent workers did not question this. However, its holotype is a specimen of *P. carditoides*. In the meanwhile, the Japanese "*P. mirabilis*," an evidently uncommon species with more prominent, zig-zag sculpture, was made the type species of the genus *Pseudoirus* Habe, 1951 (see discussion under the genus above).

Conrad's (1855a) *Petricola abrupta* was based on not infrequent specimens of this species with fairly eroded sculpture. However, the lectotype shows some of the characteristic fine radial ribs. Conrad's *S. pedroana* is certainly a synonym; its original description mentions fine

radial sculpture. Both species were found in cavities in the same rock.

Petricola buwaldi Clark, 1915, described from the Miocene of central California, was synonymized with *P. carditoides* by Bernard (1983), but it is instead a synonym of *Choristodon robustum* (see under same).

Young (1958) found the siphons of *Petricola carditoides* to be fused for half their length and capable of expansion to a distance equal to the shell length. The inhalent siphon has four rows of dendritic tentacles surrounded by a row of simple tentacles. The exhalent siphon has two rows of two rows of pinnate tentacles and one of simple tentacles. The inner demibranch is somewhat larger and extends farther forward than the outer. The animal is capable of modest expansion of its burrow by lateral pressure of the valves. D. P. Abbott & Hilgard (1987:194) figured living *Petricola carditoides*. A long, extensible foot was illustrated, as well as a terminal valvular membrane on the exhalent siphon and large labial palps.

Petricola (Petricola) linguafelis (Carpenter, 1857)

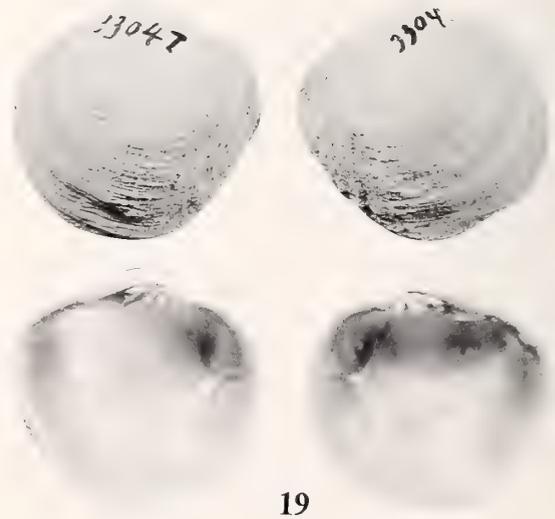
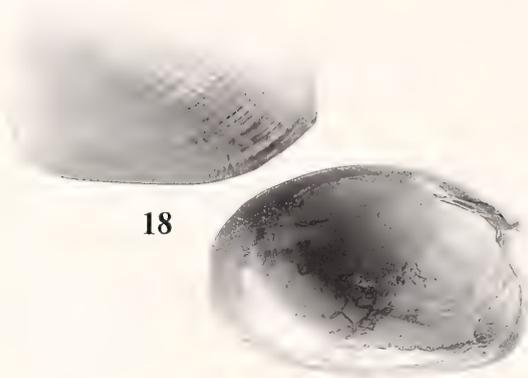
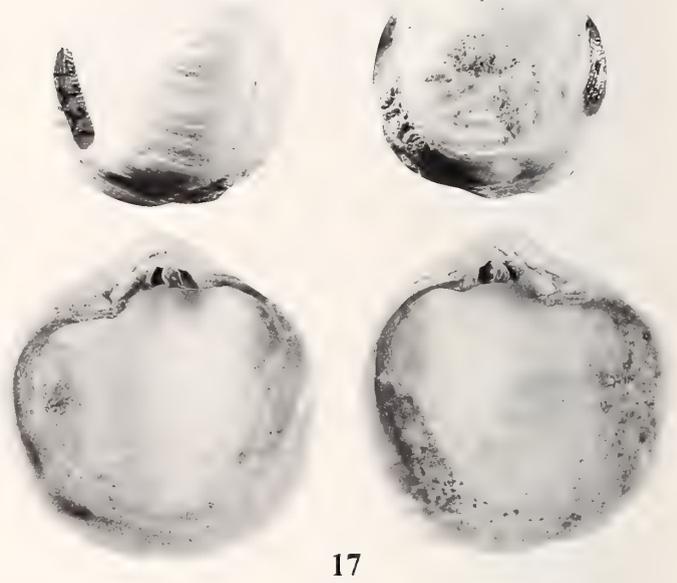
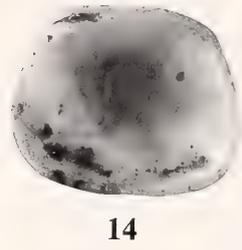
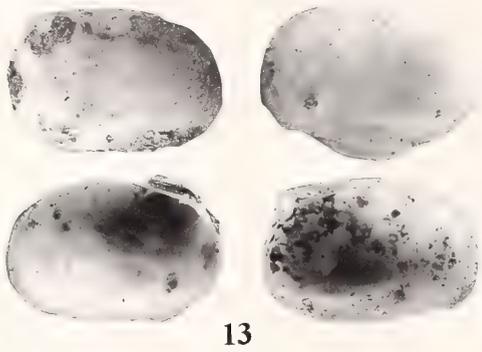
(Figures 13–16, 57)

Rupellaria linguafelis Carpenter, 1857. Carpenter, 1857b: 244, 299, *nomen nudum*; Carpenter, 1857c:20; Carpenter, 1864b:620 [1872:106]; Lamy, 1923a:285; Keen, 1958:152; Brann, 1966:27, pl. 2, fig. 27; Keen, 1968: 394, 395, fig. 17, 399 [*Petricola (Petricola)*]; Keen, 1971:197 [as a synonym of *P. exarata*]; Bernard, 1983: 57 [as a synonym of *P. exarata*].

"*Narario*" *scobina* Carpenter, 1857. Carpenter, 1857b:244, *nomen nudum*; Carpenter, 1857c:529; Tryon, 1872:258; Lamy, 1923b:341; Brann, 1966:29, pl. 4, fig. 680; Keen, 1968:394, 395, fig. 18, 399, pl. 55, fig. 11 [as a synonym of *P. (P.) linguafelis*; First Revision]; Keen, 1971: 197 [as a synonym of *P. (P.) exarata*]; Bernard, 1983: 57 [as a synonym of *P. (P.) exarata*].

Cypricardia noemi de Folin, 1867. de Folin, 1867:62–63 [repr.:24–25], pl. 4, figs. 1, 2; de Folin & Périer, 1867: 8; Kisch, 1960:162; Keen, 1971:197 [as a synonym of *P. (P.) exarata*]; Bernard, 1983:57 [as a synonym of *P. (P.) exarata*].

Type material and localities: *R. linguafelis*—BM(NH) Carpenter Mazatlán Collection tablet 72, species 27, **lectotype here designated**, the largest paired valves; length, 4.0 mm; height, 2.7 mm; thickness, approx. 2.0 mm (Figure 13). BM(NH), paralectotypes, three additional pairs. A fifth pair cited by Carpenter & Keen (1968) is no longer present. USNM 715644, paralectotypes, two pairs and two fragments. Mazatlán, Sinaloa, Mexico (23.2°N); nesting in valves of Chamidae and *Spondylus calcifer* Carpenter, 1857; F Reigen. *N. scobina*—BM(NH) Carpenter Mazatlán Collection tablet 2516, species 680, holotype, a right valve; length 4.4 mm; height, 3.5 mm; thickness approx. 1.0 mm (Figure 14). A left valve added to slide later is a Carpenter voucher specimen. USNM 716248, one left valve and one broken pair, additional Carpenter



voucher specimens. Mazatlán, Sinaloa, Mexico (23.2°N); nestling in a valve of *Spondylus calcifer* Carpenter, 1857; F. Reigen. *C. noemi*—BM(NH) 196459, **lectotype here designated**, paired valves still sealed closed; length, 2.5 mm; height, 1.9 mm; thickness, 1.4 mm (Figure 15). De Folin's figures show that he had at least one additional specimen. Archipelago de las Perlas, Panamá (approximately 8.4°N).

Description: Shell ovate; anterior end very short, rounded; posterior end rounded. Shell inflated, thin; beaks prominent. Without lunule or escutcheon. Sculpture of a network of very small beads. Pallial sinus deep, broad, dorsally directed, rounded, overlapping pallial line for a substantial distance; pallial line bowed dorsally, sometimes in discontinuous patches (Figure 57). Hinge teeth robust for size; right valve with a narrow anterior cardinal and a bifid posterior cardinal, and with an elongate posterior lateral ridge below hinge margin; left valve with a tiny anterior cardinal, a bifid central cardinal, and a small posterior cardinal. Ligament of medium length, deeply sunken; nymph stout. Color white externally and internally. Length to 7.3 mm [MNHN; La Puntilla, Guayas Province, Ecuador]. A SEM image is provided of the external sculpture (Figure 16).

Distribution and habitat: Bahía Pulmo, Baja California Sur (23.4°N) [LACM 66-19.56], and Mendia, Sinaloa (23.7°N) [USNM 532732], Mexico, to Salinas, Guayas Province, Ecuador (2.2°S) [LACM 70-9; CAS 102586], from the intertidal zone to 3 m, in rocky areas. I have examined 23 lots.

Discussion: This species is thus far known from several, widely distributed lots. It has a very distinctive beaded sculpture that sets it apart from the young of other taxa, such as *P. lucasana*, which have radial rays. However, the affinities of this small-sized species seem to be with *Petricola (Petricola)*, of which it may be a pedogenetic derivative.

I have examined a single left valve from the western Atlantic that is similar to this species. It was collected on Abaco Island in the Bahamas (Redfern Collection), and it may either be a form of *P. (P.) lapicida* (Gmelin, 1791) or a new species. It differs from *P. linguafelis* in having

a thinner, more delicate hinge, and the anterior and central cardinals are fused dorsally; they are separate in *P. linguafelis*.

Petricola (Petricola) lucasana
Hertlein & Strong, 1948

(Figures 17–20, 58)

Petricola (Petricola) lucasana Hertlein & Strong, 1948. Hertlein & Strong, 1948:194, 197, 198, pl. 2, figs. 4, 9; Keen, 1958:150, 151, fig. 345; Keen, 1971:197, 198, fig. 477; Bernard, 1983:57 [*Petricola (Petricola)*].

Petricola (Naranio) charapota Olsson, 1961. Olsson, 1961: 317, pl. 54, fig. 7; Keen, 1971:196, 197 [*Petricola (Petricola)*]; Bernard, 1983:57 [*Petricola (Petricola)*].

Type materials and localities: *P. lucasana*—CAS 06,5562, holotype, paired valves; length, 24.6 mm; height, 24.9 mm; thickness 16.6 mm (Figure 17). Cabo San Lucas, Baja California Sur (22.9°N). *P. charapota*—ANSP 218907, holotype, left valve; length, 30.1 mm; height, 21.0 mm; thickness, 9.4 mm (Figure 18). “Charapota” [Charapotó], Manabi Province, Ecuador (0.8°S).

Description: Shell ovate, sometimes as high or higher than long; anterior end short, rounded; posterior end subtruncate. Shell inflated, fairly thick; beaks prominent. Without lunule or escutcheon. Sculpture of many (more than 60) divaricating ribs in small specimens, becoming more divaricating and sometimes becoming fewer in number (about 40) in large specimens; overlain by secondary lamellose radial ribs on posterior slope in some specimens. Pallial sinus of moderate depth, broad, not dorsally directed, rounded, overlapping pallial line for a very short distance; pallial line not bowed dorsally (Figure 58). Hinge robust; right valve with a small anterior cardinal and a slightly bifid posterior cardinal, and with a low posterior lateral ridge; left valve with a small anterior cardinal, which may be lost in adult, a narrow, slightly bifid central cardinal, and a thin posterior cardinal. Ligament medium in length, deeply sunken; nymph heavy. White to tan externally; reddish-brown internally, especially on hinge and around margins of valves. Length to 43.5 mm [Skoglund Collection; Cabo Tepoca, Sonora, Mexico]. A small specimen is depicted by an SEM image (Figure 19).

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Explanation of Figures 13 to 20

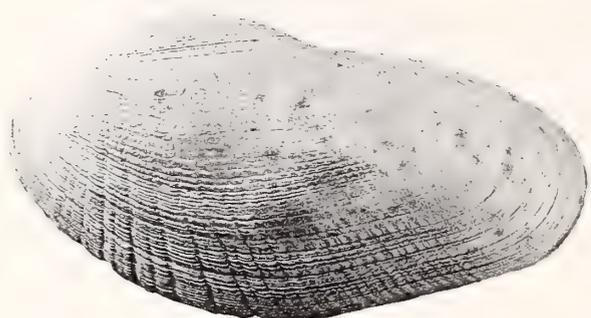
Figures 13–16. *Petricola (Petricola) linguafelis* (Carpenter, 1857). Figure 13. *Rupellaria linguafelis*; lectotype; BM(NH) Carpenter Collection 72(27); length, 4.0 mm. Figure 14. *Naranio scobina* Carpenter, 1857; holotype; BM(NH) Carpenter Collection 2516(680); length, 4.4 mm. Figure 15. *Cypricardia noemi* de Folin, 1867; lectotype; BM(NH) 196459; length, 2.5 mm. Figure 16. LACM 75-55; San Carlos, Golfo de Panama; length, 3.9 mm; SEM image. Figures 17–20. *Petricola (Petricola) lucasana* Hertlein & Strong, 1948. Figure 17. *P. lucasana*; holotype; CAS 065562; length, 24.6 mm. Figure 18. *P. charapota* Olsson, 1961; holotype; ANSP 218907; length, 30.1 mm. Figure 19. CAS 102518; Puerto Peñasco, Sonora, Mexico; length, 22.8 mm. Figure 20. CAS 102518; length, 4.6 mm; SEM image.



21



22



23



24

Distribution and habitat: Throughout the Golfo de California from its head at Puerto Peñasco, Sonora, Mexico (31.3°N) [SBMNH 27231 and other lots; CAS 102518 and other lots], to Cabo San Lucas, Baja California Sur (type locality of *P. lucasana*: USNM 75035), south to Punta Quepos, Puntarenas Province, Costa Rica (9.4°N) [LACM 72-58.57], and at Charapotó, Manabi Province, Ecuador (0.8°S) [type locality of *P. charapota*], and Salinas, Guayas Province, Ecuador (2.2°S) [CAS 105779], from the intertidal zone to 30 m, in calcareous substrata, such as corals. Also present on Pleistocene terraces in Ecuador [MNHN]. I have examined 73 lots.

Discussion: Juvenile specimens of this species are white or tan and do not develop their characteristic deep red color until about 6–7 mm. Their heavy hinge and deeply sunken ligament are readily apparent even in very small specimens.

This species is somewhat similar to the Caribbean and IndoPacific *P. (P.) lapicida* (Gmelin, 1791), from which it differs in being heavier, having a more variable outline, being red within, and in less frequently having secondary posterior radial frills.

The unique type of *Petricola charapota* from Ecuador has its beaks very close to the anterior end. In the Golfo de California, *Petricola (P.) lucasana* tends to assume an oval outline, sometimes becoming higher than long. However, some of the sparse material available of *P. (P.) lucasana* from Costa Rica and elsewhere also have beaks relatively close to the anterior end, and even some specimens of this species from the Golfo de California can also have this morphology. Indeed, *Petricola (P.) lucasana* has been reported from Ecuador (Hoffstetter, 1952: 34), but none of this material seems to be preserved in the major collections in the United States.

Petricola millestriata Brown & Pilsbry, 1913 (pp. 516–517, pl. 26, fig. 2), from the Miocene of Panamá, may be ancestral to this species, but it is as yet known from a single, now-lost specimen (Woodring, 1982:709).

Subgenus *Petricolirus* Habe, 1951

Petricolirus Habe, 1951:95–96, pl. 15, figs. 4, 5; 1952:188. Type species (original designation); *Petricola aequistriata* G. B. Sowerby II, 1874a:pl. 3, fig. 19. Recent, Japan.

Members of this subgenus have an elongate shape and

radial sculpture that is generally more conspicuous than that in *Petricola, s.s.* and is neither divaricate nor zig-zag, and the ligament is not sunken. Of the species that are tentatively included here, *Petricola californiensis*, *P. concinna*, *P. dactylus*, *P. denticulata* have each been included within *Petricolaria* because of their elongate shape, but a narrower concept of that genus is used here.

Petricola (Petricolirus) californiensis Pilsbry & Lowe, 1932

(Figures 21, 59)

Petricola californiensis Pilsbry & Lowe, 1932. Pilsbry & Lowe, 1932:97–99, pl. 13, figs. 7–9, text-fig. 6; Burch, 1944:19–20 [*Petricola (Rupellaria)*]; Bernard, 1983:57 [*Petricola (Petricolaria)*].

Petricola denticulata G. B. Sowerby I, 1834. *auctt., non* G. B. Sowerby I, 1834. Dall, 1900b:121–122 [in part]; Arnold, 1903:155–156 [*Petricola (Petricolaria)*]; Dall, 1921:44 [in part]; Willett, 1931:39, pl. 17, fig. 3.

"*Petricola tenuis* A. Adams," *non P. tenuis* G. B. Sowerby I, 1834. Jordan, 1924:153

Type material and locality: *P. californiensis*—ANSP 114337, holotype, paired valves; length, 26.5 mm; height, 12.2 mm; thickness, 10.5 mm (Figure 21). Paratypes, two additional pairs, 25.9 mm and 24.3 mm in length. San Pedro, Los Angeles County, California (33.7°N).

Description: Shell ovate-elongate; anterior end short, rounded; posterior end elongate, rounded. Shell inflated, thin; beaks somewhat inflated. Without lunule or escutcheon. Sculpture of approximately 60 radial ribs, of which the 12 most anterior are broadest, the rest becoming finer toward posterior end, and with fine commarginal ribs. Hinge teeth relatively small; right valve with a narrow anterior cardinal tooth and a slightly bifid posterior cardinal; left valve with a small anterior cardinal that is not apparent in most large specimens, a bifid central cardinal, and an elongate posterior cardinal. Ligament elongate, on a narrow nymph. Pallial sinus deep, of moderate width, rounded, closely paralleling or confluent with pallial line for a substantial distance; pallial line somewhat bowed dorsally (Figure 59). White to tan externally and internally, sometimes with brownish-purple patches externally on posterior slope, especially in small specimens. Length to 42.2 mm [CAS 105776; Long Beach, Los Angeles County, California].

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Explanation of Figures 21 to 24

Figure 21. *Petricola (Petricolirus) californiensis* Pilsbry & Lowe, 1932; holotype; ANSP 114337; length, 26.5 mm. Figure 22. *Petricola (Petricolirus) concinna* G. B. Sowerby I, 1834; lectotype; BM(NH) 1966554/1; length, 21.1 mm. Figures 23, 24. *Petricola (Petricolirus) dactylus* G. B. Sowerby I, 1823. Figure 23. *P. dactylus*; holotype; BM(NH) 1995215; length, 57.5 mm. Figure 24. *P. patagonica* d'Orbigny, 1845; lectotype; BM(NH) d'Orbigny Coll. 558, 1854.12.4.708/1; length, 42.9 mm.

Distribution and habitat: Bolinas, Marin County (37.9°N) [ANSP 39870], and Pacific Grove, Monterey County (36.6°N) [CAS 102867], California, both probably the result of larval settlement in particularly warm-water years; established populations from Coal Oil Point, Santa Barbara County, California (34.4°N) [CAS 39055], to Bahía Magdalena, Baja California Sur (24.6°N) [LACM 49–57], and in the west coast of Mexico from Puerto Peñasco (31.2°N) [LACM 152162] and Playa Cochore, Guaymas (27.9°N) [SBMNH 137767; CAS 105777], Sonora, to San Blas, Nayarit (21.5°N) [SBMNH 32588], and probably to Bahía Ventosa, Oaxaca, Mexico (16.2°N) [SBMNH 142892], from the intertidal zone to 64 m, nestling in a variety of substrata: driftwood, including in teredinid burrows, kelp holdfasts, and clumps of annelid worm tubes. Material in collections labeled as having some from Washington [LACM 56919, 56920; FMNH 142805] probably represents locality errors. I have examined 251 lots.

Also present in the Pleistocene of southern California (Playa del Rey—Willett, 1937:390; San Pedro—DeLong, 1941:242, table at p. 244; Valentine, 1961:370; Newport Bay—Bruff, 1946:232; Kanakoff & Emerson, 1959:24), and northern Baja California (Valentine, 1957:296). The only record of this species in the Pliocene of southern California (Soper & Grant, 1932:1057, taken from Cooper, in Watts, 1897:79) is more likely to have been based on a *Calyptogena* (Woodring, 1938:51).

Discussion: Early records of this species in southern California were as the Panamic species *Petricola denticulata* (for comparisons, see under that species). This species is most similar to *Petricola olssoni* (for comparisons, see under that species).

Arnold (1903:155) synonymized *P. pedroana* Conrad, 1855, with *P. californiensis* [as "*P. denticulata*"]. However, Conrad's species, of which the holotype is lost, was more likely to have been a specimen of *P. carditoides* (see under that species).

Based on specimens so labeled in the California Academy of Sciences, it seems likely that the material cited by Jordan (1924) as "*Petricola tenuis* A. Adams" from Laguna San Ignacio, Baja California Sur, were specimens of *P. californiensis* (see also Discussion under *P. rugosa*, for possibly related confusion about the species-name *tenuis*).

It has not previously been recognized that *P. californiensis* also occurs on the northwest coast of Mexico, from Sonora to Nayarit, material in collections having been identified as *P. denticulata* or *P. exarata*.

Young specimens of *Petricola californiensis* may be distinguished from *P. hertzi* in being more elongate and more produced both anterior and posteriorly, and in attaining a larger size. *Petricola californiensis* is also more heavily sculptured and has a heavier hinge.

Petricola pectorosa (Conrad, 1834:130) [see also Con-

rad, 1838:18, pl. 10, fig. 3; synonym: *P. (Claudiconcha) grinnelli* Olsson, 1914:54–55, pl. 11, figs. 7–10] from the Pliocene and Pleistocene of eastern North America may be ancestral to this species. It is smaller and has more prominent radial sculpture.

Petricola (Petricolirus) concinna

G. B. Sowerby I, 1834

(Figures 22, 60)

Petricola concinna G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:46; d'Orbigny, 1846:549; Deshayes, 1853:214; G. B. Sowerby II, 1854b:773, pl. 166, fig. 3; Tryon, 1872:256; G. B. Sowerby II, 1874a:pl. 1, fig. 3; Dall, 1909b:269; Lamy, 1923b:347; Olsson, 1961:527, pl. 54, fig. 4 [*Petricola (Petricolaria)*]; Keen, 1971:198, 199, fig. 479 [*Petricola (Petricolaria)*]; Bernard, 1983:57 [*Petricola (Petricolaria)*].

Type material and locality: *P. concinna*—BM(NH) 1966554/1, lectotype here designated, left valve; length, 21.1 mm; height, 10.2 mm; thickness, 5.0 mm (Figure 22). BM(NH) 1966544/2, paralectotype, pair, 19.6 mm in length. The lectotype selected seems to have been the specimen figured by G. B. Sowerby II (1854b). Montecristi [Manta], Manabi Province, Ecuador (1.0°S), in hard clay at low water; H. Cuming.

Description: Shell elongate; anterior end short, rounded; posterior end produced, tapered, truncate to bluntly pointed, prolonged beyond inner shell margin by outer shell layer, foliate within; posterodorsal margin slightly flared posterior to ligament, with right valve slightly overlapping left. Shell inflated, average in thickness; beaks small. Lunule absent; very small escutcheon posterior to ligament. Sculpture of heavy, well-spaced commarginal ribs, which are very lamellar and sometimes upturned on posterior end and made scabrous by about 12 radial ribs on anterior end. Pallial sinus of moderate depth and width, rounded, slightly bowed dorsally, completely detached from pallial line (Figure 60). Hinge teeth small; right valve with bifid anterior and posterior cardinals; left valve with a tiny anterior cardinal, a bifid central cardinal, and a short posterior cardinal. Ligament short, shallow; nymph thin. White externally and internally. Length to 21.1 mm (lectotype).

Distribution and habitat: Esmeraldas, Esmeraldas Province (1.0°N) (Olsson, 1961: pl. 54, fig. 4; PRI 25774); Manta, Manabi Province (1.0°S) [type locality], to La Libertad (2.2°S) [LACM 33-15.13], Guayas Province, and Bahía Bartolomé, Isla Bartolomé, Islas Galápagos (0.3°S) [LACM 71-50.1], Ecuador, from the intertidal zone to 18 m. Records from farther south, such as Perú (d'Orbigny, 1846:549) and Arica, Tarapacá Province, Chile (Deshayes, 1853:214), are doubtful and require further confirmation. I have examined eight lots.

Discussion: This is a distinctive but rare species. For

comparisons with *P. scotti*, see under that species. Small specimens of some other taxa may develop a few, low commarginal frills on the posterior slope, including *P. olssoni*, which can be differentiated by its oval outline and broad, deep pallial sinus.

Petricola (Petricolirus) dactylus

G. B. Sowerby I, 1823

(Figures 23, 24, 61)

Petricola dactylus G. B. Sowerby I, 1823. G. B. Sowerby I, 1823: *Petricola* sp. 3; Deshayes, 1853:213; Tryon, 1872: 256; ?G. B. Sowerby II, 1874a:pl. 3, fig. 4; Lamy, 1923b:345–346 [in part] [*Petricola (Petricolaria)*].

[non *Petricola dactylus* *auctt.*; see under *P. denticulata* and *Petricolaria pholadiformis*].

Petricola patagonica d'Orbigny, 1845. d'Orbigny, 1845: 547–548, pl. 82, figs. 7–10; Lamy, 1923b:346–347 [*Petricola (Petricolaria)*]; Carcelles, 1944:288, pl. 13, fig. 101 [*Petricola (Petricolaria)*]; Carcelles, 1950:80, pl. 4, fig. 77 [*Petricolaria*]; Carcelles & Williamson, 1951: 343 [*Petricolaria*]; Figueiras & Sicardi, 1969:364–365, 376, pl. 4, fig. 52 [*Petricola (Petricolaria)*].

?*Petricola chiloensis* Philippi, 1845. Philippi, 1845:53; [the next four references as a synonym of *P. rugosa*]; Dall, 1909b:289; Lamy, 1923b:351; Soot-Ryen, 1959:60; Bernard, 1983:57.

Type material and localities: *P. dactylus*—BM(NH) 1995215, holotype, paired valves; length, 57.5 mm; height, 29.7 mm; thickness, 26.9 mm (Figure 23). Original locality unknown; here restricted to southern Argentina. *P. patagonica*—BM(NH) d'Orbigny collection 558, 1854.12.4.708/1, **lectotype here designated**; length, 42.9 mm; height 21.0 mm; thickness, 18.1 mm (Figure 24). BM(NH) 1954.12.4.708/2–4, paralectotypes, three other pairs, 37.1 mm, 34.6 mm, and 33.9 mm in length. Ensenada de Ros, south of the mouth of Río Negro, Río Negro Province, Argentina (approximately 41.0°S), in calcareous rocks. *P. chiloensis*—Probably lost. Not in MNH-U (R. Kilius, in correspondence, 20 January 1996). The original material measured 8.8 mm in length, 6.6 mm in height, and 4.4 mm in thickness. Isla Chiloé, Chiloé Province, Chile (approximately 43°S); in roots of fucooid algae and in barnacle valves.

Description: Shell ovate-elongate; anterior end short, slightly produced, somewhat pointed; posterior end sharply rounded. Shell inflated, moderately to very thick-shelled; beaks somewhat inflated. Without lunule or esutcheon. Sculpture of approximately 12 strong, broad radial ribs on anterior end and about 15 on central slope, become obsolete and narrower on posterior slope; with narrow commarginal ribs that form lamellae on radial ribs of anterior end; commarginal ribs dominant in some material. Pallial sinus narrow, of moderate depth, pointed anteriorly, completely detached from pallial line; pallial line not bowed dorsally (Figure 61). Hinge teeth robust; right valve with a small anterior cardinal and a narrow,

bifid posterior cardinal; left valve with a small anterior cardinal, a bifid central cardinal, and a small posterior cardinal. Ligament short, not sunken; nymph robust. White to tan externally, with a slight flush of magenta on internal surface. Length to 57.5 mm (type specimen).

Distribution and habitat: Maldonado, Maldonado Province, Uruguay (34.9°S) [ANSP 368239], and Punta Tubul, Arauco Province, Chile (37.3°S) [UCMP D3713, D5719], to Punta Arenas, Magallanes Province, Chile (53.2°S) [SBMNH 132931, 133419; LACM 62-24.1], from the intertidal zone to 20 m. A single record from Bahía Orange, Isla Hoste, Magallanes Province, Chile (55.5°S) [USNM 17647], is improbable and requires verification. I have examined 32 lots.

It is present in the Pleistocene of southern Argentina (Feruglio, 1933: 40, 62, 65, 67, 70, 72, 76, 160, 170).

Discussion: The name *P. dactylus* was misapplied to specimens of *Petricolaria pholadiformis* (Lamarck, 1818) from the northwestern Atlantic (see under that species). As a consequence, its proper place as a senior synonym of *P. patagonica*, confirmed here by the discovery of its probable holotype, has been overlooked.

Based on the locality, it is possible that *Petricola chiloensis* belongs in synonymy here. This species was never illustrated, and the type material is presumably lost. Philippi described *P. chiloensis* as being small, ovate, inflated, with radial striae and “without prominent features.” On the other hand, it is possible that subsequent records of Philippi's taxon, such as those of Hupé (1854), are based on specimens of *P. rugosa*.

This species is most similar to *P. denticulata*, differing in lacking radial sculpture on the posterior slope, lacking brown color, attaining a larger size, and having a narrower pallial sinus.

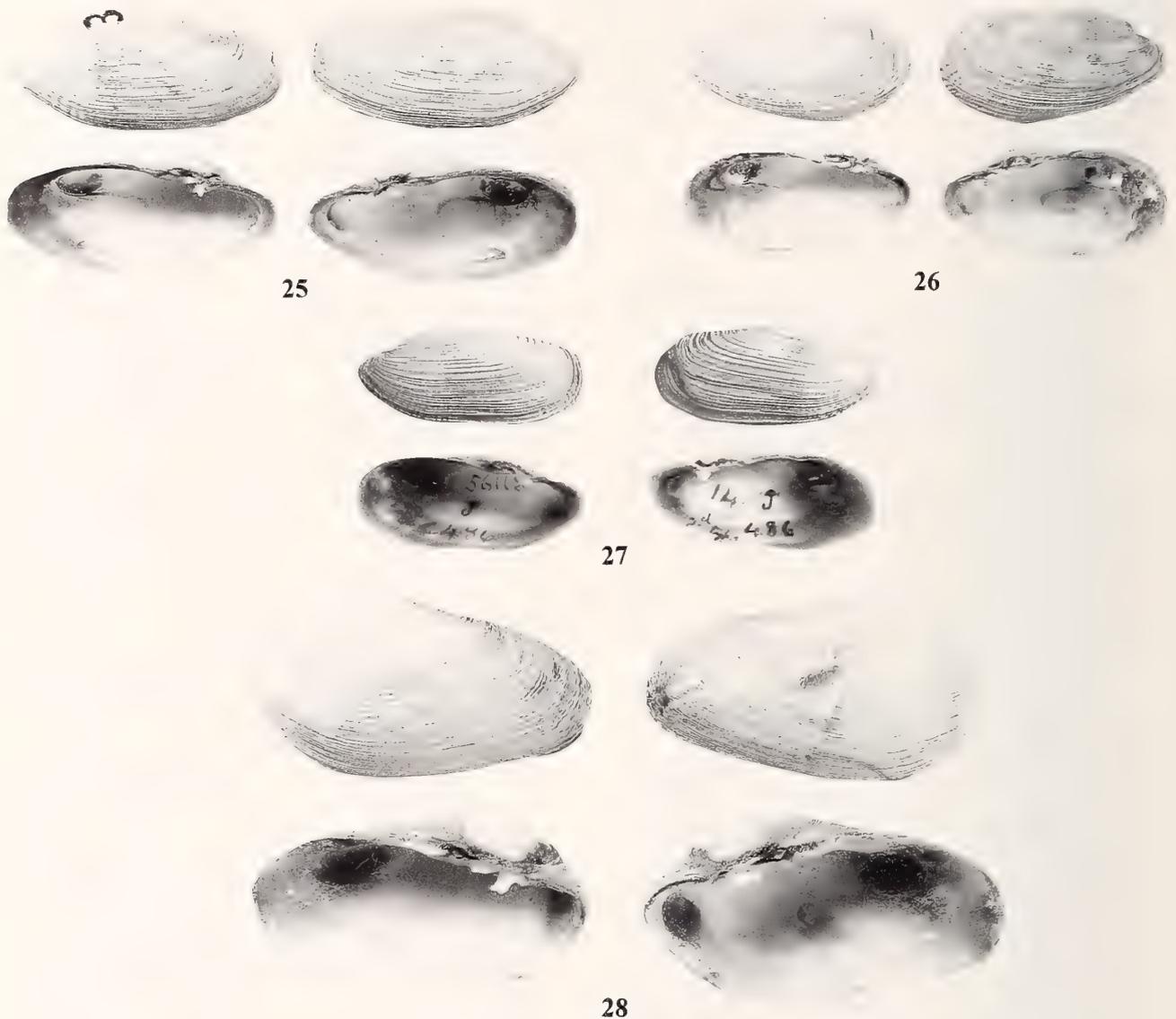
d'Orbigny (1845:548, pl. 82, fig. 8) briefly discussed and figured the soft parts of *Petricola dactylus* G. B. Sowerby I, 1823 [as “*P. patagonica*”]. He described the animal as being yellowish, the viscera reddish, and the siphons as being partly fused and stained brown. He figured the ctenidia as being elongate, but he did not depict the labial palps.

Petricola (Petricolirus) denticulata

G. B. Sowerby I, 1834

(Figures 25–28, 62)

Petricola denticulata G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:46–47; d'Orbigny, 1846:549; Troschel, 1852: 205; Deshayes, 1853:213–214; G. B. Sowerby II, 1854b:773, pl. 166, figs. 6, 7; Fischer, 1857:322, 326–327; Carpenter, 1857b:244, 297, 299; Tryon, 1872:256 [*Petricola (Petricolaria)*]; G. B. Sowerby II, 1874a:pl. 2, fig. 9; Dall, 1909b:269; Lamy, 1923b:347–349 [*Petricola (Petricolaria)*]; Grant & Gale, 1931:356–357 [in part]; Pilsbry & Lowe, 1932:98–99, pl. 13, figs. 1–3; I.



Explanation of Figures 25 to 28

Figures 25–28. *Petricola (Petricolirus) denticulata* G. B. Sowerby I, 1834. Figure 25. *P. denticulata*; lectotype; BM(NH) 199518/1; length 33.1 mm. Figure 26. *P. denticulata abbreviata* G. B. Sowerby I, 1834; lectotype; BM(NH) 1995219/1; length, 28.4 mm. Figure 27. *P. peruviana* Jay, 1839; lectotype; AMNH 56118; length, 27.2 mm. Figure 28. *P. ventricosa* Deshayes, 1853; lectotype; length, 30.9 mm.

S. Oldroyd, 1925:163 [in part]; Keen, 1958:152, 153, fig. 347 [*Petricola (Petricolaria)*]; Olsson, 1961:313–314, pl. 54, fig. 1 [*Petricola (Petricola)*]; Keen, 1971:199, 200, fig. 481 [*Petricola (Rupellaria)*]; Bernard, 1983:57 [*Petricola (Rupellaria)*].
Petricola denticulata abbreviata G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; Carpenter, 1857c:19.
Venerupis peruviana Jay, 1839. Jay, 1839:13, 113, pl. 1, figs. 14, 15; Deshayes, 1853:212 [as a synonym of *P. pholadiformis*]; Lamy, 1923a:282; Lamy, 1923b:350 [as a probable synonym of *P. denticulata*]; Keen, 1958:152 [as a synonym of *P. denticulata*]; Keen, 1971:199 [as a

synonym of *P. denticulata*]; Bernard, 1983:57 [as a synonym of *P. denticulata*].
Petricola ventricosa Deshayes, 1853 [non Krause, 1848]. Deshayes, 1853:214 [cited here as “Proc. Zool. Soc.,” but not occurring in that serial]; Carpenter, 1857b:244, 299 [as a possible synonym of *P. denticulata*]; Carpenter, 1857c:19; Carpenter, 1864b:668 [1872:154]; Tryon, 1872:256, 258 [as a synonym of *P. denticulata*]; G. B. Sowerby II, 1874a:pl. 3, fig. 23; [the following five references as a synonym of *P. denticulata*]; Dall, 1909b:289; Lamy, 1923b:348; Keen, 1958:152; Keen, 1971:199; Bernard, 1983:57.

[*non Petricola ventricosa* Krause, 1848:2, a synonym of the South African tellinid *Gastrana abildgaardiana* (Spengler, 1798)].

Petricola dactylus G. B. Sowerby I. *auctt.*, *non* G. B. Sowerby I, 1823. ?Carpenter, 1857b:232, 299, 352.

Type material and localities: *P. denticulata*—BM(NH) 1995218/1, **lectotype here designated**, paired valves; length, 33.1 mm; height, 15.7 mm; thickness, 14.6 mm (Figure 25). BM(NH) 1995218/2-3, paralectotypes, two other pairs, 33.6 mm and 33.4 mm in length. The lectotype selected was the syntype closest to the originally stated measurement of 1.3 poll. [= 33.0 mm]. Paita, Piura Province, Perú (5.1°S); in hard clay and stones at low water; H. Cuming. *P. denticulata abbreviata*—BM(NH) 1995219/1, **lectotype here designated**, paired valves; length, 28.4 mm; height, 14.5 mm; thickness, 13.1 mm (Figure 26). BM(NH) 1995219/2-4, paralectotypes, three other pairs, 13.5 mm, 31.5 mm, and 32.6 mm in length. The lectotype selected was the syntype closest to the originally stated length of 1.1 poll. [= 27.9 mm]. Isla de La Plata, Manabi Province, Ecuador (1.3°S); in stones at low water, H. Cuming. *P. peruviana*—AMNH 56118, lectotype (Richards & Old, 1969:14, as "holotype"), paired valves; length, 27.2 mm; height, 11.8 mm; thickness, 11.8 mm (Figure 27). AMNH 226533, paralectotypes, two other pairs, 31.2 mm and 29.3 mm in length. The lectotype seems to be the originally figured specimen. The statement in Boyko & Sage (1996:28) that the Richards & Old lectotype designation was not valid is incorrect. Peru. *P. ventricosa*—BM(NH) 1966556/1, **lectotype here designated**, paired valves; length 30.9 mm; height, 19.9 mm; thickness, 16.1 mm (Figure 28). BM(NH) 1966556/2-3, paralectotypes, two valves, 33.3 mm and 32.1 mm in length. Golfo de California; H. Cuming.

Description: Shell elongate; anterior end short, somewhat produced; broadly to sharply rounded posteriorly. Shell inflated, moderately to very thick-shelled; beaks low. Without lunule or escutcheon. Sculpture of strong, dense, lamellar commarginal ribs and about 50 strong radial ribs, of which approximately the 13 anteriormost are prominent and broadest, the rest becoming almost obsolete medially and narrow posteriorly. Pallial sinus short to moderate in depth, of moderate width rounded to pointed anteriorly, completely detached from pallial line; pallial line not bowed dorsally (Figure 62). Hinge teeth robust; in right valve with a pointed anterior cardinal and a bifid posterior cardinal; in left valve with a tiny anterior cardinal that is generally lost in adult, a central cardinal bifid, and a lamellar posterior cardinal. Ligament elongate, on a well-developed nymph, slightly sunken below hinge margin posteriorly. White to tan externally; interior often with brown to purplish-brown patches on posterior end, sometimes on also anterior end and along dorsal and ventral margins. Length to 42.0 mm [CAS 102588; Boca de Barranca, Puntarenas Province, Costa Rica].

Geographic distribution and habitat: Bahía Santa Maria, Pacific coast of Baja California Sur (24.8°N) [USNM 264785, 269067], into and throughout the Golfo de California to its northern end at Puerto Peñasco, Sonora, Mexico (31.5°N) [LACM 41-1], south to Bayovar, Piura Province, Perú (5.8°S) [CAS 105775, UMML 30.9589], from the intertidal zone to 22 m, in soft rock. A record by Lamy (1930:96) at "Punta," presumably La Punta near Callao, Lima Province, Peru (approximately 12°S), is suspect and requires verification. A specimen from an old collection labeled as having come from Isla Chilóe, Chilóe Province, Chile (MCZ 316109), probably represents a labeling error. I have examined 181 Recent lots. This species is also recorded in the Pleistocene of Ecuador (Hoffstetter, 1948:78).

Discussion: *Petricola denticulata abbreviata* was based on proportionately shorter specimens than the nominal subspecies. A still shorter specimen is figured by Olsson (1961:pl. 54, figs. 1a, b). This named variety has been overlooked in most subsequent synonymies.

Lamy (1923b) was the first to recognize that *Venerupis peruviana* Jay was probably a synonym of this species, and Tryon (1872) was the first to conclude that *P. ventricosa* Deshayes, based on inflated specimens, was a synonym.

Lamy (1923b) incorrectly placed *Psephis tellimyalis* Carpenter, 1864, in synonymy here; its type specimen is a *Halodakra* [Bernardinidae], and the *Petricola* for which this name has been used is here described as *P. hertzi*. Lamy (1923b) also regarded *P. costata* Philippi, 1849 [*non* Lamarck, 1801], as a variety of *P. denticulata*. However, because Philippi's description calls for material without radial ribs on the anterior slope, his taxon, described from an unknown locality, is more likely to have been a synonym of *P. rugosa* G. B. Sowerby I, 1834.

Most juvenile specimens of *P. denticulata* have more prominent radial sculpture, the commarginal sculpture becoming stronger with age.

Records of this species from southern California were based on material of *P. californiensis* Pilsbry & Lowe, 1932. The latter has a thinner, less colorful shell, a more rounded anterior end, less rugose, more predominantly radial sculpture, a more elongate pallial sinus, smaller teeth, and a less developed nymph.

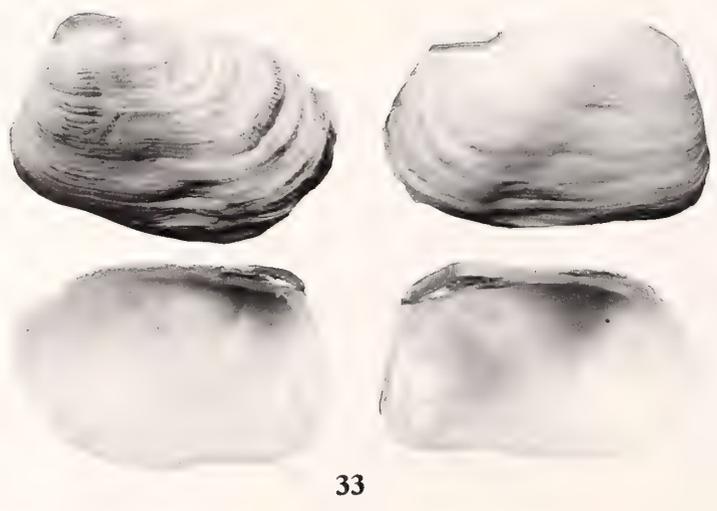
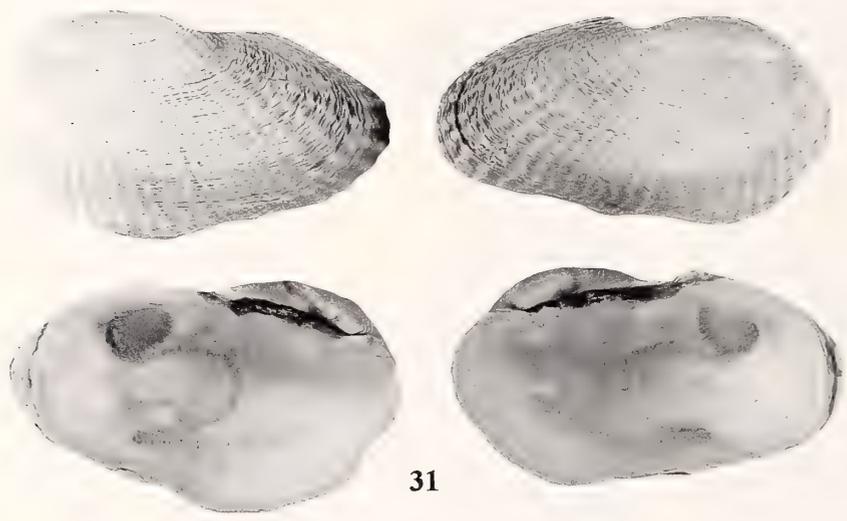
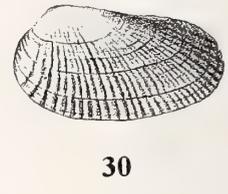
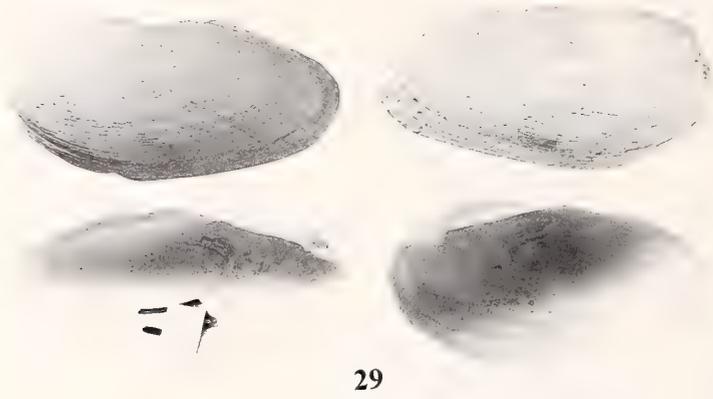
Fischer (1857:322, 326-327) noted that *P. denticulata* has an elongate foot, small, elongate, fairly equal demi-branches, and very elongate labial palps.

Petricola (Petricolirus) rugosa

G. B. Sowerby I, 1834

(Figures 29-31, 63)

Petricola rugosa G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; d'Orbigny, 1846:548; Deshayes, 1853:213; Hupé, 1854:345; Tryon, 1872:257, 258 [as a synonym of *P. nivea* "(Chemnitz, 1785)"]; Philippi, 1887:153,



- pl. 25, fig. 11; Dall, 1909b:270; Lamy, 1923b:351–352 [*Petricola (Petricolaria)*]; Carcelles & Williamson, 1951:343; Soot-Ryen, 1957:8–9; Soot-Ryen, 1959:60; Marinovich, 1973:13 [in part], fig. 17 [fig. 18 = *P. olssoni*]; Bernard, 1983:57 [*Petricola (Petricolaria)*].
- Petricola tenuis* G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; d'Orbigny, 1846:548; Troschel, 1852:204; Deshayes, 1853:215; Tryon, 1872:257, 258 [as a synonym of *P. nivea*]; Dall, 1909b:289 [as a synonym of *P. rugosa*, thus acting as First Reviser]; Lamy, 1923b:351 [as a synonym of *P. rugosa*]; Bernard, 1983:57 [as a synonym of *P. rugosa*].
- ?*Petricola costata* Philippi, 1849 [non Lamarck, 1801]. Philippi, 1849:163; Tryon, 1872:256 [as a synonym of *P. nivea*]; Lamy, 1923b:348–349 [as a variety of *P. denticulata*]; Bernard, 1983:57 [as a synonym of *P. rugosa*].
- [non *Petricola costata* Lamarck, 1801:121, = *P. lapicida* (Gmelin, 1791)]
- ?*Petricola ovata* Troschel, 1852. Troschel, 1852:204–205; Dall, 1909b:289 [as a synonym of *P. rugosa*]; Bernard, 1983:57 [as a possible synonym of *P. olssoni*].
- ?*Petricola chiloensis* Philippi, auctt., ?non Philippi, 1845. Hupé, 1854:345.
- ?[non Philippi, 1845:53]
- Laxicava* [sic for *Saxicava*] *calderensis* Conrad, 1855. Conrad, 1855b:286; Philippi, 1887:286, pl. 25, fig. 13.
- Petricola rhyssodes* Philippi, 1887. Philippi, 1887:154, pl. 25, fig. 12; Bernard, 1983:47 [as a synonym of *P. rugosa*].
- Petricola nivea* (Gmelin, 1791), auctt., non *Mytilus niveus* Gmelin, 1791. G. B. Sowerby II, 1854b:773, pl. 166, figs. 13, 14; G. B. Sowerby II, 1874a:pl. 2, fig. 8; Lamy, 1908:51.
- [non *Mytilus nivea* Gmelin, 1791:3358, ex Chemnitz ms]

Type material and localities: *P. rugosa*—Lost. None of the several lots of this species in BM(NH) can be confidently identified as the type material of this taxon. The original specimens measured: length, 35.6 mm; height, 17.8 mm; thickness, 14.0 mm. Concepción, Concepción Province, Chile (36.7°S), in barnacles at 3–7 fms. [5–13 m], H. Cuming. *P. tenuis*—BM(NH) 1995217/1, **lectotype here designated**, paired valves; length, 26.0 mm; height, 12.9 mm; thickness, 11.2 mm (Figure 29). BM(NH) 1995217/2–3, paralectotypes, two other pairs, 23.1 mm and 19.0 mm in length. The lectotype selected is the pair closest to the originally stated length of 25.4 mm. Lambayeque, Lambayeque Province (6.7°S), and Pascamayo, La Libertad Province (7.4°S), Perú; in hard clay at low water; H. Cuming. *P. costata* Philippi—Probably

lost. Not in MNH-U (R. Kiliias, in correspondence, 20 January 1996). The original specimen measured 23.0 mm in length, 11.5 mm in height, and 11.0 mm in thickness. The original locality was unknown. *P. ovata*—Probably destroyed in World War II (Dance, 1986:210, 229). Not in MNH-U (R. Kiliias, in correspondence, 20 January 1996). The original specimen measured 31 mm in length, 18 mm in height, and 16 mm in thickness. Perú. *L. calderensis*—Probably lost. Conrad did not provide a size or a figure. [?Puerto Caldera, Atacama Province (27.1°S)], Chile. *P. rhyssodes*—Not in the Museum at the Universidad de Chile, in Santiago, Chile (D. Frassinetti, in correspondence, 30 July 1996). The original specimen measured 48 mm in length, 25 mm in height, and 22 mm in thickness (Figure 30). Pleistocene and Recent material from Coquimbo, Coquimbo Province, Chile (30.0°S). The original figure is of a Recent specimen.

Description: Shell elongate, cylindrical; anterior end short, rounded; posterior end rounded to somewhat truncate, sometimes with an extension formed by outer layer of shell. Shell generally inflated, but large specimens sometimes flattened, moderately heavy to thin-shelled; beaks low. Without lunule or escutcheon. Sculpture of about 40 radial ribs that are moderate in strength and broad on anterior slope; ribs obscure on central slope, and about 10 very heavy, narrow radial ribs on posterior slope. Pallial sinus of moderate depth and width, rounded to somewhat pointed anteriorly, completely detached from pallial line; pallial line not bowed dorsally (Figure 63). Hinge teeth small; right valve with two produced cardinals, the posterior slightly bifid; left valve with two elongate cardinals, the anteriormost slightly bifid, lacking any sign of an anterior cardinal in the smallest specimens available. Ligament elongate, shallow, on a somewhat developed nymph. White to tan externally; white within. Length to 50 mm [SBMNH 125291; Lima, Lima Province, Perú].

Distribution and habitat: Lambayeque, Lambayeque Province, Perú (6.7°S) [one of the type localities of *P. tenuis*]; Viru, La Libertad Province, Perú (8.4°S) [SBMNH 138131], to Bahía Concepción, Concepción Province, Chile (37.1°S) [LACM 72–207.7]; Bahía de Lota, Concepción Province, Chile (37.1°S) (Soot-Ryen, 1959); the only habitat data recorded on labels is the in-

←

Explanation of Figures 29 to 34

Figures 29–31. *Petricola (Petricolirus) rugosa* G. B. Sowerby I, 1834. Figure 29. *P. tenuis* G. B. Sowerby I, 1834; lectotype; BM(NH) 1995217/1; length, 26.0 mm. Figure 30. *P. rhyssodes* Philippi, 1887; original figure; original specimen length, 48 mm. Figure 31. BM(NH) 06.6.9.798; Coquimbo, Chile; length, 42.3 mm. Figures 32–34. *Petricola exarata* (Carpenter, 1857). Figure 32. *Rupellaria exarata*; lectotype; BM(NH) Carpenter Coll. 73(28); length, 4.7 mm; Figure 33. CAS 102591; Altata, Sinaloa, Mexico; length, 13.5 mm; Figure 34. CAS 102591; length, 4.0 mm; SEM image.

tertidal zone. Records in Chile from Archipelago de los Chonos, Aisen Province (approx. 44.5°S) (Soot-Ryen, 1959), and Bahía Orange, Isla Hoste, Magallanes Province (55.5°S) [USNM 17648], are doubtful and require additional verification; I have examined 37 Recent lots.

This species is recorded in the Pliocene of Chile (Herm, 1969:58).

Discussion: *Petricola tenuis* was based on thin-shelled specimens. This name was confused by Carpenter (1864a: 29 [1872:203], 1864b:552 [1872:33]) with *Saxicava tenuis* G. B. Sowerby I, 1834:88, in his discussions of the C. B. Adams collection, because Adams had specimens of a *Petricola* identified as the *Saxicava*.

This species is also highly variable in shape and sculpture, with some specimens almost cylindrical and others flattened and expanded. The sculpture varies from subdued to fairly heavy (Figure 30).

It seems possible that *P. costata* Philippi was based on material of this species (see Discussion under *P. denticulata*).

Based on the locality, it is likely that *Petricola chilensis* Philippi, 1845, belongs in synonymy of *P. dactylus* (see under it). However, it is possible that subsequent records of Philippi's taxon, such as those of Hupé (1854), are based on specimens of *P. rugosa*.

It is with some hesitancy that I assign *P. ovata* to synonymy here. The original specimen had fewer ribs than does *P. olssoni*, which normally has 50–60 ribs. *Petricola rugosa* occasionally has a fairly oval shape, and can have as few as the 36 ribs counted by Troschel.

Conrad's "*Laxicava*" [*Saxicava*] *calderensis* is certainly this species. Many specimens of *P. rugosa* have a pattern of strong ribs on the ends, with the ribbing obsolete on the central slope. Given the species name, it seems likely that the original material came from Puerto Caldera, although Conrad did not supply a locality or a size, nor did he provide a figure.

Given the large size of the specimen and the figure, it is likely that *Petricola rhyssodes* belongs in synonymy here, and it is unfortunate that it has not been located among the Philippi material in the Museum at the Universidad de Chile.

Gray (1825:136) was the first to assign Gmelin *Mytilus niveus* Gmelin, 1791:3358, to the genus *Petricola*, and subsequent illustrations by G. B. Sowerby II seem to be the present species. Gmelin's taxon was based on the unavailable *Mytilus niveus* Chemnitz, 1785:154, pl. 82, fig. 734, reportedly from the Nicobar Islands in the Indian Ocean, and some material of *P. rugosa* in BM(NH) was subsequently labeled as having come from there. The figure in the non-binomial Chemnitz, upon which Gmelin's species rests, is interminable, as is the description by Chemnitz: shell semi-transparent, edge knifelike, inner surface smooth and shiny, external surface with striae (not ribs).

Petricola, sensu lato

A variety of morphologies are represented by the following taxa, but with present knowledge, none can confidently be assigned to named subgenera.

Petricola exarata (Carpenter, 1857)

(Figures 32–34, 64)

Rupellaria exarata Carpenter, 1857. Carpenter, 1857b:244, 299, *nomen nudum*; Carpenter, 1857c:20–21; Lamy, 1923a:285; Coan, 1962:92; Brann, 1966:29, pl. 4, fig. 28; Keen, 1968:394, 395, fig. 16, 399 [*Petricola (Petricola)*]; Keen, 1971:197, 198, fig. 476 [*Petricola (Petricola)*]; Bernard, 1983:47 [*Petricola (Petricola)*].

Type material and locality: *R. exarata*—BM(NH) Carpenter Mazatlán Collection, Tablet 73, species 28, **lectotype here designated**, paired valves; length, 4.7 mm; height, 3.0 mm; thickness, 1.6 mm (Figure 32). BM(NH), paralectotypes, two additional pairs, one in a barnacle. A fourth syntype mentioned by Carpenter & Keen (1968) not located. USNM 715645, paralectotypes, six fragmentary valves on a glass slide. Mazatlán, Sinaloa, Mexico (23.2°N); in barnacles attached to *Muricanthus princeps* (Broderip, 1833); F. Reigen.

Description: Shell ovate; anterior end very short, truncate to slightly rounded; posterior end rounded; posterior slope demarcated by a low keel. Young shells moderately inflated; adult generally flattened. Shell moderate in thickness; beaks very small. Lunule absent; long, narrow escutcheon in left valve. Sculpture of very fine, closely spaced radial threads (adult specimen with more than 100), slightly larger posteriorly, and irregular commarginal growth checks. Pallial sinus of moderate depth, broad, rounded, slightly overlapping pallial line; pallial line slightly bowed dorsally (Figure 64). Hinge teeth small; right valve with a small anterior cardinal and a bifid posterior cardinal, plus an elongate posterior lateral ridge; left valve with a very small anterior cardinal (lacking in many specimens), bifid central cardinal, and small posterior cardinal. Ligament of medium length, not sunken; nymph of moderate thickness. White externally, except for young portion of shell, which has broad brownish radial patches. Length to 15 mm [LACM 655645; Puerto Pizarro, Tumbes Province, Perú]. A photograph of large specimen (Figure 32) and an SEM view of a small specimen (Figure 34) are provided here.

Distribution and habitat: Altata, Sinaloa, Mexico (24.5°N) [CAS 102591, UCMP E8125], to Puerto Pizarro, Tumbes Province, Perú (3.5°S) [LACM 72–84.16; SBMNH 142893; USNM 655644, 655645], from the intertidal zone, nesting in crevices in rocky areas near muddy mangrove swamps and sand flats. I have examined 34 lots.

Discussion: This is a distinctive species with a number

of unique features. It is known mostly from very small specimens.

Petricola hertzana Coan, sp. nov.

(Figures 35, 36, 65)

Petricola tellimyalis (Carpenter), *auctt.*, non *Psephis tellimyalis* Carpenter, 1864. Dall, 1900a:100; Willett, 1931: 39, pl. 17, figs. 1, 2; Pilsbry & Lowe, 1932:96–97, pl. 13, figs. 12, 13; Burch, 1944:18–19; Burch, 1948:9–10; Bernard, 1983:57 [*Petricola* (*Rupellaria*)].

[non *Psephis tellimyalis* Carpenter, 1864]. Carpenter, 1864b: 641 [1872:127]; Carpenter, 1865:135–136 [1872:303–304]; Palmer, 1958:100–101, pl. 12, figs. 1–5.

Petricola denticulata G. B. Sowerby I, *auctt.*, non G. B. Sowerby I, 1843. Dall, 1900b:121–122 [in part].

Type material and locality: *P. hertzi*—CAS 104559, holotype, an articulated pair, length, 5.3 mm; height, 4.0 mm; thickness 2.8 mm (Figure 35). Paratypes, CAS 106035, 26 articulated and 5 disarticulated pairs, two of which are also figured here (CAS 104518) (Figure 36). San Pedro, Los Angeles County, California (33.7°N); on kelp.

Description: Shell ovate; anterior end shortest, sharply rounded; posterior end rounded. Shell inflated, thin; beaks broad. Without lunule or escutcheon. Sculpture primarily of irregular commarginal striae and low radial ribs, especially on ends; some specimens entirely lacking radial ribs, and some specimens with radial ribs over entire surface. Pallial sinus of moderate depth, broad, rounded, slightly confluent with pallial line; pallial sinus somewhat bowed dorsally (Figure 65). Hinge teeth relatively small, delicate, broken in most specimens; right valve with a narrow anterior cardinal and a slightly bifid posterior cardinal; left valve with a tiny anterior cardinal, a bifid central cardinal, and a narrow posterior cardinal. Ligament elongate, shallow, on a narrow nymph. Color variable, from cream to dark chocolate brown, in patches or radial bands; occasional specimens white. Length to 7 mm [CAS 106035, a paratype; San Pedro, Los Angeles County, California].

Distribution: Santa Monica, Los Angeles County, California (34.0°N) [ANSP 15759; CAS 104552, 104556, 104560; SBMNH 143007, 143008; LACM 19264, and other lots], to Bahía Magdalena, Baja California Sur (24.6°N) [ANSP 151718, SBMNH 15807], from the intertidal zone to 27 m, on algae. Two lots labeled as having come from Guaymas, Sonora, Mexico (27.9°N) [USNM 602882, UCMP A4200], both from old collections, may represent locality errors because no other material has come from that well-studied locality. However, the species should be looked for in that area because several other Californian species occur in isolated central Golfo de California populations. I have examined 55 lots.

This species has been reported, as *P. tellimyalis*, from the Pleistocene of southern California at Playa del Rey,

Los Angeles County (Willett, 1937:390), and Newport Bay, Orange County (Kanakoff & Emerson, 1959:24).

Etymology: This species is named in honor of Carole and Jules Hertz of San Diego, California.

Discussion and comparisons: Dall (1900a) was the first to identify this species of *Petricola* as *Psephis tellimyalis* Carpenter, which he presumed had been based on a very small specimen. This assignment is hard to explain because Carpenter specifically mentioned elongate lateral teeth, and the type was in the USNM. Dall (1900b) then became convinced that it was merely the young of *Petricola denticulata*. Willett (1931) eventually showed that it was a separable species, and Pilsbry & Lowe (1932) agreed, noting this as they reassigned southern Californian material that has been known as *P. denticulata* to their new species *P. californiensis*.

When I examined the tiny holotype of *Psephis tellimyalis* (length, 2.5 mm) [USNM 15554], I realized that it was not a *Petricola* at all, but rather a member of the Bernardinidae and a previously unrecognized synonym of *Halodakra* (*Halodakra*) *subtrigona* Carpenter, 1857:82 (this species discussed by Coan, 1984:231). This has left the small *Petricola* without a name.

Petricola olssoni Bernard, 1983

(Figures 37, 38, 66)

Petricola (*Petricola*) *peruviana* Olsson, 1961, non (Jay, 1839). Olsson, 1961:315, pl. 55, fig. 9; Keen, 1971:199, 200, fig. 482 [as *Petricola* (*Rupellaria*)].

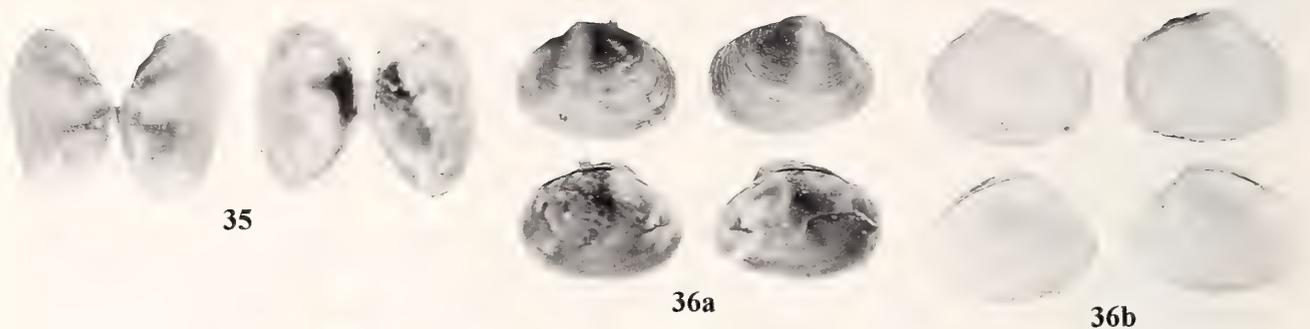
[non *Venerupis peruviana* Jay, 1839, a synonym of *P. denticulata*]

Petricola olssoni Bernard, 1983, *nom. nov. pro P. peruviana* Olsson, non (Jay, 1839). Bernard, 1983:57, 70 [*Petricola* (*Rupellaria*)].

Petricola rugosa G. B. Sowerby I, 1834, *auctt.*, non G. B. Sowerby I, 1834. Marincovich, 1973: fig. 18.

Type material and locality: *P. peruviana* Olsson/*olssoni*—ANSP 218905, a right valve; length, 30.0 mm; height, 19.0 mm; thickness, 5.6 mm (Figure 37). Negritos, Piura Province, Perú (4.7°S). ANSP 218906, paratype, a left valve, 30.0 mm in length, from Lobitos, Piura Province, Perú (4.4°S) (Figure 38).

Description: Shell ovate; anterior end shortest, rounded; posterior end broadly expanded, rounded to slightly truncate. Small specimens moderately inflated; larger material sometimes flattened. Shell inflated, thin; beaks prominent. Without lunule or escutcheon. Sculpture of about 50–60 fine, narrow radial ribs over entire surface, ribs varying somewhat in width, becoming somewhat less conspicuous posteriorly, and strong, irregular commarginal growth checks. Pallial sinus of moderate depth and width, pointing somewhat anterodorsally, rounded, overlapping pallial line for a substantial distance; pallial line greatly bowed dorsally, often broken into irregular patches (Fig-



ure 66). Hinge teeth relatively small; right valve with a narrow anterior cardinal and a produced, slightly bifid posterior cardinal; left valve with a tiny anterior cardinal, a slightly bifid central cardinal, and a thin posterior cardinal. Ligament elongate, shallow; nymph fairly robust. White to tan externally, often with wide radial brownish bands; internally mottled with orange-brown. Length to 30 mm (type material of *P. peruviana* Olsson). A complete pair is also illustrated here (Figure 39).

Distribution and habitat: Between Zorritos and Mancora, Tumbes Province, Peru (3.9°S) [SBMNH 125769], to Antofagasta, Antofagasta Province, Chile (23.7°S) [LACM 54743], from the intertidal zone to 3 m, in nesting situations. I have examined 22 lots.

Discussion: This species is most similar to *P. californiensis*, which attains a larger size, is more elongate and proportionately longer posteriorly, and has heavier sculpture in general, particularly anteriorly.

Petricola scotti Coan, sp. nov.

(Figures 40, 41, 67)

Petricola (Narario) sp., auctt. Olsson, 1961: 528, pl. 55, fig. 11 [plate expl. makes reference to p. 317, but species not mentioned there].

Type material and locality: *P. scotti*—PRI 25782, holotype, paired valves; length, 16.9 mm; height, 8.6 mm; thickness, 7.2 mm (Figure 40). Esmeraldas, Guayas Province, Ecuador (1.0°N); habitat not recorded; A. A. Olsson. CAS 102509, paratype, paired valves; length, 11.0 mm (Figure 41); Manta, Manabi Province, Ecuador (1.0°S); Don L. Frizzell

Description: Shell ovate-elongate; anterior end very short, rounded to subtruncate; posterior end rounded, extended beyond inner shell layer by outer shell layer in some specimens; posterodorsal margin somewhat flared, with right valve overlapping left. Shell inflated, average in thickness; beaks slightly inflated. Lunule absent; small escutcheon posterior to ligament in some material. Sculpture on initial portion of shell of approximately 50 radial ribs, becoming somewhat finer posteriorly; at approximately 6 mm in size, sculpture transitioning entirely to thin, evenly spaced commarginal lamellae, which can be as high as their interspaces. Pallial sinus of moderate depth and width, rounded anteriorly, overlapping or very

closely paralleling pallial line for a short distance; pallial line slightly bowed dorsally (Figure 67). Hinge fairly robust; right valve with a projecting anterior cardinal and a bifid posterior cardinal; left valve with a very low, inconspicuous anterior cardinal, a bifid central cardinal, and a thin, elongate posterior cardinal. Ligament short, shallow. Shell white externally and internally. Length to 18.5 mm [MNHN; La Puntilla, Guayas Province, Ecuador].

Distribution and habitat: Ft. Amador, Panamá Province, Panamá (9.0°N) [SBMNH 142891], to Salinas, Guayas Province, Ecuador (2.2°S) [USNM 635362]; the only habitat noted was in algae. This species is as yet known from 9 lots.

Referred material: Skoglund Collection—Venado Beach, Panamá Province, Panamá (8.9°N); LACM 75-56.19—Playa de Farfan, Panamá Province, Panamá (8.9°N); LACM 65461—Ft. Amador, Panamá Province, Panamá (9.0°N); SBMNH 142891—Ft. Amador, Panamá Province, Panamá (9.0°N); PRI 25782—Esmeraldas, Guayas Province, Ecuador (1.0°N)—Holotype; CAS 102509—Manta, Manabi Province, Ecuador (1.0°S)—Paratype; NMNH—La Puntilla, Guayas Province, Ecuador (2.2°S); NMHN—Peninsula Santa Elena, Guayas Province, Ecuador (2.2°S); USNM 635326—Salinas, Guayas Province, Ecuador (2.2°S).

Etymology: This species is named for Paul H. Scott of the Santa Barbara Museum of Natural History.

Discussion: I initially mistook specimens of this species for *Petricola concinna*, from which it differs in being more ovate and less tapered posteriorly, in having even radial sculpture on the early portion of the shell rather than a few radial ribs concentrated anteriorly, and in having a pallial sinus that overlaps the pallial line for a short distance. Two of the four lots from Panama include some very tiny specimens that can only be tentatively assigned here. This species differs from young *P. denticulata* in having a more rounded outline, with a less produced anterior end, in developing frills on the posterior slope, and in having lower radial sculpture.

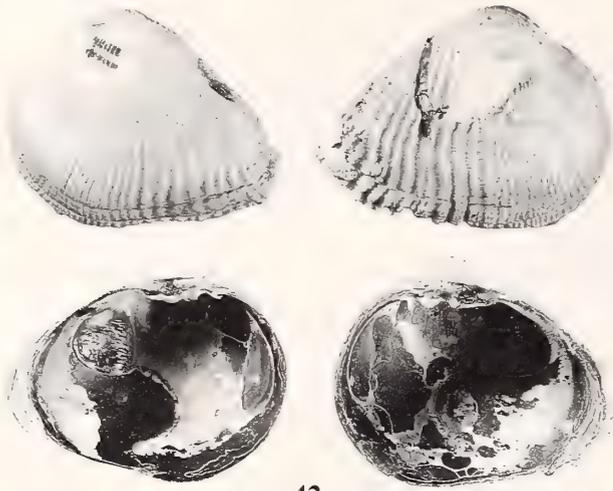
Genus *Choristodon* Jonas, 1844

Choristodon Jonas, 1844:185 [Type species (M): *C. typicum* Jonas, 1844:185, =*Petricola robusta* G. B. Sowerby I, 1834:47; Recent, Caribbean and eastern Pacific].

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Explanation of Figures 35 to 41

Figures 35, 36. *Petricola hertzana* Coan, sp. nov. Figure 35. Holotype; CAS 104559; length, 5.3 mm. Figure 36a, b. Paratypes; CAS 104518; same magnification. Figures 37–39. *Petricola olssoni* Bernard, 1983. Figure 37. Holotype; ANSP 218905; length, 30.0 mm. Figure 38. Paratype; ANSP 218906; length, 30.0 mm. Figure 39. SBMNH 126151; Pisco, Ica Province, Peru; length, 12.0 mm. Figures 40, 41. *Petricola scotti* Coan, sp. nov. Figure 40. Holotype; PRI 25782; length, 16.9 mm. Figure 41. Paratype; CAS 102509; length, 11.0 mm.



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This genus is characterized by a heavy shell, heavy radial sculpture, a sunken ligament, a hinge that becomes distorted in large specimens, and a tendency to become inequivalve, the right valve overlapping the left postero-dorsally. It was synonymized with the Mediterranean *Rupellaria* by Keen (1969); the latter genus is thin-shelled and equivalve, has fine radial ribs, and the ligament is not deeply sunken. Moreover, the foot is elongate in *Petricola* (*Rupellaria*) *lithophaga* (Retzius, 1788), as are the siphons, and the pallial sinus is very large (Deshayes, 1848:Atlas, pp. 139–145, pls. 66, 67, 67a). In contrast, *Choristodon robustum* has a small foot, short siphons, and a smaller pallial sinus (Narchi, 1974).

Choristodon robustum (G. B. Sowerby I, 1834)

(Figures 42–48, 68)

Petricola robusta G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; Deshayes, 1853:210–211; G. B. Sowerby II, 1854b:775, pl. 166, figs. 16, 17; Gould & Carpenter, 1857:198; Carpenter, 1857b:184, 226, 232, 234, 244, 265, 295, 299, 352, 364, 365; Fischer, 1857:323, 325, 327–329; Carpenter, 1857c:17–19, 547; Carpenter, 1864b:529, 543, 620 [1872:15, 29, 106]; Tryon, 1872:257, 258 [as a synonym of *P. lithophaga* (Retzius, 1788)]; G. B. Sowerby II, 1874a:pl. 3, fig. 30; Dall, 1909b:270; Lamy, 1923b:330–332; Hertlein & Strong, 1948:194 [*Petricola* (*Petricola*)]; Durham, 1950:87, 168, pl. 23, fig. 15; Keen, 1958:152, 153, fig. 349 [*Petricola* (*Rupellaria*)]; Olsson, 1961:215 [*Petricola* (*Petricola*)]; Emerson & Hertlein, 1964:359; Brann, 1966:pl. 2, fig. 24; Keen, 1971:199, 200, fig. 483 [*Petricola* (*Rupellaria*)]; Woodring, 1982:709 [as a synonym of *P. typica* Jonas, 1844].

Choristodon typicum Jonas, 1844. Jonas, 1844:185; Jonas, 1846:101–103, 133 [repr.:1–3, 33], pl. 7, fig. 3, 3a, 3b; [the following references mostly as *Petricola*]; Deshayes, 1853:510; G. B. Sowerby II, 1874a:pl. 3, fig. 21; Carpenter, 1857b:244, 364 [as a probable synonym of *P. robusta*]; Fischer, 1857:324 [as a synonym of *P. robusta*]; Carpenter, 1857c:19, 529, 547 [as a probable synonym of *P. robusta*]; Carpenter, 1864b:543 [1872:29]; Tryon, 1872:257, 258 [as a synonym of *P. lithophaga*]; Dall, 1900c:1059; Lamy, 1923b:332–333; Weisbord, 1964:329–332, pl. 47, fig. 15, pl. 48, figs. 1–6 [*Petricola* (*Rupellaria*)]; Narchi, 1974:123–129; Woodring, 1982:709–710, pl. 118, fig. 2 [*Rupellaria*]; Rios, 1994:290, pl. 99, fig. 1419.

Petricola robusta Philippi, 1849 (March) [non *P. robusta* G. B. Sowerby I, 1834]. Philippi, 1849:163; Carpenter,

1857b:295 [as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Carpenter, 1857c:17 [as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Tryon, 1872:257, 258 [as a synonym of *P. lithophaga*].

Petricola sinuosa Conrad, 1849 (pre-16 June). Conrad, 1849a:155; 1849c:229; 1850:279, pl. 39, fig. 2; [the following three references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Carpenter, 1857a:209; Carpenter, 1857b:226, 244, 265; Carpenter, 1857c:547; Tryon, 1872:257, 258 [as a synonym of *P. lithophaga*]; [the following five references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Lamy, 1923b:331; Hertlein & Strong, 1948:194; Keen, 1958:152; Keen, 1971:199; Bernard, 1983:57.

Petricola bulbosa Gould, 1851. Gould, 1851:16, 408, pl. 15, fig. 5; [the following four references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Gould & Carpenter, 1857:198; Carpenter, 1857b:226, 232, 244; Carpenter, 1857c:547; Gould, 1862:210; Tryon, 1872:255, 257 [as a synonym of *P. lithophaga*]; [the following six references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Lamy, 1923b:331; Hertlein & Strong, 1948:194; Keen, 1958:152; R. I. Johnson, 1964:48; Keen, 1971:199; Bernard, 1983:57.

Petricola anchoreta de Folin, 1867. de Folin, 1867:56–58 [repr.:18–20], pl. 3, figs. 1–4; de Folin & Périer, 1867:8; Tryon, 1872:255; Lamy, 1923b:320; Kisch, 1960:162; Bernard, 1983:57 [as a synonym of *P. exarata*].

Petricola venusta de Folin, 1867. de Folin, 1867:58–59 [repr.:20–21], pl. 3, figs. 5–7; de Folin & Périer, 1867:8; Tryon, 1872:258; Kisch, 1960:162.

Petricola buwaldi Clark, 1915. Clark, 1915:471, pl. 60, fig. 6; Adegoke, 1969:149; ?Woodring & Bramlette, 1951:66, 90.

Petricola (*Rupellaria*) *riocanensis* Maury, 1917. Maury, 1917:384 [220], 414 [250], pl. 37, fig. 12; Woodring, 1982:709 [as a synonym of *P. typica*].

Type material and localities: *P. robusta* G. B. Sowerby I—BM(NH) 1966558/1, **lectotype here designated**, paired valves; length, 30.6 mm; height, 24.4 mm; thickness, 21.2 mm (Figure 42). BM(NH) 1966558/2–3, paralectotypes, two additional pairs, 26.2 mm and 21.5 mm in length. Panamá and “Isla Muerto” [?Isla Santa Clara], Golfo de Guayaquil, El Oro Province, Ecuador (3.2°S). The label now with the specimens says: “Panamá, found in rocks at 6–11 fms.” [11–20 m]. *C. typicum*—Probably lost. Not in MNH-U (R. Kiliyas, in correspondence, 20 January 1996). The original specimen measured 16.5 mm in length, 11.0 mm in height, and 8.8 mm in thickness (Figure 43). St. Thomas, Virgin Islands (about 18.3°N).

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Explanation of Figures 42 to 48

Figures 42–48. *Choristodon robustum* (G. B. Sowerby I, 1834). Figure 42. *Petricola robusta*; lectotype; BM(NH) 1966558/1; length, 24.4 mm. Figure 43. *Choristodon typicum* Jonas, 1844; figure from Jonas (1846); length, 16.5 mm. Figure 44. *Petricola sinuosa* Conrad, 1849; as figured in Conrad (1850); length, 19 mm. Figure 45. *P. bulbosa* Gould, 1851; holotype; MCZ 169065; length, 27.8 mm. Figure 46. *P. anchoreta* de Folin, 1867; lectotype; BM(NH) 1995222/1; length, 12.4 mm. Figure 47. *P. venusta* de Folin, 1867; holotype; BM(NH) 1995223/1; length, 16.3 mm. Figure 48. *P. buwaldi* Clark, 1915; holotype; UCMP 11657; length, 29.5 mm.

P. robusta Philippi—Probably lost. Not in MNH-U (R. Kiliyas, in correspondence, 20 January 1996). The original specimen measured 15.4 mm in length, 14.3 mm in height, and 12.1 mm in thickness. Panamá, in association with the pearl oyster “*Avicula margaritifera*” [= *Pinctada mazatlanica* (Hanley, 1856)]. *P. sinuosa*—Probably lost. The original specimen measured 19 mm in length, 15 mm in height, and 14 mm in thickness (Figure 44). Either Baja California or Peru. *P. bulbosa*—MCZ 169065, holotype, paired valves; length, 27.8 mm; height, 22.2 mm, thickness, 17.4 mm (Figure 45). Guaymas, Sonora, Mexico (27.9°N); T. P. Green. *P. anchoreta*—BM(NH) 1995222/1, **lectotype here designated**, paired valves; length, 12.4 mm; height, 10.8 mm; thickness 8.2 mm (Figure 46). BM(NH) 1995222/2-5, paralectotypes, one pair of 20 mm in length, and three valves, 8.8 mm, 7.0 mm, and 3.6 mm in length. Archipelago de las Perlas, Panamá (approximately 8.4°N). The lectotype selected is the specimen closest to de Folin’s figures 1 and 2 and is reasonably close to his stated measurements. *P. venusta*—BM(NH) 1995223/1, **lectotype here designated**, left valve; length, 16.3 mm; height, 15.2 mm; thickness, 4.8 mm (Figure 47). BM(NH) 1995223/2-3, paralectotypes, one pair of 11.2 mm and a left valve of 15.6 mm in length. Archipelago de las Perlas, Panamá (approximately 8.4°N). Because none of the specimens is a close match for de Folin’s figure or measurements, the largest specimen was selected as lectotype. *P. buwaldi*—UCMP 11657, holotype, left valve [mis-labeled as right on plate explanation]; length, 29.5 mm; height, 25.0 mm; thickness, 10.5 mm (Figure 48). Southeast of Walnut Creek, Contra Costa County, California (37.9°N); Upper San Pablo Group; Upper Miocene; UC Locality 1942 [not in locality list in Clark, 1915:505–512]. *P. riocanensis*—PRI 42067 [not examined], holotype, right valve; length, 21 mm; height, 17 mm; thickness, 8 mm. Río Cana, Caimito, Dominican Republic; Miocene.

Description: Shell ovate to ovate-trigonal; anterior end short, rounded; posterior end often produced, broadly to narrowly truncate; right valve sometimes overgrowing left valve especially posterodorsally. Shell inflated, moderately thick; beaks prominent. Without lunule or escutcheon. Sculpture of about 50 narrow, heavy radial ribs that are lowest and most dense anteriorly and heaviest and most widely spaced posteriorly, and fine commarginal threads. Ribs scalloping posterior margin. Pallial sinus of moderate depth, broad, rounded anteriorly, not confluent with pallial line; pallial line not bowed dorsally (Figure 68). Hinge teeth very robust, often becoming gerontic in adult; right valve with a produced anterior cardinal and an elongate, slightly bifid posterior cardinal; left valve with a very small anterior cardinal, which is obliterated in adult, a narrow, slightly bifid central cardinal, and an elongate posterior cardinal. As first pointed out by Fischer (1857:323), with a tendency for the teeth of one valve to

fuse into those of the opposite valve, and, when the valves are separated, to break off and either remain embedded there or to become detached and lost. Ligament short, on a heavy nymph, deeply sunken. White to tan externally; reddish purple to dark purple within, especially posteriorly. Length to 42.5 mm [Skoglund Collection; Guaymas, Sonora, Mexico].

Distribution and habitat: Laguna Ojo de Liebre [Scammons], Baja California Sur (27.8°N) [ANSP 263845; SDNHM 29611], into the Golfo de California as far north as Puerto Peñasco, Sonora (31.3°N) [SBMNH 32484 and other lots; CAS 102500], Mexico, to Panamá (approximately 9°N) [CAS 105778; USNM 22832, 105228, 131808, 620701], and south to Paita, Piura Province, Peru (5.1°S) [MNHN], and and Isla Baltra, Islas Galápagos, Ecuador (0.4°S) [MNHN]; in the western Atlantic from North Carolina [USNM 602882] to Rio Grande do Sol, Brazil (Narchi, 1974), from the intertidal zone to 55 m, in calcareous substrata, such as shells of *Spondylus*, colonial corals, and calcareous bryozoans, as well as in colonies of polychaetes made of agglutinated sand. I have examined 82 Recent eastern Pacific lots.

Recorded from the Pleistocene of Bahía Magdalena, Baja California Sur (Jordan, 1936:112); Isla Coronados (Durham, 1950:87, Emerson & Hertlein, 1964:349, 359) and Isla San Marcos (Durham, 1950:87), in the Golfo de California; and Ecuador (Hoffstetter, 1948:78; MNHN). Occurring in the Late Miocene of northern California (type of *P. buwaldi*), central California (Gale, in Preston, 1931:15; Woodring & Bramlette, 1951:66, 90; Adegok, 1969:149), the Dominican Republic (type of *P. riocanensis*), and Panama (Woodring, 1982:709–710). Also in the Pliocene and Pleistocene of Venezuela (Weisbord, 1964:331) and the Pliocene of Florida (Dall, 1900c:1059).

Discussion: Carpenter (1857c) was the first to conclude that *P. robusta* Philippi, 1849, was not only a homonym but also a synonym of *P. robusta* G. B. Sowerby I, 1834. Perhaps Philippi had in hand a specimen labeled *robusta* and thought it was only a manuscript name.

It has long been recognized that *C. robusta* is very similar to the Caribbean *C. typica* Jonas, 1844, type species of *Choristodon*. Carpenter (1857c:19) thought they might be synonyms, and Woodring (1982:709) synonymized them (unfortunately placing the senior *P. robusta* into the synonymy of the younger *P. typica*). Some possible morphological differences were noted and should be made the subject of statistical study of their significance: eastern Pacific material may attain a larger size, may be more produced and attenuate posteriorly, may have heavier ribs, and its internal color may tend to be purplish-brown, whereas Caribbean material seems to be greenish or brownish-green within. On the other hand, Weisbord’s (1964) contention that *P. robusta* has a shorter pallial sinus than Caribbean material does not seem to be true. However, in the course of the present study, insufficient

material from both coasts was available simultaneously to test these differences, and they have been left in synonymy pending future, more detailed study by other workers.

Although the type specimen of *P. sinuosa* Conrad is missing, its illustration in Conrad (1850) makes clear that it is a synonym, and the type specimen of *P. bulbosa* proves that it is as well. Both have relegated to synonymy since Carpenter (1857c).

The type specimens of *Petricola anchoreta* and *P. venusta*, both deFolin, 1867, thought to have been lost (Kisch, 1960), have been located and are both based on small specimens of this species.

Woodring (1982) placed *Petricola (Rupellaria) riocanensis* Maury, 1917, from the Miocene of Dominican Republic, into the synonymy of *P. typica*, and also reported the species from the Miocene of Panamá. Examination of the type specimen of *P. buwaldi*, as well as the specimen cited by Adegoke (1969), demonstrates that this material is within the range of variability of the Recent species. A detailed study of Recent material from both coasts should take this sparse fossil material into account as well.

Records of this species from South Africa, both as *P. robusta* and as *P. typica* (for example, G. B. Sowerby III, 1890:157, 1892:60, 61, 1897:33; Smith, 1906:65; Turton, 1932:246), were based on specimens *Petricola bicolor* G. B. Sowerby II, 1854b:776, pl. 166, fig. 22 (Barnard, 1964:513). This species has a much thinner shell, finer sculpture, and a less robust hinge.

Fischer (1857) noted that *Choristodon robustum* has elongate siphons, a very small foot, very unequal ctenidia, and very small labial palps. Narchi (1974) described the functional morphology of *Choristodon robusta* [as "*Petricola (Rupellaria) typica*"]. Its burrows in calcareous substrata are shallow, oval, and presumably enlarged by mechanical rasping. The siphons are short, subequal, and fused for half their length. The inhalent siphon is fringed by large pinnate tentacles of two sizes plus two ranks of simple tentacles. The exhalent siphon has smaller, less complex tentacles and a terminal valvular membrane. The ctenidia have 14–18 shallow plicae. The outer demibranch is only about half the size of the inner. The labial palps are small and triangular. The foot is small.

Genus *Petricolaria* Stoliczka, 1870

Petricolaria Stoliczka, 1870:139–140 [Type species: *Petricola pholadiformis* Lamarck, 1818:505; subsequent designation of Stoliczka, 1871:xvii]

Stoliczka's text included two species within his new genus and no type designation, the later-published table at the front of his book, which is headed "Synoptical list of the families and genera noticed in the present volume, together with the respective type-species," constitutes a subsequent designation.

Members of this genus are elongate, thin shelled, with strong, scaly radial ribs on the anterior end and radial threads posteriorly. The hinge is thin and delicate.

Petricolaria cognata (C. B. Adams, 1852)

(Figures 49, 50, 69)

- Petricola cognata* C. B. Adams, 1852. C. B. Adams, 1852a: 510–511, 546–547 [1852b:286–287, 322–323]; Carpenter, 1857b:279, 299, 363; Carpenter, 1864a:29 [1872:203] [as a possible synonym of *P. pholadiformis*]; Carpenter, 1864b:552 [1872:38] [as a possible synonym of *P. pholadiformis*]; Tryon, 1872:256; Arnold, 1903:156; Lamy, 1923b:347 [as a synonym of *P. pholadiformis*]; Grant & Gale, 1931:356 [as a synonym of *P. pholadiformis*]; Pilsbry & Lowe, 1932:99, pl. 13, figs. 10, 11; Turner, 1956:38, 130, pl. 19, figs. 3, 4; Soot-Ryen, 1957:9; Keen, 1958:152, 153, fig. 346; Olsson, 1961:316, pl. 54, figs. 5, 5a; Keen, 1971:197, 198, fig. 478.
- Petricola gracilis parallela* Pilsbry & Lowe, 1932. Pilsbry & Lowe, 1932:99–100, pl. 13, figs. 4, 5, 5a, 6; [the following five references as *Petricola parallela*]; Hertlein & Strong, 1948:195; Keen, 1958:152, 153, fig. 348; Olsson, 1961:315–316, pl. 54, figs. 3–3b; E. J. Moore, 1968:66–67, pl. 31, fig. e; Keen, 1971:198, 199, fig. 480; Bernard, 1983:57 [as a synonym of *P. gracilis*]; Avilés & Sánchez, 1983:102, fig. 2.
- Petricola gracilis* Deshayes, *auctt.*, non Deshayes, 1853. Bernard, 1983:57 [*Petricola (Petricolaria)*]. [non *Petricola gracilis* Deshayes, 1853]. Deshayes, 1853:214; Deshayes, 1854:pl. 18, fig. 6; G. B. Sowerby II, 1854b:772, pl. 164, fig. 12.
- P. pholadiformis* Lamarck, *auctt.* non Lamarck, 1818. Carpenter, 1864b:537 [1872:23]; Grant & Gale, 1931:356 [in part].

Type material and localities: *P. cognata*—MCZ 186308, holotype, paired valves, the right substantially broken, the left chipped posteriorly; length, 22.3 mm; height, 10.2 mm; thickness, 5.4 mm (Figure 49). Panamá, presumably near Ciudad de Panamá (9.0°N); C. B. Adams, 27 November 1850–2 January 1851. *P. gracilis parallela*—ANSP 155591, holotype, formerly filed in SDNHM 50799 as "paratype"; length, 28.7 mm; height, 10.2 mm; thickness, 9.6 mm (Figure 50); ANSP 398891, paratypes, three left valves measuring 43.5 mm, 31.6 mm, and 26.9 mm in length; the first was illustrated in Pilsbry & Lowe (1932:pl. 13, fig. 6). Corinto, Chinandega Province, Nicaragua (12.5°N); H. N. Lowe.

Description: Shell elongate to very elongate, cylindrical; anterior end very short, somewhat pointed; posterior end elongate, rounded to truncate, somewhat laterally flattened in large specimens. Shell inflated, thin; beaks small. With a lunule demarcated by anteriormost radial rib and lacking prominent sculpture; without escutcheon. Anterior end with about eight heavy, well-spaced radial ribs; ribs with nodes dorsally and produced, ventrally curved scales toward anteroventral margin; central and posterior slopes with approximately 20 thin radial threads. Hinge



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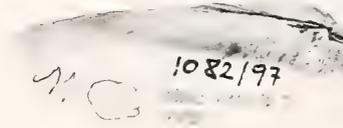


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TYPE

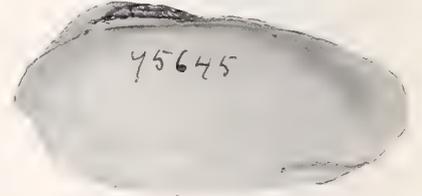
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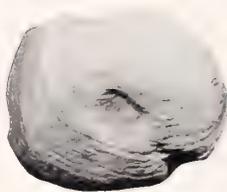


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teeth small; right valve with a small anterior cardinal and a bifid posterior cardinal; left valve with a small anterior cardinal, a bifid central cardinal, and an elongate posterior cardinal. Pallial sinus deep, narrow, pointed anteriorly, paralleling but completely detached from pallial line; pallial line not bowed dorsally (Figure 69). Ligament relatively short, not sunken; nymph thin. External and internal color white, stained with brown posteriorly. Length to 80 mm [CAS 105784; Laguna Ojo de Liebre, Baja California Sur].

Distribution and habitat: Isla Cedros, Baja California [Norte] (28.4°N) [LACM 72-113], and Laguna Ojo de Liebre [Scammon], Baja California Sur (27.9°N) [CAS 105784; LACM 72-1.1], to and throughout the Golfo de California to Puerto Peñasco, Sonora (31.3°N) [SBMNH 124920], Mexico, and south to Isla Puná, Golfo de Guayaquil, Guayas Province, Ecuador (2.8°S) [CAS 105785; MNHN], from the intertidal zone to 15 m, in soft substrata, such as clay banks. I have examined 91 lots. Dall (1900b:122) cited San Diego, California, as a locality, but no specimens have been located from there.

This species is also present in the Pleistocene of southern California (San Pedro—Arnold, 1903:156; Valentine & Meade, 1961:8, 24; Huntington Beach—Valentine (1959:53, 54); Newport Bay—Bruff, 1946:232; Kanakoff & Emerson, 1959:24, 35; Valentine & Meade, 1961:24, 28; and San Diego—Dall, 1878a:11; 1878b:28; Kanakoff, in Emerson & Chace, 1959:338, 341; E. J. Moore, 1968:66).

Discussion: The holotype of *P. cognata* is a short, thick but not highly unusual specimen (for example, USNM 153348, also from Panamá). Insufficient material was available in 1932 when Pilsbry & Lowe described *P. gracilis parallela*.

Pilsbry & Lowe (1932) appropriately recognized the similarity of their new species to *P. gracilis* Deshayes, 1853. Described from an unknown locality, *P. gracilis* has subsequently been recognized from the Indian Ocean and the Red Sea (Oliver, 1992: 194, pl. 44, fig. 7). The syntypes of this species are extant [BM(NH) 196953]. It differs in having (1) a less produced anterior end, (2) denser sculpture on the anterior end, (3) sharper, narrower scales on the radial ribs near its anteroventral margin, and (4) a less demarcated lunule.

Two other tropical members of this genus have been

described, but their relationships to *P. gracilis* have yet to be resolved. The first is *Petricolaria serrata* (Deshayes, 1853), described in error from New Zealand (Deshayes, 1853:212, 1854:pl. 18, fig. 11), where petricolids are as yet unknown (Powell, 1979). It matches material I have seen from West Africa that has a very rugose anterior end, with very broad scales, and that lacks a lunule. However, it may be a synonym of *P. gracilis*. The second is *P. stellae* Narchi, 1975, occurring from Brazil to Uruguay; its anterior end is, in general, less produced and more densely sculptured than *P. cognata*. Its scales are also broader than those of *P. cognata*, and there is no demarcated lunule, with heavy commarginal ribs running onto the anterodorsal slope. It also has a poorly developed anterior cardinal in the left valve; there may also be some other subtle differences in dentition among these taxa, as discussed by Narchi (1975); the source of his specimens of "*P. pholadiformis gracilis*" is not made clear. In any event, these tropical species account for all records of the Northern Hemisphere *Petricolaria pholadiformis* in the Southern Hemisphere.

For comparisons with *P. pholadiformis*, see under next species.

Narchi (1975) described the anatomy of *Petricolaria stellae*, which forms burrows in polychaete worm colonies, a fairly hard substratum, by valve abrasion. The siphons are fused for half of their length and can be extended to a distance equal to the shell length. The inhalent siphon has four ranks of tentacles, the inner dentritic, the second and third pinnate, and the outermost simple. The exhalent siphon has three ranks of tentacles, the innermost pinnate, the outer two simple, and an rudimentary terminal valvular membrane. The outer demibranch is smaller than the inner, does not extend as far forward, and has a dorsal supra-axial extension. Each demibranch has 10–13 folds, with an average of 12 filaments per fold. The labial palps are small and triangular, and the coil and uncoil actively.

Petricolaria pholadiformis (Lamarck, 1818)

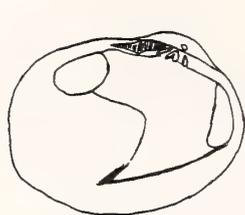
(Figures 51–53, 70)

Petricola pholadiformis Lamarck, 1818. Lamarck, 1818: 505; G. B. Sowerby I, 1823:figs. 1, 2; Conrad, 1832: 37, pl. 7, fig. 3; Say, 1834:[2 pp.], pl. 60, fig. 1; De Kay, 1844:228, pl. 28, fig. 282; Deshayes, 1853:211–

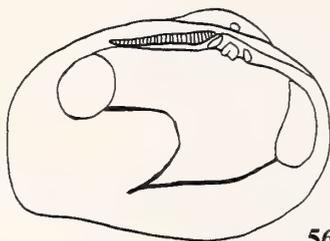
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Explanation of Figures 49 to 54

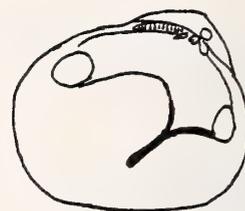
Figures 49, 50. *Petricolaria cognata* (C. B. Adams, 1852). Figure 49. *Petricola cognata*; holotype; MCZ 186308; length, 22.3 mm. Figure 50. *P. gracilis parallela* Pilsbry & Lowe, 1932; holotype; ANSP 155591; length, 28.7 mm. Figures 51–53. *Petricolaria pholadiformis* Lamarck, 1818. Figure 51. *Petricola pholadiformis*; holotype; MHNG; length, 46.0 mm. Figure 52. *Gastranella tumida* Verrill, 1872; lectotype; PMYU 8845a; length, 2.2 mm. Figure 53. *Petricolaria pholadiformis lata* Dall, 1925; lectotype; USNM 95645; length, 53.4 mm. Figure 54. *Thracia curta* Conrad, 1837. *Ungulina luticola* Valenciennes, 1846; lectotype; MNHN; length, 10.4 mm.



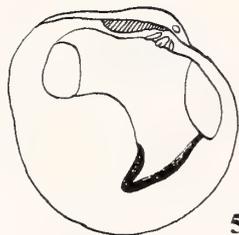
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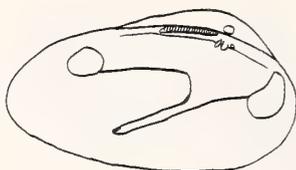
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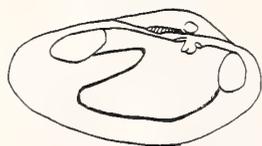
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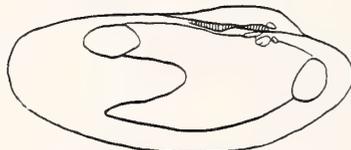
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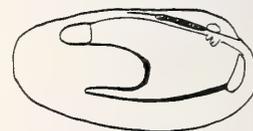
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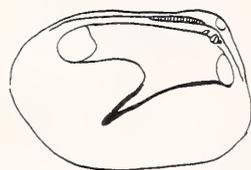
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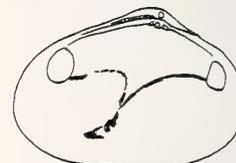
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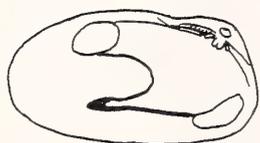
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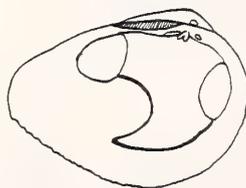
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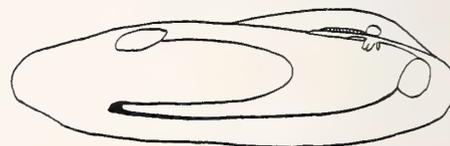
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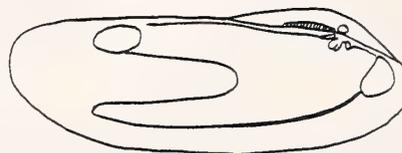
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- 212; G. B. Sowerby II, 1854b:771, pl. 166, fig. 1; Tuomey & Holmes, 1856:87–88, pl. 21, fig. 5; Gould, 1870:90–92, figs. 398, 399; Tryon, 1872:257; G. B. Sowerby II, 1874a:pl. 1, fig. 7; Dall, 1889:58–59, pl. 59, fig. 15, pl. 64, fig. 140a; Dall, 1900c:1061; Lamy, 1921:435–436; Lamy, 1923b:342–344; Grant & Gale, 1931:356 [in part]; Jacobson, 1943:142; Burch, 1944:18; Hanna, 1966:60, fig. 69; Bernard, 1983:57, 70 [*Petricola* (*Petricolaria*)]; Campbell, 1993:46, pl. 20, fig. 181 [pp. 212–213]; Poppe & Goto, 1993:127, pl. 23, fig. 6.
- Petricola fornicata* Say, 1822. Say, 1822:319–320; Conrad, 1832:37 [as a synonym of *P. pholadiformis*]; Deshayes, 1853:212; Tryon, 1872:257 [as a synonym of *P. pholadiformis*].
- Petricola flagellata* Say, 1834. Say, 1834:[1 p.] [in synonymy of *P. dactylus* G. B. Sowerby I, of Say].
- Petricola carolinensis* Conrad, 1863. Conrad, 1863:576; Dall, 1900c:1060; Campbell, 1993:46 [as a synonym of *P. pholadiformis*].
- Gastranella tumida* Verrill, 1872. Verrill, 1872:211, 286, pl. 6, figs. 3, 3a; Verrill, 1873:678–679, pl. 26, fig. 190; Verrill, 1882:568; Dall, 1900c:1061 [as a synonym of *P. pholadiformis*]; R. I. Johnson, 1989:71.
- Petricolaria pholadiformis lata* Dall, 1925. Dall, 1925:90.
- Petricola rogersi* McGavock, 1944. McGavock, 1944:2; Campbell, 1993:46 [as a synonym of *P. pholadiformis*].
- Petricola dactylus* G. B. Sowerby I, *acutt*, non G. B. Sowerby I, 1823. Say, 1834:[1 p.], pl. 60, fig. 2; De Kay, 1844:228–229, pl. 28, fig. 283; Gould, 1870:92–93; Dall, 1889:58 [as a variety of *P. pholadiformis*]; Dall, 1900c:1061 [as a separable species]; C. W. Johnson, 1914:95; Lamy, 1923b:345–346 [in part].
- [non *Petricola dactylus* G. B. Sowerby I, 1823:*Petricola* sp. 3; see under this species above]

Type material and localities: *P. pholadiformis*—MHNG 1082/97, holotype, paired valves; length, 46.0 mm; height, approx. 16 mm; thickness [measurement not obtained] (Figure 51). Original locality unknown; the type locality is here clarified to be Massachusetts, USA. *P.*

fornicata—Lost. The original dimensions were: height, 43 mm; width, 15 mm; thickness, 23 mm. [east coast] of North America. *P. carolinensis*—Possibly in AMNH (L. Campbell, in correspondence, 2 February 1996). Not listed in Moore (1962). Based on the material discussed and illustrated by Tuomey & Holmes (1856:87–88, pl. 21, fig. 5) as *P. pholadiformis*, from Pee Dee River [Raysor Marl] and Smith, Goose Creek [lower Waccamaw Formation], South Carolina; Pliocene. *G. tumida*—PMYU 8845a, **lectotype here designated**, a right valve (with broken hinge), glued in a mount, formerly part of a set of paired valves; the left valve has been lost; length, approx. 4 mm; height, approx. 2.2 mm; thickness could not be measured (Figure 52). PMYU 1845b, paralectotypes, two smaller, sealed pairs glued in the same mount. Long Island Sound near New Haven, New Haven County, Connecticut. Label adds: “off South End [Point], 4–6 fms. [7–11 m]; A. E. Verrill” (41°N). *P. pholadiformis lata*—USNM 95645, **lectotype here designated**, paired valves; length, 53.4 mm; height, 26.5 mm; thickness, 19.0 mm (Figure 53). The lectotype selected is the largest specimen in the lot. USNM 880151, paralectotypes, 3 pairs (48.8 mm, 45.1 mm, 36.0 mm in length), one left valve (52.6 mm in length). Quahog Bay, Cumberland County, Maine (43.8°N). *P. rogersi*—ANSP 16015, syntypes [not studied]. Yorktown, Virginia (37.2°N); “Yorktown formation; Pliocene,” but more likely late Pleistocene [L. Campbell, in correspondence, 2 February 1996].

Description: Shell elongate, cylindrical; anterior end very short, sharply rounded; posterior end elongate, broadly rounded. Shell inflated, thin; beaks small. Without lunule; anterodorsal slope with commarginal sculpture; without escutcheon. Anterior end with approximately eight well-spaced, scaly radial ribs; central and poste-

←

Explanation of Figures 55 to 70

- Figures 55–70. Diagrammatic sketches of the inside of left valves of the species discussed here.
- Figure 55. *Petricola* (*Petricola*) *botula*; based on Skoglund Collection; Tizate, Nayarit, Mexico; length, 15.0 mm.
- Figure 56. *P.* (*P.*) *carditoides*; CAS 102524; Monterey, California; length, 32.7 mm.
- Figure 57. *P.* (*P.*) *linguafelis*; LACM 70-9; Salinas, Guayas Province, Ecuador; length, 4.2 mm.
- Figure 58. *P.* (*P.*) *lucasana*; CAS 102518; Puerto Peñasco, Sonora, Mexico; length, 22.3 mm.
- Figure 59. *P.* (*Petricolirus*) *californiensis*; Socorro, Baja California [Norte], Mexico; length, 28.3 mm.
- Figure 60. *P.* (*P.*) *concinna*; LACM 71.50.1; Bahía Bartolomé, Isla Bartolomé, Islas Galápagos; length, 20.3 mm.
- Figure 61. *P.* (*P.*) *dactylus*; SBMNH 133419; Punta Arenas, Magallanes Province, Chile; length, 25.6 mm.
- Figure 62. *P.* (*P.*) *denticulata*; CAS 024296; Canoa, Manabi Province, Ecuador; length, 33.5 mm.
- Figure 63. *P.* (*P.*) *rugosa*; ANSP 323775; Lurin, Lima Province, Peru; length, 24.8 mm.
- Figure 64. *P. exarata*; CAS 102591; Altata, Sinaloa, Mexico; length, 13.5 mm.
- Figure 65. *P. hertzana*; CAS 106035; paratype.
- Figure 66. *P. olsoni*; ANSP 252061; Peninsula Paracas, Ica Province, Peru; composite of two specimens; lengths, 12.3 mm and 15.0 mm.
- Figure 67. *P. scotti*; holotype; length, 16.9 mm.
- Figure 68. *Choristodon robustum*; SBMNH 143212; Bahía San Carlos, Sonora, Mexico; length, 21.8 mm.
- Figure 69. *Petricolaria cognata*; SBMNH 143213; Cochore, Guaymas, Sonora, Mexico; length, 43.7 mm.
- Figure 70. *P. pholadiformis*; CAS 102508; Woods Hole, Barnstable Co., Massachusetts; length, 39.8 mm.

rior slope with approximately 36 radial threads; dense commarginal threads also present. Pallial sinus of moderate depth, narrow, pointed anteriorly, paralleling but not confluent with pallial line; pallial line not bowed dorsally (Figure 70). Hinge teeth proportionately small, thin; right valve with a sharp, projecting anterior cardinal and a projecting, bifid posterior cardinal; left valve with a small anterior cardinal, a slightly bifid central cardinal, and a narrow posterior cardinal. Ligament shallow; nymph thin. Color white to light tan externally and internally. Length to 60 mm in eastern Pacific material [CAS 105782; Coyote Point, San Francisco Bay, California], to 71.3 mm in western Atlantic material [USNM 27089; Staten Island, New York].

Distribution and habitat: According to Carlton (1979: 514–517, 1992:495), this species was introduced, perhaps with *Crassostrea virginica* (Gmelin, 1791), in three localities in the northeastern Pacific: Willapa Bay, Pacific County, Washington (46.7°N), in about 1943 [LACM 17787, SBMNH 43253, CAS 105781, and many other lots; Kincaid, 1947]; San Francisco Bay, California (approx. 37.7°N), in about 1927 [SBMNH 17377, CAS 105782, and many other lots]; Upper Newport Bay, California (33.6°N), in about 1972 (V. L. Human, in Carlton, 1979:515), but not now surviving there (R. Seapy, e-mail, 28 January 1996). A lot in the CAS labeled Monterey, California [CAS 105783], is thought to represent a labeling error (Carlton, 1979:516). It does not seem to have spread beyond Willapa and San Francisco bays, where it occurs from the intertidal zone to 10 m, burrowing in clay, mud or other soft substrata. It is not common and populations are very patchy (J. T. Carlton, e-mail, 16 April 1996; A. Cohen, e-mail, 16 April 1996). I have examined 32 eastern Pacific lots.

In its native habitat in the western Atlantic, it occurs from Prince Edward Island, Canada [USNM 27105], to the Gulf of Mexico (R. T. Abbott & Morris, 1995:74). It was also introduced into the eastern Atlantic in 1890, and it now occurs from Norway to the Black Sea (Tebble, 1966:126). There are several papers that track the expansion of this species in the eastern Atlantic: Cooper (1896), Boettger (1907a, b), Schouteden (1907), Sikes (1910), Grahle (1932), Schlesch (1932), Rustad (1955). Records from west Africa and the southern Caribbean are based on other taxa (see Discussion under the previous species).

Discussion: Lamarck (1818) described *Petricola pholadiformis* from an unknown locality. Four years later, Say (1822) redescribed this species as *P. fornicata* from the western Atlantic. Conrad (1832) was the first to recognize that they were the same thing. Two years later, Conrad (1834) also identified some specimens of this species as *P. dactylus*, but eventually Dall (1925) was able to conclude that the name of this South American species had been misapplied, and he proposed the name *P. pholadiformis lata* for such specimens.

Gastranella tumida Verrill, 1872, was based on juvenile specimens, as first deduced by Dall (1900c:1061).

Campbell (1993) synonymized the eastern North American Pliocene *P. carolinensis* Conrad, 1863, and (probably) Pleistocene *P. rogersi* McGavock, 1944, with this species.

Petricolaria pholadiformis differs from *P. cognata* in having a broader, less produced posterior end; flat rather than curved scales on its radial ribs; heavier commarginal sculpture; and a narrower, more pointed pallial sinus. It differs from *Petricola dactylus* in being more elongate, thinner, having scales on its radial ribs, having more delicate hinge teeth, and in having a longer, narrower pallial sinus.

There are many accounts on the anatomy and biology of this species. The following are the most important of these: *Anatomy & Morphology*—Russell, in Gould (1841: 64–65), Perkins (1869:149), Gould (1870:92), Rice (1897:36, 66–67), Morse (1919:179–180), White (1942: 73), Purchon (1955), Taylor et al. (1973:275, table 15); *Reproduction & Development*—Coe (1943:182–183), Sullivan (1948:22–23, pl. 13), Loosanoff & Davis (1963: 115–117), Brousseau (1981); *Ecology*—Connell (1955), Burton (1958); *Burrowing*—Duvall (1963), Ansell & Nair (1969:862–863), Ansell (1970).

Excluded Taxa

Petricola amygdalina G. B. Sowerby I, 1834:47, was described without illustration from the Islas Galápagos, Ecuador. It was said to have been found in pterioid valves at 3–6 fms. [6–11 m]. By 1854, G. B. Sowerby II (1854b: 777) could not identify it, and no type material has been located at BM(NH). The original specimen, which measured 33 mm in length, 20 mm in height, and 12.7 mm in thickness, was described as being thin, subhyaline, yellowish, and with commarginal lamellae. Both Pilsbry & Vanatta (1902:551) and Bernard (1983:57) revived the Galápagos record of this species, the latter allocating it the subgenus *Petricolaria*. No museum specimens that might have been the basis of these records has come to light (Yves Finet, in correspondence, 23 January 1996), although the Galápagos specimen of the very different looking *P. concinna* [LACM 71–50.1] may account for Bernard's report. This species is best regarded as a *nomen dubium* and/or extralimital.

Choristodon cancellarus Verrill, 1885:435–436, described on the basis of a single, eroded left valve (USNM 44839) measuring 7.7 mm in length dredged off Chesapeake Bay in 70 fms. [128 m], has never been recollected. First figured by Verrill & Bush (1898:778, 896, pl. 96, fig. 2), it is probably not a petricolid because the sculpture is very even and the hinge has a broad dorsal area that lacks teeth (Coan, 1996:122, fig. 20). It may be from an offshore fossil deposit.

Petricola cordieri Deshayes, 1839:358, 1840:pl. 18, is

a long-recognized synonym of *Irusella lamellifera* (Conrad, 1837) (for example, Lamy, 1923b:322).

Petricola discors G. B. Sowerby I, 1834:46, was described from Lambayque, Lambayque Province, Perú (6.7°S), was said to have been obtained from hard clay. No illustration was ever published, and type material has not been located in BM(NH). The original specimen measured 20.3 mm in length, 14.0 mm in height, and 7.6 mm in thickness. An argument might be advanced that this is what is here known as *P. olssoni*: the locality, shape, brownish color, and the presence of only radial sculpture fit this species. On the other hand, the described smooth posterior end and clay habitat do not. Little point would be served by salvaging this taxon, for which a neotype would be required to achieve stability, and it is best regarded as a *nomen dubium*.

Petricola elliptica G. B. Sowerby I, 1834:46, is the original combination for the venerid *Irus* (*Paphonotia*) *elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Venerupis foliacea Deshayes, 1853:192–193, is a synonym of *Irus* (*Paphonotia*) *elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182). This species was listed as a *Rupellaria* by Carpenter (1857b:299, 1864b:668 [1872:154]) and by Tryon (1884:174, 435).

Venus lamellifera Conrad, 1837:251, is the original combination for the venerid *Irusella lamellifera* (Conrad, 1837). It was listed as a *Rupellaria* by Carpenter (1857a:214, 1857b:299, 349, 1864b:536, 539, 540, 641 [1872:22, 25, 26, 127]) and also as a *Petricola* (Carpenter, 1857b:229).

Ungulina luticola Valenciennes, 1846:pl. 24, figs. 5, 5a, b, was described on the basis of four specimens that are now conserved in the MNHN. It was been regarded as a synonym of *Petricola carditoides* (Conrad, 1837) (Dall, 1900c:1155; Bernard, 1983:57). However, the originally figured specimen, here designated **lectotype** (Figure 54), is instead paired valves of *Thracia curta* Conrad, 1837; it measures 10.4 mm in length, 9.1 mm in height, and 8.4 mm in thickness (this species was discussed by Coan, 1990:33–35). The paralectotypes are: 16.9 mm in length [*Petricola carditoides*], 12.8 mm in length [*Thracia curta*], and 7.0 mm in length [*Sphenia luticola* (Valenciennes, 1846), a different species described in the same work under the generic name *Corbula*].

Petricola oblonga G. B. Sowerby I, 1834:46, is a synonym of *Irus* (*Paphonotia*) *elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Venerupis paupercula Deshayes, 1854:5, described in error from New Zealand, has been synonymized with *Irus* (*Paphonotia*) *elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182). It was listed by Carpenter (1857b:299) as a *Rupellaria*.

Petricola solida G. B. Sowerby I, 1834:46, is a synonym of *Irus* (*Paphonotia*) *elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Petricola solidula G. B. Sowerby II, 1854a:770, is a

synonym of *Irus* (*Paphonotia*) *elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Petricola subglobosa G. B. Sowerby I, 1823:fig. 6, was described without a known locality, with only an internal view of the valves provided. No original material is present in BM(NH). Carpenter (1864b:559 [1872:45]) associated the species with some of the synonyms of *P. carditoides*, perhaps because the ribs were described by Sowerby as being “decussatis.” It is now best regarded as a *nomen dubium*.

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Calyptogena packardana, A New Species of Vesicomimid Bivalve from Cold Seeps in Monterey Bay, California

by

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Abstract. *Calyptogena packardana*, a new bivalve species of the family Vesicomidae, is described from specimens collected from sulfide seeps near 600 m depth in the Monterey Submarine Canyon, Monterey Bay, California. Shell characteristics of *C. packardana* differ considerably from those of sympatric confamilial species (*Calyptogena pacifica*, *C. kilmeri*, *C. gigas*, and *Vesicomya stearnsii*) found at cold seeps in Monterey Bay and elsewhere in the northeastern Pacific. They are most similar to those of two fossil species (*C. gibbera*, *C. lasia*), from Pleistocene and Pliocene deposits in southern California. The soft anatomy, including mantle and siphons, ctenidia, and foot, are discussed. Ratios of stable carbon isotopes near -36‰ PDB units and presence of endosymbiotic bacteria in ctenidial tissues indicate that chemosynthesis, via thiotrophic chemoautotrophic endosymbiotic bacteria, is the primary nutritional source for *C. packardana*, as reported for other vesicomids.

INTRODUCTION

The family Vesicomidae was erected by Dall & Simpson (1901) to include a number of large, thick-shelled species with heterodont dentition and dehiscent periostraca. Fossil representatives of the Vesicomidae are known from as early as the Eocene from the Pacific Northwest (Goedert & Squires, 1990, 1993), and span the Paleogene and Neogene from collections at several locations (Kanno et al., 1989; Niitsuma et al., 1989; Goedert & Squires, 1993). While the taxonomic relationships among species within the family are not completely understood (Kojima et al., 1995; Vrijenhoek et al., 1995), extant species are presently assigned to five genera (Krylova & Moskalev, 1996; Goto & Poppe, 1996). Most species belong to the genera *Vesicomya* Smith, 1885 and *Calyptogena* Dall, 1891. Vesicomimid bivalves have been collected principally or perhaps exclusively (exact location of dredge samples are not known) in sulfide-rich habitats (e.g., hydrothermal vents, cold seeps, whale falls) from 400 m to greater than 3000 m depth.

Prior to the discovery of hydrothermal vent and cold seep communities, vesicomids were regarded as noteworthy for their large size and robust shells, collected from deep sea habitats where the bivalve fauna typically included small, thin-shelled species (Boss, 1970). Recent

studies have shown that all living species examined contain sulfur-oxidizing endosymbiotic bacteria from which much of their nutrition derives (Fiala-Médioni et al., 1994). Knowledge that vesicomimid nutrition is based largely or entirely on thioautotrophic production by endosymbiotic bacteria, thereby potentially increasing the energy available to sustain high rates of metabolism and growth compared to non-chemosynthetic deep sea species, resolves the paradox of differences between vesicomids and other deep sea bivalves.

Discoveries of new vesicomimid species have been frequent in the past 20 years, owing to investigations of seep and vent communities using submersibles and ROVs. The relatively recent discovery of many sulfide-rich environments inhabited by vesicomids partially explains the rarity of their collection and poor representation in museum collections. Historically, most collections were from bottom trawls, which are not deployed in areas of rough terrain where vesicomids often occur. Much new information concerning the diversity, biology, and ecology of vesicomids is arising from studies of seep and vent sites.

Several cold seep sites have been discovered recently in the Monterey Bay region from 600 m to 1000 m depth, in which the fauna is dominated by up to five species of vesicomimid clams (Barry et al., 1996). In this paper we

describe a new species of vesicomimid bivalve which inhabits two of these cold seep sites.

COLLECTION INFORMATION

Observations and collections were made at the "Mt. Crushmore" cold seep site (36°46.9'N, 122°2.6'W) in Monterey Canyon, Monterey Bay, California (Barry et al., 1996), during dives of the remotely operated vehicle (ROV) *Ventana*, operated by Monterey Bay Aquarium Research Institute. This site includes numerous small seeps distributed near 600 m depth along exposures of the Purisima Formation sandstones in Monterey Canyon. Clusters of vesicomimids are common at these seeps. Following close examination of 210 living and dead unidentified specimens of vesicomimids collected from 1992 to 1994, coupled with review of the taxonomic literature concerning vesicomimids, comparisons with specimens housed at the United States National Museum of Natural History (USNM), the Museum of Comparative Zoology at Harvard University (MCZ), Los Angeles County Museum of Natural History (LACM), and the Santa Barbara Museum of Natural History (SBMNH), and consultations with experts on vesicomimid taxonomy, we concluded that these specimens differed significantly from any described vesicomimid species. Although the taxonomic affinities within the family Vesicomimididae remain unresolved, the unidentified specimens were most similar morphologically (i.e., periostracum, dentition, and other characters) to other species assigned to the genus *Calyptogena*. In addition, unpublished genetic analyses also indicate high relatedness of the new species to other *Calyptogena* sp. (G. Matsumoto, personal communication). We therefore propose the following new species of *Calyptogena*.

SPECIES DESCRIPTION

Calyptogena packardana, Barry, Kochevar,
Baxter & Harrold, sp. nov.

(Figure 1)

Holotype: Length—77.8 mm, height—42.1 mm, width—27.8 mm, sex unknown (Figure 1), USNM, Department of Invertebrates, Mollusks, no. 880188.

Paratypes: Length—46.4 mm, height—22.7 mm, width—12.4 mm, sex, unknown, USNM, no. 880189; Length—52.7 mm, height—28.4 mm, width—15.4 mm,

sex, female, USNM, no. 880190; Length—72.1 mm, height—37.9 mm, width—23.3 mm, sex, male, USNM, no. 880191; Length—79.2 mm, height—40.5 mm, width—25.7 mm, sex, unknown, USNM, no. 880192; Length—69.3 mm, height—35.4 mm, width—19.9 mm, sex, female, USNM, no. 880193; Length—78.9 mm, height—43.5 mm, width—29.2 mm, sex, unknown, USNM, no. 887520.

Paratypes are accessioned at the LACM, SBMNH, and the MCZ at Harvard University.

Type-locality: "Mt. Crushmore" cold seep, (36°47.1'N, 122°2.6'W), Monterey Bay, California, in 635 m depth.

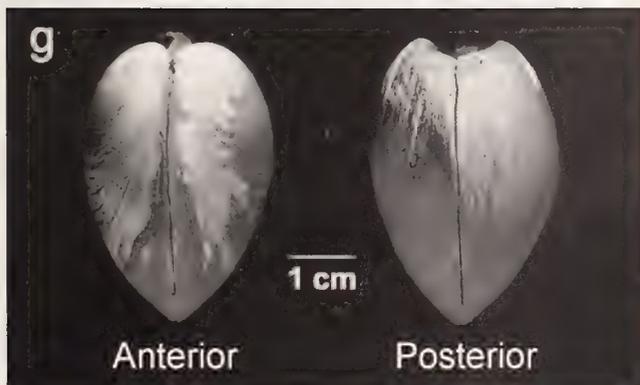
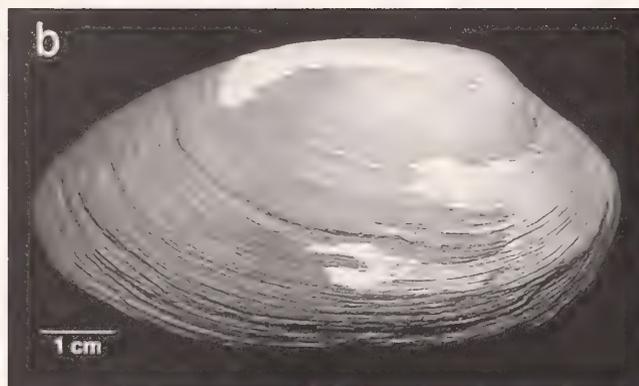
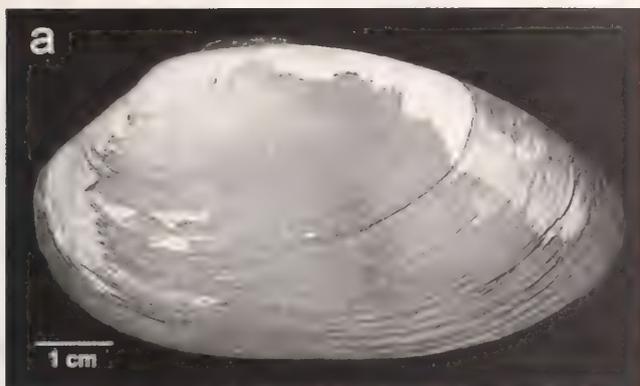
Description: Shell whitish, chalky, covered by yellowish brown periostracum. Juvenile color light brown, with intact, smooth periostracum. Large individuals with flaky dehiscent periostracum. Periostracum overlapping shell margin slightly to provide complete seal when shell valves close. Shell (Figure 1) to 87.2 mm long, 46.8 mm high, and 31.0 mm wide, subtrigonal, elongate, inequilateral, heavy and solid, slightly compressed. Small individuals have a more transparent and indehiscent periostracum, and a lower W/L ratio. Large individuals are more inflated and have a slightly greater height/length ratios than shorter, presumably younger individuals.

Valves strongly inequilateral, with slightly inflated and introrse umbo positioned far anterior (20–25% of total shell length [TL]) along shell length. Umbonal cavity moderately deep; beaks mildly inflated. Anterior margin short, rounded, with very slight or no gape; posterior margin pointed in largest specimens. Ventral margin generally convex, nearly flat medially. Anterodorsal margin short, slightly convex in small individuals, flat to slightly concave in large individuals. Lunule short, sublanceolate, deeply incised in large individuals. Posterodorsal margin elongate, convex. Escutcheon little developed in small specimens, becoming deeply incised, steeply walled in larger, presumably older specimens, extending from umbo to posterior end of shell (Figures 1, 2). Ligament opisthodontic, dark brown, lanceolate, inflated, deeply embedded, extending 38 to 45% of posterodorsal margin. Sculpture consisting of weak commarginal lirations, most crowded and conspicuous near anterior end and within escutcheon. Growth rings weakly evident; no obvious radial sculpture. Viewed ventrally, slight flexure evident along ventral margin, most notably near posterior end. From dorsal perspective, mild flexure along posterodorsal

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Figure 1

Shell characteristics of the holotype of *Calyptogena packardana* Barry, Kochevar, Baxter & Harrold, sp. nov. (USNM, no. 880188) a. Left valve, external view; b. Right valve, external view; c. Left valve, internal view; d. Right valve, internal view; e. Dorsal view of shell; f. Ventral view of shell; g. Anterior and posterior view of shell; h. View of hinge structure for left and right valves.



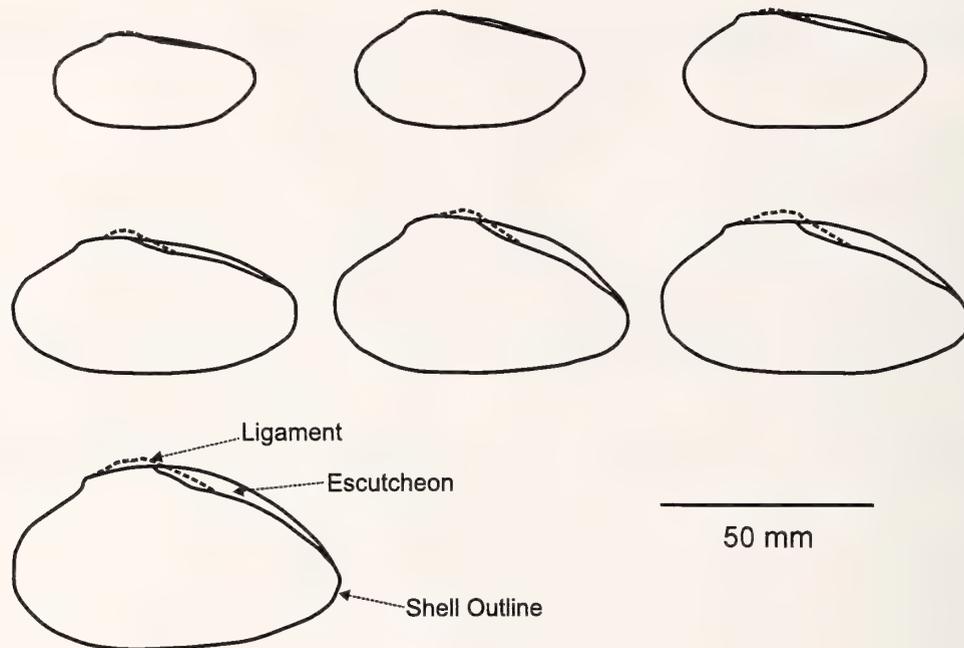


Figure 2

Size series of *Calyptogena packardana* Barry, Kochevar, Baxter & Harrold, sp. nov. showing allometric changes in the depth of the escutcheon.

shell margin apparent, as is slight overlap (~1-1.5 mm in 75 mm long specimen) of right valve over left valve near posterior third of escutcheon, particularly in larger specimens.

Right valve with three cardinal teeth radiating from the umbo (Figure 1). Anterior cardinal tooth thin, only mildly protuberant, with nearly parallel dorsal and ventral margins, pointed ventrally and merging with hinge plate. Medial tooth nearly parallel to and positioned ventrally to anterior tooth; strongly protuberant, blunt on medial face, but narrow and massive compared to anterior cardinal. Posterior cardinal massive, strongly protuberant, blunt, bifid, subtrigonal, subconvex along dorsal margin, mildly concave along anterior face. Anterior and posterior cardinals joined at beak. Three sockets are formed amongst the right cardinal teeth and posterior-dorsal margin, to accept cardinal teeth from the left valve. The central socket is deepest and pyramidal. Right posterior hinge plate massive, forming wide solid nymph subtending the ligament. Left valve (Figure 1) with three cardinal teeth forming two sockets to accept central and posterior cardinal teeth of the right valve. Anterior cardinal thin, pointed, ventral to and merging with hinge plate. Central tooth protuberant, massive, slightly bifid in most specimens, trigonal. Posterior cardinal protuberant, subconvex along dorsal margin, roughly parallel to dorsal shell margin. Anterior and posterior cardinal teeth joined at or slightly anterior to beak.

Internal surface of shell porcelaneous, white, without internal ribs. Anterior adductor muscle scar incised dorsally and posteriorly, subovate, slightly pointed dorsally (Figure 1). Posterior adductor muscle scar irregularly ovate. Pallial line weakly to moderately impressed, subarcuate anteriorly; sinuous and angular posteriorly, forming small pallial sinus. Anterior pedal retractor muscle scar deeply recessed, subtending anterior margin of hinge plate immediately posterior to dorsal end of adductor scar.

Soft anatomy: The anatomy of *C. packardana* is generally very similar to that described for *C. pacifica* and *C. kilmeri* by Bernard (1974), and *C. magnifica* by Boss & Turner (1980). The most conspicuous features of *C. packardana* are the greatly enlarged ctenidia, often yellow in color owing to their content of elemental sulfur; large and heavily vascularized foot; reduced digestive system; and presence of red, hemoglobin-rich blood, all of which relate to the life style of this group, which harbor chemoautotrophic bacteria.

Mantle and siphons: The mantle lobes are bilaterally symmetrical, and slightly thickened anteriorly. The mantle is attached to the shell ventrally by broad pallial muscles, and dorsally by smaller pallial muscles, except near the hinge plate, where pallial musculature is enlarged. The mantle cavity opens ventrally, leaving a pedal gape which extends from the ventral margin of the anterior

adductor muscle to the ventral anterior margin of the incurrent siphon. The inner mantle folds are fused posteriorly to form inhalant and exhalant siphons and continue fused dorsally between the adductor muscles. The mantle lobes of *C. packardana*, as in *C. kilmeri* and *C. pacifica*, are thickened along their ventral margin and hypertrophied along the posteroventral margin, but do not exhibit the greatly thickened anterior and posterior margins observed in *C. magnifica* (Boss & Turner, 1980).

The siphons are conical to cylindrical in shape and elliptical in cross section. The inhalant siphon is larger and more elliptical in cross section than the exhalant siphon, with two to three rows of papillae on its distal margin. The inner row includes approximately 35 short papillae. An outer row has about 35 long, similar sized, club-shaped papillae along its inner edge, and about 85 variably sized, club-shaped papillae along its outer edge. The base of the inhalant siphon includes internally a branched flaplike structure apparently acting as a filter for rejecting large particles. The exhalant siphon is smaller and more ovate in cross section than the inhalant siphon, and has a single row of approximately 60 papillae of variable size on its distal margin. Like *C. kilmeri* and *C. pacifica*, the base of the exhalant siphon of *C. packardana* also bears an inner collar of thin translucent epithelium, which acts as a one-way valve.

Ctenidia: The ctenidia are greatly enlarged, enveloping the body and extending dorsally into the umbonal cavity and ventrally greater than half the distance to the ventral shell margin. Ctenidia lie on either side of the body and have nearly equally sized inner and outer demibranchs, both with ascending and descending lamellae. The inner demibranchs are fused along their distal margins to the midline of the visceral mass and joined together posteriorly, thereby isolating the inhalant and exhalant pallial chambers. Ctenidia are sulfur-laden, varying in color among specimens from bright sulfur-colored to purplish red.

Foot and visceral mass: The foot is large, conical, pointed distally, highly muscular, and distensible, particularly in its ventral half. It is also highly vascularized, and in live specimens is a deep red color, owing to its hemoglobin content. Live animals have been observed to extend the foot through the pedal gape greater than 1 body length. Dorsally, the foot grades into the visceral mass, which includes a large gonad surrounded laterally and ventrally by the foot musculature, and dorsally by the stomach, digestive glands, intestinal tract, and heart. The stomach and intestine are greatly reduced, as are the labial palps, similar to that described for other vesicomyids by Bernard (1974) and Boss & Turner (1980).

Reproductive system: A fairly large gonad is embedded in the dorsal portion of the visceral mass, adjacent to and partially merging with the digestive glands. The species

is dioecious, with little difference in size among sexes (Figure 3) and no apparent sexual dimorphism of the shells.

Etymology: *Calyptogena packardana* is named in honor of David and Lucille Packard, the founders of the Monterey Bay Aquarium Research Institute.

DISCUSSION

Calyptogena packardana inhabits cold seeps in Monterey Bay, California, near 600 m depth. The clams house endosymbiotic thioautotrophic bacteria in their ctenidia (Kochevar & Barry, 1994). Sulfide levels at the center of these cold seeps are near 200 μM (Barry et al., 1997). Shell length reaches 87.2 mm in Monterey Bay, but the average size of 210 specimens examined was 63.5 mm (Figure 3). Shells of *C. packardana* have also been collected by dredge from 800 m in southern California (C. Fisher, personal communication). Inspection of approximately 35 shell valves collected by dredge near Point Conception, California (housed in the MCZ at Harvard University) showed their maximum length near 70 mm.

The most diagnostic shell characters of *Calyptogena packardana* are its moderate to large size and stout shell thickness, narrow width, long, deep escutcheon, and pointed posterior margin. The depth of the escutcheon and sharply pointed posterior are most evident in the largest specimens, while small individuals are characterized by a remarkably narrow width, and a smooth and almost pearly periostracum.

Comparison with Other Vesicomyids

Few extant sympatric species can be confused with *Calyptogena packardana*. *Calyptogena pacifica* Dall, 1891, inhabits the same cold seeps as *C. packardana*, but is considerably smaller in size (maximum length near 62.1 mm; Table 1), and has a more ovate outline. Recent data concerning *C. pacifica* indicate that shell morphology differs between the sexes (Barry, unpublished data); males of *C. pacifica*, have a slightly pointed posterior shell margin, and may therefore be confused with *C. packardana*, especially among smaller individuals. These species are easily differentiated, however, by the smoother periostracum and very narrow width/length ratio of *C. packardana* (~ 0.31) compared to *C. pacifica* (W/L ~ 0.38), and the greatly pronounced escutcheon, especially in large specimens, unlike that of *C. pacifica*. *Calyptogena pacifica* can also be distinguished by the presence of a long narrow posterior cardinal tooth on the hinge plate of the right valve subtending the length of the ligament, which is absent in *C. packardana*.

Calyptogena kilmeri Bernard, 1974, is also found amongst *C. packardana* (Barry et al., 1996). *Calyptogena kilmeri* has a generally smoother and transparent periostracum, a rounded shell margin both anteriorly and pos-

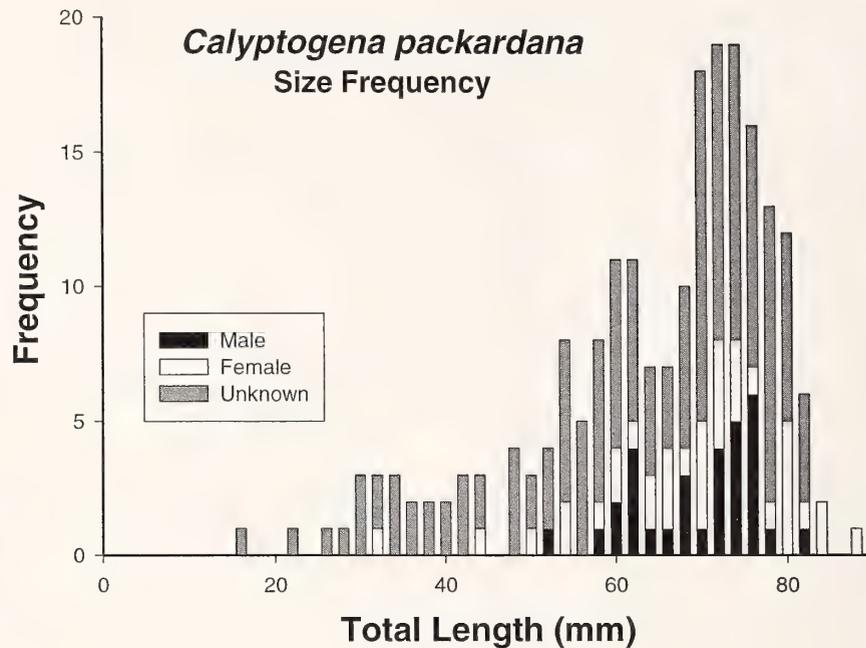


Figure 3

Size frequency of *Calypptogena packardana* Barry, Kochevar, Baxter & Harrold, sp. nov. (total length), collected from cold seeps in Monterey Bay, California.

teriorly, lacks a posterior cardinal tooth in the right valve, and is considerably greater in width/length ratio (Table 2); *C. kilmeri* also attains a much greater size (Table 1).

Calypptogena gigas Dall, 1896, is sympatric with and co-occurs at seeps with *C. packardana*, and attains a similar length in Monterey Bay (Barry unpublished data). *C. gigas* is considerably more similar to *C. kilmeri* than to *C. packardana*, however, and is easily distinguished by its greatly inflated shell compared to both *C. kilmeri* and *C. packardana* (Table 2).

Vesicomya stearnsii Dall, 1895, is a small vesicomimid found rarely at cold seeps in Monterey Bay (Barry et al., 1996), though it may be common elsewhere. Its shell morphology is quite dissimilar to *C. packardana*. *Vesi-*

comya stearnsii attains a total length of only ~33 mm, has a nearly transparent periostracum, and a much greater width/length ratio (0.52).

Ectenagena extenta Krylova & Moskalev, 1996, was described from Monterey Canyon and is found elsewhere in the North Pacific, but is difficult to confuse with *C. packardana*, owing to its great length (to 174 mm) and low width/length ratio (0.18). *Ectenagena extenta* also appears to inhabit deeper depths (> 3000 m) than *C. packardana*.

Shells of *C. packardana* have also been collected from dredge collections off southern California, where *Calypptogena elongata* Dall, 1916, has also been found. *Calypptogena elongata* is similar in height/length ratio (0.58) to *C. packardana* (0.53), but has a much thinner shell and lacks an escutcheon.

Two fossil species, *Calypptogena lasia* Woodring, 1938, from the Pliocene Towsley formation of Ventura County, California, and *Calypptogena gibbera* Crickmay, 1929, from the Timms Point Silt Pleistocene deposits of Los Angeles County, California (Squires, 1991), have shell morphologies similar to *C. packardana*. Although *C. lasia* and *C. gibbera* were recently synonymized (Squires, 1991), we treat them separately here, owing to the greater morphological variation between the three fossil specimens inspected for each of the former species, compared to intraspecific variation within *C. packardana*.

Calypptogena lasia is easily distinguished from *C. pack-*

Table 1

Maximum dimensions (total length, height, and width) for vesicomimid bivalves from collections at cold seeps in Monterey Bay, California. Dimensions in millimeters.

Species	Length	Height	Width
<i>Calypptogena gigas</i>	100.3	49.0	46.2
<i>Calypptogena kilmeri</i>	129.4	60.6	46.9
<i>Calypptogena pacifica</i>	62.1	36.6	26.6
<i>Calypptogena packardana</i> , sp. nov.	87.2	46.8	31.0
<i>Ectenagena extenta</i>	174.0	44.2	30.6
<i>Vesicomya stearnsii</i>	33.0	22.8	17.5

Table 2

Morphometric comparisons among vesicomymid species inhabiting the eastern Pacific, including species from Monterey Bay cold seeps, seep communities in Costa Rica (*C. angulata* Dall 1896), dredged *C. elongata* from near Pt. Conception, California, and fossil species (*C. gibbera*, *C. lasia*) deposits.

Species	Height/length (H/L)			Width/length (W/L)			Width/height (W/H)		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
<i>Calyptogena angulata</i>	0.61	0.02	2	0.38	0	2	0.62	0.02	2
<i>Calyptogena elongata</i>	0.45	0.02	12	0.26	0.08	12	0.58	0.19	12
<i>Calyptogena gibbera</i>	0.53	0.03	3	0.31	0.04	3	0.58	0.03	4
<i>Calyptogena gigas</i>	0.56	0.05	14	0.46	0.04	14	0.84	0.11	14
<i>Calyptogena kilmeri</i>	0.51	0.03	1805	0.33	0.03	1826	0.65	0.06	1825
<i>Calyptogena lasia</i>	0.54	0.05	3	0.37	0.05	3	0.67	0.08	4
<i>Calyptogena pacifica</i>	0.58	0.03	1275	0.38	0.02	1272	0.66	0.05	1272
<i>Calyptogena packardana</i> , sp. nov.	0.53	0.03	210	0.31	0.03	210	0.58	0.04	210
<i>Ectenagena extenta</i>	0.25	—	1	0.18	—	1	0.69	—	1
<i>Vesicomyma stearnsii</i>	0.70	0.04	69	0.52	0.05	68	0.74	0.07	68

ardana by its greater W/L ratio (0.37 vs. 0.31) and greater W/H ratio (0.67 vs. 0.58). Furthermore, *C. lasia* lacks a deep escutcheon and sharply pointed posterior outline, which are distinguishing characters of *C. packardana*.

Inspection of three specimens of *C. gibbera* show that this species is similar in general outline to *C. packardana*, with a pointed posterior margin and deep escutcheon, but these features are less pronounced than in *C. packardana*. The W/L, W/H, and H/L ratios for both species are very similar (Table 2); however, these measures do not reflect shell differences in margin shape, escutcheon, etc. The cardinal teeth of *C. packardana* differ greatly from *C. gibbera*. On the left valve, the anterior cardinal of *C. packardana* is not as heavy, being narrower and longer. The middle cardinal of *C. packardana* is triangular, with the anterior vertex displaced steeply anteriorly, such that the anterior margin of the tooth is nearly parallel to the anterior cardinal, forming a steep lanceolate recess between them. In contrast, the middle cardinal of the left valve of *C. gibbera* is strongly bifid, with a strong, posteriorly directed posterior ridge, which is entirely lacking in the modern species. Furthermore, the anterior ridge of the middle cardinal in *C. gibbera* is set at a much greater angle from the anterior cardinal, pointing almost directly away from the beak, thus forming a nearly ovate recess to accept the middle cardinal of the right valve. The posterior cardinal in the left valve of *C. packardana* is considerably shorter than in *C. gibbera*, and is set at 20 to 30 degrees to the dorsal margin, compared to nearly parallel in *C. gibbera*. In the right valve of *C. packardana*, the anterior cardinal is slender and set nearly parallel to the anterodorsal margin. This feature is not easily distinguished on *C. gibbera* fossils, due to poor preservation. Nevertheless, the recess formed by the anterior and middle cardinal teeth of the right valve is narrowly and sharply lanceolate in *C. packardana*, and wide and triangular in *C. gibbera*. The middle cardinal of *C. packardana* is

longer and less massive or bifid, than in *C. gibbera*. The posterior cardinal of the right valve in *C. packardana* is massive, slightly bifid, broadly trigonal, and set at nearly 45 degrees from the dorsal margin. In *C. gibbera*, this tooth is slightly bifid, but is set at an angle near 10 degrees from the dorsal surface (nearly parallel). No details of the pallial line or other interior shell characteristics are available from specimens of *C. gibbera*.

Natural History of the Vesicomymidae

Although numerous species of vesicomymids were described prior to the discovery of chemosynthetic communities at hydrothermal vents and cold seeps, little was known of the life style of most species of this group. Because most specimens have been collected from dredge samples, little information was available regarding characteristics of the environments inhabited by vesicomymids. Recent observations and collections using manned and unmanned submersibles have shown that nearly all species are associated with sulfide-rich environments at hydrothermal vents (e.g., *Calyptogena magnifica* Boss & Turner 1980), cold seeps (various species; Paull et al., 1984; Kennicutt et al., 1985; Laubier et al., 1986; Hashimoto et al., 1987; Embley et al., 1990; Barry et al., 1996), and whale carcasses on the sea floor (Bennett et al., 1994). Moreover, all living species of vesicomymids investigated to date have been shown to rely on endosymbiotic thioautotrophic bacteria harbored in gill tissues as their principal source of nutrition (Fiala-Médioni et al., 1994). Observations by Vetter (1985) and Kochevar & Barry (1994) suggest that variation in the color of gill tissues is due to their content of elemental sulfur, apparently related to the physiology of endobacterial symbionts. The frequency of yellowish gill coloration among specimens held in laboratory aquaria for weeks decreased, apparently related to utilization by endosym-

biotic bacteria of sulfur stored in the ctenidia. Bacteria in gill tissues of *C. packardana* have features characteristic of other thiotrophic bacteria studied by Kochevar & Barry (1994). Their sulfur-laden ctenidia and stable carbon isotopic ratios ($\delta^{13}\text{C}$) near -36‰ PDB units (expressed here as per mil [‰] values relative to Peedee belemnite) further suggest bacterial thioautotrophic production.

Evidence for the uniformity of thioautotrophic-based nutrition for vesicomyids largely explains the paradox of large size and robust shell morphology for a deep sea bivalve species. While much of the deep sea may be food limited, thus favoring reduced metabolism, small body size, and perhaps reduced shell calcification, chemosynthetic systems in the deep sea are comparatively food-rich, thus enabling the existence of large species with high metabolic needs. Although little information is available concerning rates of metabolism and growth for *C. packardana*, rapid growth and high nutritional requirements identified for chemosynthetic fauna (i.e., the vestimentiferan worm, *Riftia pachyptila*, 85 cm/y; Lutz et al., 1994) from hydrothermal vents at 2500 m along the East Pacific Rise, and for vesicomyids from Monterey Bay (*Calyptogena kilmeri*, 2 cm/y; Barry unpublished data), supports the notion that these sulfide-rich sites are truly deep sea oases. Similarly, vesicomyids appear to have been released from food limitation characteristic of much of the deep sea, owing to their chemosynthetic nutritional mode.

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Differences in Shell Morphology between the Sibling Species *Littorina scutulata* and *Littorina plena* (Gastropoda: Prosobranchia)

by

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Abstract. Three shell characters are described for the sibling species *Littorina scutulata* Gould, 1849, and *L. plena* Gould, 1849: (1) a thin, translucent band at the base of the shells, more frequently observed in *L. plena*; (2) a thin, well-defined ridge near the base of *L. plena* shells; (3) larger checkers on shells of *L. scutulata* than on *L. plena*. A fourth character was observed in the Pacific Northwest: a difference in the number of color bands in banded varieties of each species. On a banded form of *L. scutulata* there are two light bands on the body whorl, and on a banded variety of *L. plena* only observed north of California there are three light bands. Specimens collected along the California coast were examined for variation in shell morphology with geographic location and degree of wave exposure. Variation in shell morphology was primarily observed in relation to degree of wave exposure. Both species were smaller and had a larger shell aperture height relative to shell length where wave action was higher. The mean size of *L. plena* is almost always smaller than that of *L. scutulata* regardless of the amount of wave action. *Littorina plena* appears to be most common on the shores of large bays and where rivers and creeks enter the ocean. *Littorina scutulata* appears to be most common on the exposed outer coast.

INTRODUCTION

It has been established that the prosobranch gastropod *Littorina scutulata* Gould, 1849, a species common on rocks and pilings of exposed and sheltered shores of the west coast of North America, is actually a complex of two sibling species (Murray, 1979; Mastro, et al., 1982). These species are now recognized as *L. scutulata* (*sensu stricto*) and *L. plena* Gould, 1849. Among recent studies on the ecology of eastern Pacific littorinids (Mastro, 1985; Chow, 1989; Voltolina & Sacchi, 1990; Yamada, 1992; Boulding & Van Alstyne, 1993), few have distinguished between *L. scutulata* and *L. plena* (Mastro, 1985; Chow, 1989), and fewer have compared the two (Mastro, 1985). Part of the reason for the lack of work on the ecology of *L. scutulata* and *L. plena* may be that it is difficult to tell these species apart. Since the discovery of the *L. scutulata*-*L. plena* complex by Murray (1979), two books on intertidal invertebrates (Ricketts et al., 5th ed., 1985; Brandon & Rokop, 1985), a key to Pacific Northwest marine invertebrates (Kozloff, 1987), a review of the literature on intertidal ecology (Foster, et al., 1988),

and a study of northeastern Pacific littorinids (Yamada, 1992) have cited the work by Murray (1979) and Mastro et al. (1982), but have not described any new differences between the two species. Mastro (1985) and Chow (1989) relied primarily on the distinct differences between penis and egg capsule shapes to identify these species. In this paper I include shell characters for *L. scutulata* and *L. plena* not previously described, and provide observations on the distribution and abundance of each of these species.

METHODS

Shells of *L. scutulata* and *L. plena* from California, Oregon, and Washington, positively identified by penis and egg capsule morphology (Figure 1a, b), were provided by E. Mastro. These were examined for characters that could be used to help identify the species. Three characters were identified, and the frequency of each of these characters in 238 male *L. plena* and 142 male *L. scutulata* was recorded. The usefulness of these characters for iden-

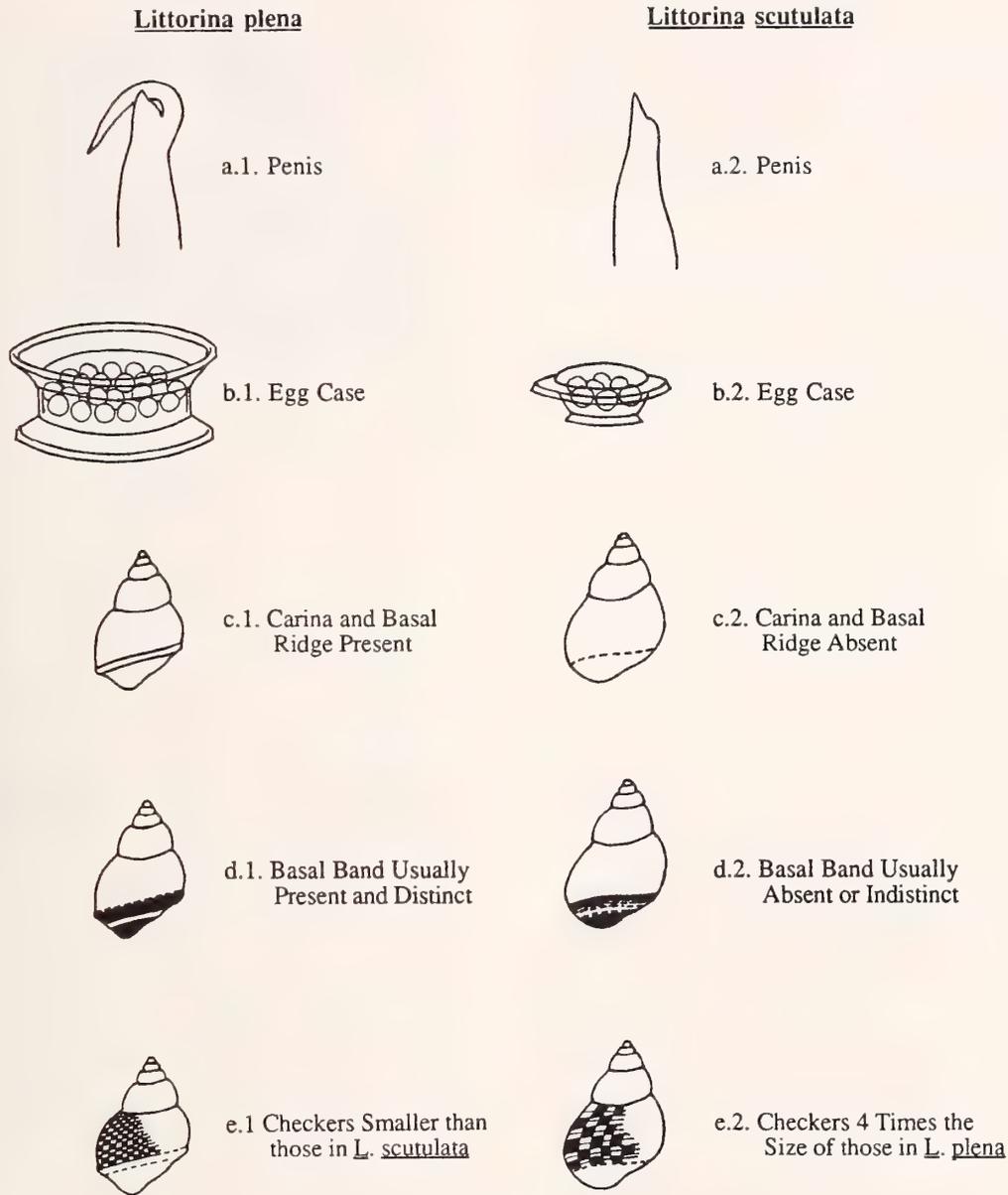


Figure 1

Reproductive (a & b) and shell (c-e) characters compared for *Littorina scutulata* and *Littorina plena*.

tification was then tested as follows: A sample of *L. scutulata* and *L. plena* was collected from the breakwater at Harbor Island, San Diego Bay, California. Before examining the snails for reproductive characters, they were identified and separated into species groups by shell characters alone. Next, males in each group were identified by penis morphology to test identification based on the shell characters. The mean shell length for populations of *L. scutulata* and *L. plena* was obtained from different locations along a wave exposure gradient from the protected south shore of San Diego Bay near Sweetwater

Marsh to the exposed shoreline at Pacific Beach. Samples of *L. scutulata* and *L. plena* were obtained primarily from 1 m² quadrats, except along the south shore of San Diego Bay where snail densities were less than or equal to 10/m², band transects parallel to the shore and about 2 m wide by 75 m long were sampled. Species were identified using shell characters. The length of each specimen was measured from the apex to the base of the shell with an ocular micrometer lens under a dissecting microscope. In addition to samples from San Diego County, small collections of *L. scutulata* and *L. plena*, also identified using

shell characters, were made from exposed rocky shores along the California coast and from the protected shores of Newport Bay, San Francisco Bay, and Humboldt Bay. Shells from the California coast, including San Diego, were examined for possible variation in shell morphology with different degrees of wave exposure and different geographic locations.

In a population of *L. scutulata* and *L. plena* found on cobblestones along the shore of the Puget Sound in Lincoln Park, West Seattle, banded varieties were frequent and appeared to be present in both species. A sample of these snails was collected and separated into species groups by shell characters alone. Then, males in each group were identified by penis morphology to verify identification based on shell characters.

RESULTS

On shells from California, Oregon, and Washington, three shell characters were apparent (Figure 1c–e). The first is a thin, light-colored band seen on the base of shells of both *L. scutulata* and *L. plena* (Figure 1d). This band is less distinct on some specimens than on others, or it may not be visible at all. Murray (1982) first observed this band in 15.9% of the *L. scutulata* shells and 84.3% of the *L. plena* shells he examined. The basal band is translucent to light, and by observing the band inside the shell aperture, illuminated by a small bright light from behind, I observed the band in 42.2% of the *L. scutulata* shells and 97.4% of the *L. plena* shells I observed (Figure 2).

On specimens of *L. plena*, I identified a second character: a thin, well-defined ridge (a raised spiral cord) near the base of most shells (Figure 1c). At the base of *L. plena* the whorl is usually angled in toward the central axis of the shell, forming a keel or carina. The basal ridge runs spirally along the periphery of the angle. In contrast, specimens of *L. scutulata* are generally rounded smoothly near the base of the shell. Some *L. scutulata* shells may be somewhat angled with the appearance of having a slight ridge, but this is never as sharply defined a ridge as is found in a typical specimen of *L. plena*. To highlight this feature, a light was shone on the specimen from directly above the apex. The resulting shadow was sharply defined by a line running along the ridge in *L. plena*. In *L. scutulata*, the resulting shadow faded indistinctly from light to dark.

The third character I identified was a difference between the species in the size of the markings on the shells. A checker pattern is commonly seen in both species, but the checkers in the pattern of a *L. plena* shell are usually one quarter the size of the checkers on a *L. scutulata* shell of the same size (Figure 1e). Although zig-zag and tentlike markings are occasionally observed on the shells of both species, most of the pattern variation is produced by a modification of the basic checker pattern.

For the sample of shells (238 male *L. plena* and 142

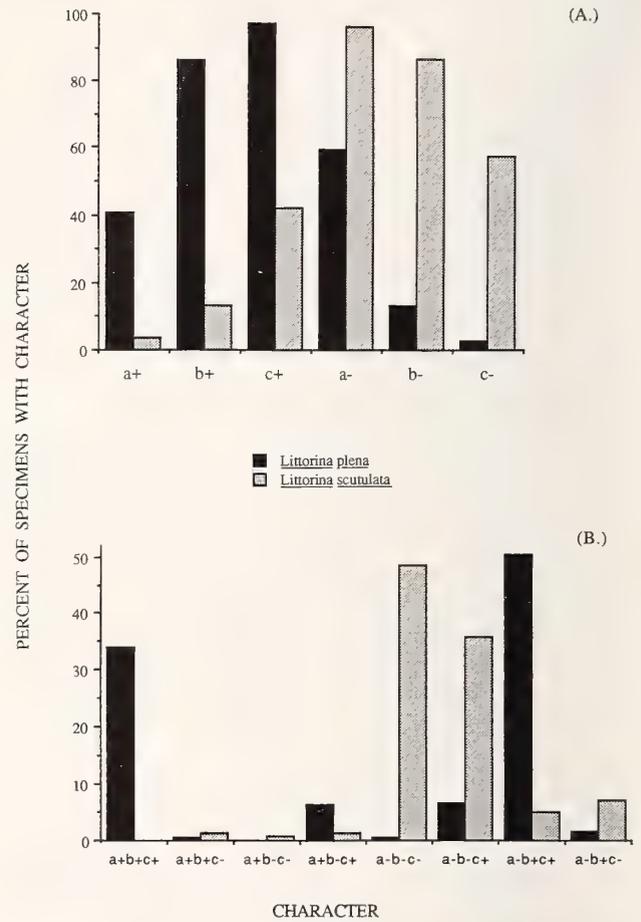


Figure 2

Frequency distribution of shell characters in *L. scutulata* and *L. plena*. (A) Individual characters, (B) Total possible combinations of all characters; a+ = small checkers present, a- = small checkers absent, b+ = basal ridge present, b- = basal ridge absent, c+ = basal band present, c- = basal band absent. Data based on sample size of 238 *L. plena* and 142 *L. scutulata*. All shells from males.

male *L. scutulata*), the frequency of the presence or absence of each of the three characters was determined (Figure 2a). If the absence of a character is considered itself to be a character, then eight combinations of these are possible. The frequency of each of these combinations of shell characters was determined for each species (Figure 2b). Most *L. scutulata* (85%) have no small checkers and no apparent basal ridge, and may or may not have a basal band. Most *L. plena* (85%) have both a basal ridge and a basal band and may or may not have small checkers (*L. plena* without small checkers are usually specimens that lack checkers altogether, and *L. scutulata* without small checkers lack checkers or have large checkers). *Littorina scutulata* with small checkers are occasionally ob-

served, especially in areas exposed to moderate or low wave shock.

In the population of *L. scutulata* and *L. plena* collected from the rock breakwater at Harbor Island, San Diego Bay, I found 17 male *L. scutulata* in the *L. scutulata* group and nine male *L. plena* in the *L. plena* group. Based on shell characters alone, 100% of the male *Littorina* in the Harbor Island sample were correctly identified.

The usefulness of these characters for distinguishing between *L. scutulata* and *L. plena* was again confirmed during spring 1995 when egg capsules were observed along the sides of two 5 L buckets, each containing a few hundred snails of each species identified using shell characters. All of the egg capsules deposited in each bucket were of the type characteristic of that species (Figure 1b). *Littorina plena* capsules are pink, and *L. scutulata* capsules are light brown and approximately half the diameter of *L. plena* capsules.

An additional character that will help distinguish between banded varieties of each species in the Pacific Northwest is the number of bands in these varieties. A variety of *L. scutulata* with two light bands is common in almost every population from Seattle, Washington to San Diego, California (Figure 5a). In *L. plena* a similar banded variety with three light bands occurs (Figure 5b), but I have never observed this variety in shells collected from California. In my samples of shells from E. Mastro that were collected in Oregon, there was one banded *L. plena* from Siletz Bay. This variety was also observed in the Puget Sound in various locations. In my collection of banded *L. scutulata* and *L. plena* from Lincoln Park, West Seattle, of the 66 *L. scutulata* snails I collected and identified by shell characters, 22 were male *L. scutulata*, and of the 44 *L. plena* snails, 16 were male *L. plena*.

Besides the three widely observed characters described above and the additional variety of *L. plena* with three light bands observed north of California, differences in shell color are somewhat helpful for identifying *L. scutulata* and *L. plena* from most locations. In both species, the shell color may be a checker pattern of gray or light blue-gray (occasionally white) alternating with light golden-brown, dark green, or black. Shells of *L. scutulata* are more frequently checkered light blue-gray alternating with light golden brown. Shells of *L. plena* are more frequently checkered light gray or white alternating with dark green or black. Orange-brown color varieties of *L. plena* are also often observed.

Checker patterns in both species are generally more clearly visible on specimens from protected shores. On exposed shores, both species tend to have darker shells, and the checker pattern is often obscured. *Littorina plena* shells from exposed shores are usually completely dark brown or black, but some individuals display a remnant of the checker pattern as tiny whitish spots on the dark background. Shells from female *L. scutulata* and *L. plena* identified by E. Mastro exhibited no apparent sexual di-

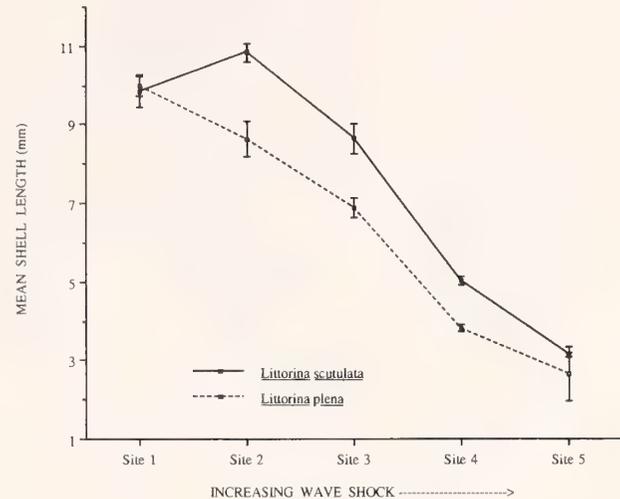


Figure 3

Mean size of individual species of *Littorina* in sympatric populations of both species along a gradient of increasing wave shock. Error bars are 95% confidence intervals. Site 1: South San Diego Bay; Site 2: Harbor Island; Site 3: Shelter Island; Site 4: Mission Bay Inlet Channel; Site 5: Pacific Beach.

morphism for all the characters or color patterns described.

In general, shell morphology appeared to vary more in relation to degree of wave shock than with geographic location. Size varied with exposure; snails of both species were an average of 10 mm in length in the most protected locations, whereas populations exposed to surf had a mean length of around 3 mm. In any given location, *L. plena* was always smaller than *L. scutulata*, with the exception of the most protected location in the south San Diego Bay where the mean size of both species was equal (Figure 3). This trend in species size was also observed by Mastro, et al. (1982) and Murray (1982). Mean shell length appeared to be inversely related to density; the smallest snails were found on the outer coast where densities of *L. scutulata* and *L. plena* often exceed 1000/m², and the largest snails were found in the more protected areas of San Diego Bay where density was as low as 10/m².

Shells of both species have a greater aperture height to shell length ratio on the open coast where wave shock is highest (Figure 4). Shells of both *L. scutulata* and *L. plena* have a relatively smaller aperture in protected locations, and the whorls of both species are rounder where wave action is lowest. The shell surface of *L. scutulata* is usually smooth and polished, regardless of geographical location or degree of wave exposure, unless the specimen has been eroded by heavy surf. *Littorina plena* from the least and most exposed shores commonly have shells with a dull, textured surface, but snails from shores exposed to intermediate levels of wave shock frequently

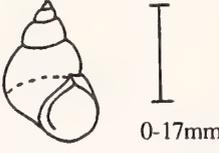
SPECIES	MINIMUM WAVE SHOCK	MODERATE WAVE SHOCK	HEAVY WAVE SHOCK
<i>Littorina plena</i>			
LOCATION EXAMPLES	South San Diego Bay Coyote Point, San Mateo County	Shelter Island, San Diego Bay Bodega Bay	Shell Beach, La Jolla Baker's Beach, San Francisco
<i>Littorina scutulata</i>			
LOCATION EXAMPLES	South San Diego Bay Humboldt Bay	Shelter Island, San Diego Bay Bodega Bay	Shell Beach, La Jolla Andrew Molero State Park, Monterey County

Figure 4

Trends in shell morphology and ranges of individual shell length of *Littorina* exposed to different degrees of wave shock. Vertical bars represent the relative maximum shell length attained by snails in each habitat. Representative locations are given for southern and northern California.

have smooth, polished shells, with the basal ridge typical of this species generally poorly defined or absent. The thinnest shells of *L. plena* appear to be found on the most exposed shores.

Although both species occur together over much of their known local and geographic range, there were observed differences between the relative abundance and local distribution of each species. *Littorina scutulata* is usually most abundant on the outer coast, but where rivers or creeks meet rocky shores of the open coast, the relative abundance of *L. plena* in populations of *L. scutulata* and *L. plena* approaches 100% (e.g., Rincon Creek, Ventura County, California and Wilson Creek, Del Norte County, California). In Humboldt Bay, San Francisco Bay, and the south end of San Diego Bay, the relative abundance of *L. plena* is higher than that of *L. scutulata*. These observations suggest that *L. scutulata* is best adapted to wave shock and *L. plena* is best adapted to lowered salinities. I am currently investigating these ideas.

DISCUSSION

Six species of native *Littorina* are recognized on the west coast of North America between Alaska and Baja California; *L. scutulata* Gould, 1849; *L. plena* Gould, 1849; *L. keenae* Rosewater, 1978 (synonym: *L. planaxis* Philippi, 1847); *L. sitkana* Philippi, 1847; *L. subrotundata* (Carpenter, 1864) (synonym: *L. newcombiana* (Hemphill, 1876)); and an undescribed species (Yamada, 1992). *Littorina scutulata sensu lato* ranges from Baja, California, Mexico, to Kodiak Island, Alaska (determined from older collections containing unknown proportions of *L. scutulata* and *L. plena*). Presently, *L. scutulata* and *L. plena* are known to share the same vertical and local ranges from southern California to at least southern British Columbia (Yamada, 1992). It remains to be determined if both species occupy the entire range of *L. scutulata s. l.*

In this paper I describe three shell characters for *L. scutulata* and *L. plena* that appear to be present through-

out the geographical range of each species. One of these characters, the basal band (Figure 1d), was first compared between the species by Murray (1982). The presence of this character alone should not lead to the conclusion that a specimen is *L. plena*; although it is observed in virtually all *L. plena* shells, it is also frequent in shells of *L. scutulata* (Figure 2a). More reliable than the presence of the band is the nature of this character in each species. In *L. plena* this band is usually sharply defined and stands out distinctly against an opaque shell wall when observed with a bright light shone from behind the specimen (Figure 1d 1). In *L. scutulata* the band is often poorly defined and blends in somewhat with a semi-translucent shell wall (Figure 1d 2). However, shells of young *L. scutulata* (<5 mm in length) frequently have a more opaque shell than adults with a well-defined basal band similar to that of a typical *L. plena*.

A second, newly described character is a difference in the relative size of the squares in the checker pattern of the two species. *Littorina scutulata* shells are generally marked by a checker pattern with squares that are 4 times the size of squares on a *L. plena* shell of equal size. This character is most difficult to use on exposed shores where most *L. scutulata* and *L. plena* have dark shells so that most or all of the checker pattern is obscured.

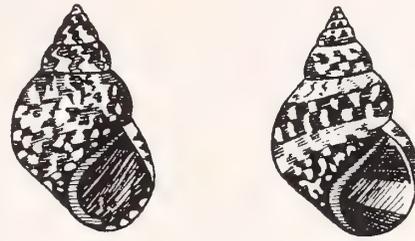
Another newly described character is a thin, well-defined ridge bordering the typically keeled base of *L. plena* shells. On shores exposed to intermediate wave shock, this ridge is often very reduced or absent from shells and is therefore not as useful a character in these locations.

Since the expression of each of the above three characters is highly variable, these will be most useful for identification when used in combination. Most specimens with large checkers (or no checkers) and no basal ridge are *L. scutulata*, and most specimens with small checkers (or no checkers), a basal band, and a basal ridge are *L. plena* (Figure 2).

A variety of *L. scutulata* with two light bands is common throughout the range of this species (Figure 5a). In California, where no similar variety of *L. plena* is observed, this banded variety can easily be identified as *L. scutulata*. North of California, a similar variety of *L. plena* can be distinguished from banded *L. scutulata* by the presence of a third light band (Figure 5b).

Shell morphology in both species varies with degree of wave shock (Figure 4). On exposed shores, *L. scutulata* and *L. plena* both have smaller shells and a larger aperture relative to the shell length than do specimens collected from protected shores (Figure 3). In both species, whorls are rounder on shells from protected shores, and *L. plena* has thicker shells where wave shock is reduced. The same trends in shell morphology have been observed for several other species of *Littorina*, as well as for species in another prosobranch family, the Thaidae (review in Boulding, 1990). This trend in habitat-related morphology is most likely related to differences in selec-

a. *Littorina scutulata* Gould, 1849



b. *Littorina plena* Gould, 1849

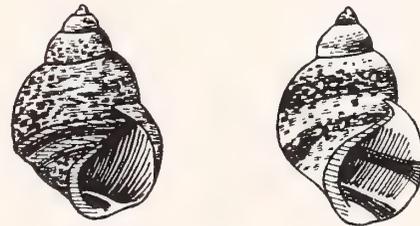


Figure 5

Banded and unbanded forms of the *Littorina scutulata* complex species.

tion pressures between exposed and sheltered localities. On exposed shores, a smaller body size may increase the number of crevice refuges available, and a larger aperture size and foot area may decrease the probability of dislodgment. On protected shores a large, thick shell with a small aperture reduces predation by crabs. A small aperture also increases resistance to desiccation, and a thick shell will reduce damage from shifting stones (Janson, 1982; Yamada, 1989; Boulding, 1990).

Intraspecific differences in shell sculpture on specimens from different habitats have also been noted. *Littorina picta* Philippi, a Hawaiian species, exhibits a high degree of variation in shell sculpture in relation to degree of wave exposure. Extreme ribbed and noded forms live on relatively dry raised benches not generally subject to horizontal water swash, while extreme smooth forms predominate on low, moist benches subject to strong wave swash. The same characters found in parents of the distinct ecotypes also occurred in progeny raised in the laboratory, indicating that the phenotypic differences have a genetic basis (Struhsaker, 1968). Extreme phenotypic variation was found in *Littorina saxatilis* Olivi from exposed shores in northwestern Spain at different intertidal

levels. A form of *L. saxatilis* with a white, ridged shell is found in the upper barnacle zone. Another form with a smooth, darkly colored or tessellated shell is confined to the lower mussel zone. The offspring from parents of these two distinct forms developed the same characters, indicating the phenotypic differences between the forms are genetic (Johannesson, et al., 1993). In other species, phenotypic plasticity in shell sculpture may be environmentally induced. Laboratory-reared offspring of typical heavily ridged *L. sitkana* developed ridging at slow growth rates, but those cultured at high growth rates were completely smooth (Boulding, et al., 1993). In my study, *L. plena* shells from shores exposed to intermediate wave shock were thicker, more polished, and more rounded at the base than their counterparts on the most exposed and protected shores. It is possible that a greater abundance of crabs such as *Pachygrapsus crassipes* (a species known to prey on *L. scutulata* and *L. plena* (E. Mastro, personal communication)) along shores exposed to intermediate wave shock has selected against the basal ridge typically expressed in this species on more or less exposed shores. A smoother, rounder, and thicker shell would be more difficult for a crab to handle and crush. The inability of two Pacific Northwest *Littorina* species to resist crab predation has prevented them from occupying shores of intermediate wave exposure altogether (Yamada, 1992).

Shells of both *L. scutulata* and *L. plena* from exposed habitats are noticeably darker than those from protected shores. I painted a sample of black shells of snails of both species from an exposed jetty and transferred them to a protected site inside Mission Bay. After a few weeks, new shell material had been added in each species and was a considerably lighter color typical of natural populations from protected areas. This observation suggests that differences in shell color in these species between exposed and protected shores are controlled by the environment. What specific factors are responsible for this are uncertain, but differences in the algae species available for food or a difference in growth rates in each habitat are two possible explanations. Boulding & Hay (1993) found that the undescribed species (Yamada, 1992) produced a lighter colored shell when grown in a low density treatment. It may be relevant that the lowest densities of *L. scutulata* and *L. plena* occur along protected shores where the lightest shells are observed.

There are few studies on the ecology of *L. scutulata* and *L. plena* (Mastro, 1985; Chow, 1987; Chow, 1989; Voltolina & Sacchi, 1990). More work is needed. Earlier ecological studies (North, 1954; Bock & Johnson, 1967; Chow, 1975) will have to be re-examined. Principal-component analysis of measured shell characters has been used to describe size and shape variation in *Littorina* on a geographic scale (Lewis & Williams, 1995), and on a local scale where variation may occur in relation to differences in habitat (Johannesson et al., 1993) and could

prove useful for further describing the differences in the shell morphology of the California sibling species between exposed and protected habitats. Studies in which the F₁ generation from distinct ecotypes of *Littorina* species were raised in the laboratory have provided good evidence that the habitat-specific characteristics of these forms are inherited in some species (Struhsaker, 1968; Johannesson, et al., 1993) and are environmentally induced in others (Boulding et al., 1993). Studies of allele frequencies in distinct phenotypes of *Littorina* obtained from different intertidal heights have produced evidence that an allele can be selected for within a given intertidal level (Johannesson & Johannesson, 1989; Johannesson et al., 1993). Thus, breeding experiments and electrophoresis studies could provide information on whether phenotypic differences in *L. scutulata* and *L. plena* associated with habitat differences are a result of environmental or genetic differences.

It is worthwhile to attempt to separate species with similar morphology on the basis of their shell characters because such characters can be measured on museum specimens and on fossils (Boulding, 1993). The newly described shell characters presented in this paper should facilitate future work. Fortunately, because the larger, more eye-catching *L. scutulata* (with larger, more noticeable checkers) retains the same species name, the specimens typically illustrated in popular field guides to shells of western North America (e.g., Morris, 1966; Abbott, 1968) are correctly identified as such. The common name for *L. scutulata* is the checkered periwinkle. At the present time, *L. plena* does not have a common name. I offer as a suggestion the name starry periwinkle because of the resemblance of the fine checker pattern on this species to stars in a clear night sky, and because the common names for both *L. scutulata* and *L. plena* would then refer to the color patterns on their shells.

ACKNOWLEDGMENTS

I wish to thank Dr. T. Cohn for his encouragement and guidance. E. Mastro provided positively identified specimens and demonstrated identification of male *Littorina* of both species. Thanks to S. Shelton for providing access to specimens of *Littorina* in the San Diego Museum of Natural History collection. I am grateful for early comments on the manuscript provided by E. Mastro and D. Dexter. Additional comments by E. Boulding, B. Roth, and an anonymous reviewer submitted during the review process greatly improved the manuscript.

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Pacific Mexican Affinities of New Species of the
Gastropod Genera *Macron* (Pseudolividae) and
Neorapana (Muricidae) from the Cantaure Formation
(Early Miocene) of Venezuela

by

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Abstract. *Macron constrictus* sp. nov. and *Neorapana rotundata* sp. nov. from the Cantaure Formation (Early Miocene) of Venezuela are the earliest known members of their respective genera, and the only species of *Macron* and *Neorapana* known from the Atlantic Ocean. Both are extremely similar to Recent species from northwestern Mexico, *Macron orcutti* Dall, 1918, and *Neorapana tuberculata* (Sowerby, 1835).

INTRODUCTION

The very rich early Miocene fauna of the Cantaure Formation of Venezuela contains representatives of many genera that are rarely preserved as fossils. Here we describe two new species, *Macron constrictus* (Pseudolividae) and *Neorapana rotundata* (Muricidae). Not only are these species the earliest known members of their respective genera, but they also provide evidence of geographical restriction of *Macron* and *Neorapana* to the eastern Pacific, notably to northwestern Mexico. The two species are characterized by a labral tooth, a common feature among Cantaure neogastropods. Abbreviations used in the text: LACM, Los Angeles County Museum of Natural History; NMB, Naturhistorisches Museum, Basel; UCMP, University of California, Museum of Pa-

leontology, Berkeley; USNM, United States National Museum of Natural History.

SYSTEMATICS

Family PSEUDOLIVIDAE Cossmann, 1901

Genus *Macron* H. & A. Adams, 1853

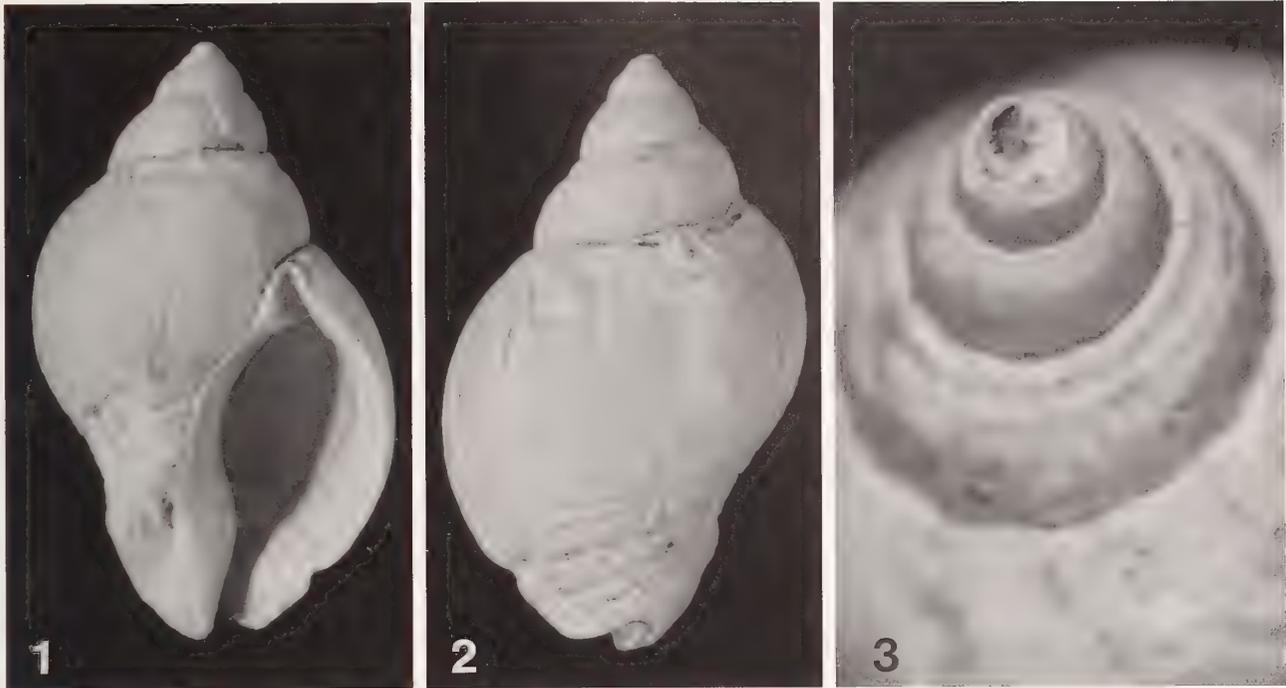
Type species: *Macron aethiops* (Reeve, 1847).

Macron constrictus J. Gibson-Smith &
W. Gibson-Smith & Vermeij, sp. nov.
(Figures 1-3)

Macron orcutti Dall: Gibson-Smith & Gibson-Smith, 1979:22.

Diagnosis: *Macron* with very finely threaded, rounded last whorl, narrowly channeled suture in adult stage, and inner side of outer lip bearing 13 to 16 lirae on recessed ridge.

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Figures 1–3

Ventral, dorsal, and oblique apical views of *Macron constrictus* J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.; holotype, NMB 17776; 36.7 mm in height.

Description: Shell medium-sized, maximum height 36.6 mm, fusiform; spire relatively high, last whorl comprising 68–72% of total shell height; protoconch consisting of two and one-half to three smooth, bulbous whorls; junction between protoconch and teleoconch indistinct; teleoconch consisting of four to five whorls separated by distinct suture, which becomes narrowly channeled between penultimate and last whorl of adult specimens; last whorl without shoulder, evenly rounded on upper part, weakly constricted near base; area immediately below suture on last two whorls weakly concave; spiral sculpture of first teleoconch whorl consisting of five cords; spiral sculpture of first teleoconch whorl consisting of five cords; spiral sculpture of later whorls consisting of very fine striae, which continue to the upper part of the last whorl; lower part of last whorl with deep spiral groove (pseudolivid groove), below which are two or three flat, low spiral cords; axial sculpture absent; outer lip planar, its edge crenulated most strongly by the ends of interspaces between basal cords; labral tooth present, consisting of a blunt projection at the edge of the outer lip, situated at the end of a deep spiral groove (pseudolivid groove); inner side of outer lip thickened by ridge parallel to edge, sculptured by 13 to 16 short lirae; adapical end of outer lip with weak notch; inner lip adherent, smooth, with broad, rounded fold at entrance of siphonal canal; adapical end of inner lip bearing rounded parietal rib; colu-

mellar and parietal callus of very limited extent; aperture ovate, its height-to-breadth ratio 2.4 to 2.6; siphonal fasciole prominent, bounded adapically by low keel; umbilicus absent.

Holotype: NMB Number 17776; height 36.7 mm, diameter 21.5 mm, height of aperture 26.5 mm.

Paratypes: 18 specimens. Paratype 1: NMB H-17777, height 36.2 mm, diameter 22.6 mm. Paratype 2: NMB H-17778, height 34.2 mm, diameter 20.3 mm. Paratype 3: NMB H-17779, height 29.2 mm, diameter 17.8 mm. Paratype 4: NMB H-17780, height 30.5 mm, diameter 18.1 mm. Paratype 5: NMB H-17781, height 10.9 mm, diameter 6.5 mm. UCMP 152334, three specimens, largest height 35.5 mm, diameter 22.3 mm, height of aperture 24.2 mm.

Type locality: GS-1-PGNA, NMB 17516, lower shell bed, Cantaure Formation, 300 m south southeast of the new (1952) Casa Cantaure near San José de Cocodite, Paraguaná Peninsula, Falcón State, Venezuela.

Stratigraphic and geographic distribution: Cantaure Formation (Early Miocene), Venezuela.

Discussion: In reviewing the fauna of the Cantaure Formation of Venezuela, Gibson-Smith & Gibson-Smith (1979:22) listed *Macron orcutti* Dall, 1918, and recog-

nized this species as Paciphilic, that is, as having become restricted to the eastern Pacific from a broader distribution that also included the Atlantic. This fossil is indeed strikingly similar to *M. orcutti*, which occurs in the Recent fauna from Bahía Magdalena south to Punta Marquez, on the Pacific side of Baja California Sur, Mexico. Because the fossil form differs significantly and consistently from the Recent *M. orcutti*, we here distinguish it as a separate species, *M. constrictus*. The material of *M. orcutti* on which the comparisons below are based consists of the holotype (USNM 218185) from Magdalena Bay, and two additional lots, LACM 79-26.27 (Punta Marquez) and LACM 71-3.26 (Punta Abreojos). The latter two lots were kindly loaned to GJV by J. H. McLean.

The Miocene *Macron constrictus* from the Cantaure Formation resembles the Recent *M. orcutti* in maximum adult size (36 mm in both species), spire height (last whorl comprising 68–72% of shell height in *M. constrictus*, 60–75% in *M. orcutti*), aperture shape (height-to-breadth ratio 2.4–2.6 in both species), number of lirae on the inner side of the outer lip (13–16 in *M. constrictus*, 13–17 in *M. orcutti*), and in having the last whorl evenly rounded and mostly smooth, with spiral sculpture being confined to the basal part. *M. constrictus* differs from *M. orcutti* by having the suture narrowly channeled instead of appressed between the last two whorls, by being somewhat more constricted basally, by having a concave zone just below the suture, and by having the inner side of the outer lip thickened.

With the recognition of *M. constrictus*, the genus *Macron* must be added to the list of Paciphilic taxa. *M. constrictus* is only the second pseudolivid known from the Neogene in the western Atlantic. The only other Neogene member of the family there is *Pseudoliva guppyi* Mansfield, 1925, from the Miocene of Trinidad.

All the available specimens are from the lower shell bed of the Cantaure Formation. Stratigraphic relations and the fauna of planktonic Foraminifera indicate that the Cantaure Formation is of Early Miocene (Burdigalian) age (Díaz de Gamero, 1974; Gibson-Smith & Gibson-Smith, 1979; González de Juana et al., 1980).

The holotype and two paratypes each have one repaired break on the last whorl. The incidence of shell repair among the 22 available specimens is therefore 14%.

Family MURICIDAE Rafinesque, 1815

Subfamily RAPANINAE Gray, 1853

Genus *Neorapana* Cooke, 1918

Type species: *N. muricata* (Broderip, 1832).

Neorapana rotundata J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.

(Figures 4–9)

Diagnosis: *Neorapana* with the periphery below the shoulder at the third of five primary spiral cords on last whorl.

Description: Shell of medium size, maximum height estimated to be 38 mm, broadly fusiform; protoconch not preserved; teleoconch consisting of about four whorls separated by impressed suture; spire relatively high, last whorl comprising 69–79% of total shell height; last whorl with low, angulated shoulder above, tapering without constriction below; last whorl sculptured by five primary spiral cords, each bearing eight tubercles in the adult and 15 in the immature shell; second primary cord from suture forms shoulder; third primary cord forms periphery of last whorl; aperture ovate, its height-to-breadth ratio 2.2 to 2.5; outer lip incompletely preserved, but shows a trace of a labral tooth at end of groove below fifth primary cord; inner side of outer lip smooth or with six weak denticles; columella straight, smooth, its upper end marked by parietal rib; inner lip adherent along most of its length, but forming excavated, free-edged flange below prominent siphonal fasciole; umbilicus absent.

Holotype: NMB H-17784; height 35.6 mm, maximum diameter 28.22 mm, height of aperture 24.5 mm.

Paratypes: Paratype 1: NMB H-17783; height 33.3 mm, maximum diameter 30.6 mm (incomplete). Paratype 2: NMB 17782; height 17.7 mm, maximum diameter 13.7 mm.

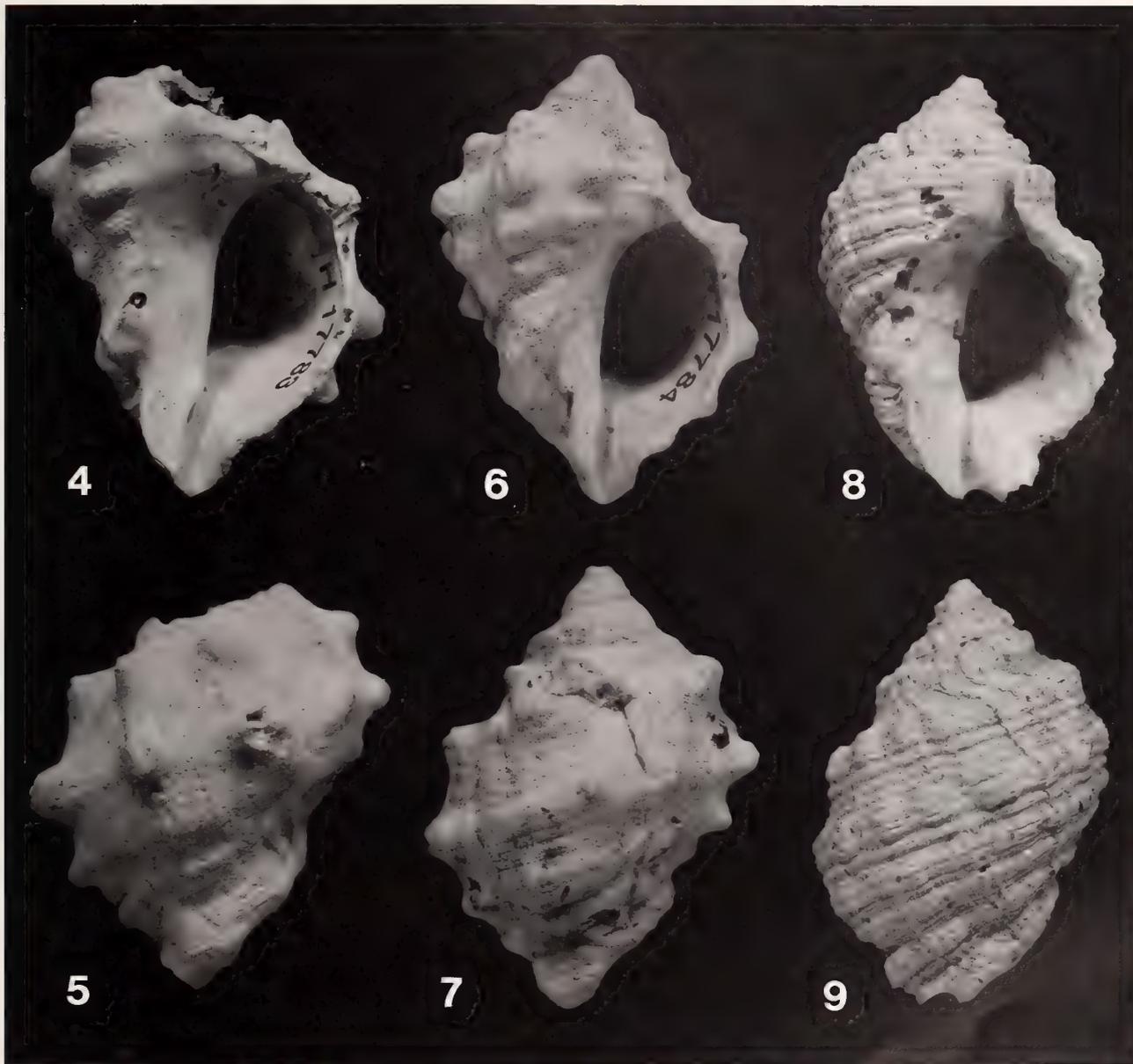
Type locality: GS-122-PGNA, NMB 17519, upper shell bed, Cantaure Formation, 550 m southeast of the new (1952) Casa Cantaure near San José de Cocodite, Paraguaná Peninsula, Falcón State, Venezuela.

Stratigraphic and geographic distribution: Cantaure Formation (Early Miocene, Burdigalian), Venezuela.

Etymology: *rotundata*, Latin “rounded,” referring to the profile of the upper part of the last whorl.

Discussion: The above description is based on three specimens, none of which is wholly intact. In the holotype, collected by J. and W. Gibson-Smith at their Locality GS-122-PGNA from the upper shell bed in the Cantaure Formation, the excavated anterior portion of the inner lip is abraded. Paratype 1, also from the upper shell bed, has the spire missing, and with a maximum shell diameter of 30.6 mm, is the largest of the three specimens, with an estimated height of 38 mm. The labral tooth is preserved only on Paratype 2, an immature shell from Locality GS-1-PGNA in the lower shell bed of the Cantaure formation.

We assign this species to the genus *Neorapana* on the basis of the following characters: five tuberculated primary spiral cords; presence of labral tooth at end of groove below fifth primary cord; lower part of inner lip free-edged and slightly excavated; broadly ovate aperture; smooth, straight columella; parietal rib present. The only character inconsistent with assignment to *Neorapana* is the smooth inner side of the outer lip in the two apparently mature specimens (the holotype and



Figures 4, 5

Ventral and dorsal views of *Neorapana rotundata* Gibson-Smith & Vermeij, sp. nov.; paratype 1, NMB H-17783; height 33.3 mm.

Figures 6, 7

Ventral and dorsal views of *Neorapana rotundata* J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.; holotype, NMB H-17784; height 35.6 mm.

Figures 8, 9

Ventral and dorsal views of *Neorapana rotundata* J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.; paratype 2, NMB H-17782; height 17.7 mm.

paratype 1). In the immature paratype 2, the inner side of the outer lip bears six weak denticles or riblets. The three Recent species of *Neorapana* are characterized by a lirate outer lip, in which discontinuous riblets occur

on the inner side. In two immature specimens of *N. tuberculata* (Sowerby, 1835) in the Vermeij collection from Estero de Bahía Falso (southern Gulf of California, Baja California Sur), however, the inner side of the

outer lip is smooth as it is in the two larger *N. rotundata* from Venezuela.

The fossil *N. rotundata* very closely resembles the Recent northwest Mexican *N. tuberculata* (Sowerby, 1835). *N. rotundata* differs from *N. tuberculata* mainly in having the widest part of the shell at cord three, below the shoulder; whereas in *N. tuberculata* the widest part of the shell encompasses the sector bounded by the second and third primary cords. *N. rotundata* therefore gives a more rounded aspect than does *N. tuberculata*.

In a phylogenetic analysis of the subfamily Rapaninae, Vermeij & Carlson (in review) identified the Indo-West Pacific genus *Mancinella* Link, 1807, as the sister group of *Neorapana*. The Miocene *N. rotundata* resembles species of *Mancinella* more closely than do any of the three Recent species of *Neorapana*. Both *N. rotundata* and species of *Mancinella* have the widest part of the shell at the third primary spiral cord of the last whorl, below the shoulder; whereas in the living *Neorapana*, the widest part is either at the shoulder (the second primary cord), as in *N. muricata* and *N. grandis* (Sowerby, 1835), or in the sector bounded by the second and third primary cords, as in *N. tuberculata*.

As pointed out by Vermeij & Kool (1994) and Vermeij & Carlson (in review), the labral tooth of *Neorapana* evolved independently of that in *Mancinella*. In *Neorapana*, the labral tooth is formed at the end of a groove situated below the fifth primary cord. In *Mancinella alouina* (Röding, 1798), the type species of *Mancinella*, it forms at the end of a groove between the fourth and fifth primary cords. Other Indo-West-Pacific species of *Mancinella* lack a labral tooth (see Vermeij & Carlson, in review, for a review of species of *Mancinella* and *Neorapana*). The discovery of *N. rotundata* shows that the evolution of the labral tooth in *Neorapana* had already occurred by Early Miocene time.

Neorapana rotundata is phylogenetically interesting for three additional reasons. First, it is the earliest known member of its genus. Previously, the genus had been recorded from the Pliocene of the Gulf of California (as *Acanthina* cf. *A. tuberculata* Sowerby by Durham, 1950, and Emerson & Hertlein, 1964) and from the La Vaca Formation (Pliocene) of Costa Rica (as *Neorapana* sp. in a list by Woodring, 1973). Second, *N. rotundata* is the only species of its genus from the Atlantic side of tropical America. The genus *Neorapana* must therefore be added to the list of clades that have become restricted since Late Neogene time to the eastern Pacific. Third, like *Macron constrictus*, *N. rotundatus* has as its closest apparent relative a Recent species from northwestern Mexico. The two other Recent species of *Neorapana*, *N. muricata* from the mainland coasts of Central and northwestern South America, and *N. grandis* from the Islas Galápagos, differ from *N. tuberculata* and *N. rotundata* in being much larger and in having a markedly triangular last whorl whose widest point coincides with the sharply angular shoulder.

DISCUSSION

The molluscan fauna of the Cantaure Formation is remarkable not only for its richness, with more than 600 species being recorded (see Jung, 1965, and Gibson-Smith & Gibson-Smith, 1979, for a partial account), but also because it records the earliest appearance of many genera in tropical America, including *Macron* and *Neorapana*. Many taxa in the Cantaure Formation, moreover, belong to Pacific clades. At least one taxon in the Cantaure Formation other than *Macron* and *Neorapana* has as its closest living relative a species in northwestern Mexico. The turrid *Glyphostoma* (*Euglyphostoma*) is represented today by a species in the Gulf of California.

Both *Macron* and *Neorapana* possess a labral tooth on the edge of the outer lip. Other species in the Cantaure formation with a labral tooth include *Panamurex gatunensis* (Brown & Pilsbry, 1911) (see Vokes, 1992) and new species of *Ocinebrina* and *Pterorytis* (*Microrhytis*) (see Vermeij & Vokes, 1997). A labral tooth therefore occurs in four of at least 20 muricids (20%) in the Cantaure Formation. This is the highest incidence of labral teeth in any muricid assemblage in tropical America, fossil or Recent. Work in progress by Vermeij indicates that this high incidence is typical of communities living under condition of high planktonic productivity.

ACKNOWLEDGMENTS

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NOTES, INFORMATION & NEWS

"*Aclis*" *californica* Bartsch, 1927: A Land Snail Misinterpreted (Gastropoda: Pulmonata: Subulinidae)

by

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Bartsch (1927) described the new species of gastropod, *Aclis californica*, as follows:

Shell small, pupiform, thin, bluish white. Nuclear whorls not differentiated from the postnuclear turns. All the whorls well rounded, appressed at the summit which is finely crenulated, the rest marked by fine lines of growth which are somewhat retractorily slanting. The type is slightly worn and shows no indication of spiral sculpture. Sutures moderately constricted. Periphery of the last whorl inflated and strongly rounded. Base short, strongly rounded, narrowly umbilicated, marked like the spire. Aperture subquadrate; posterior angle decidedly obtuse; outer lip thin; columella almost straight, reflected over and appressed to the base for its posterior fifth; parietal wall covered with a thin callus (Bartsch, 1927:4).

The holotype, in the National Museum of Natural History (USNM 362455) is the only known specimen and supposedly was collected by R. H. Tremper on rocks at San Clemente Island, California. Bartsch interpreted it as a marine species and assigned it to the genus *Aclis* Lovén, 1846 (Aclididae).

Subsequently, the species was included in various compilations covering the marine gastropods of California but no additional Recent specimens were reported. Oldroyd (1927:578) copied Bartsch's description and placed the species under the subgenus *Graphis* Jeffreys, 1869. Keen (1937:28) listed it, as *Aclis californica*, from latitude 34°N (apparently an attempt, although an inaccurate one, to render the San Clemente Island range numerically). In the three editions of Keen's generic reviews of north-eastern Pacific mollusks (Keen & Pearson, 1952; Keen, 1963; and Keen & Coan, 1974), a line drawing taken from Bartsch's original figure was used to represent the genus *Aclis*.

Burch (1945:17) reported under *Aclis californica*: "We have specimens so labelled fossil from the Pleistocene of the Lomita gravel pits, but no Recent specimens." Those Pleistocene specimens undoubtedly represent some other species.

The collections of the Section of Malacology, Natural

History Museum of Los Angeles County (LACM), which include the results of extensive sampling of diverse shallow-water habitats in southern California, contain no specimens of "*Aclis*" *californica* (James H. McLean, personal communication).

In connection with the preparation of a checklist of west American marine gastropods, Dr. McLean referred the subject to me, based on a comment by Anders Warén that "*A.*" *californica* looked like a pulmonate. The holotype turns out to be a juvenile specimen of the subulinid land snail *Allopeas gracile* (Hutton, 1834), a species widely spread by commerce throughout tropical and subtropical regions of the world.

Subulinidae Crosse & Fischer, 1877

Allopeas H. B. Baker, 1935

Type-species: *Bulimulus gracilis* Hutton, 1834; by original designation.

The genus is circumtropical, with some species so widely dispersed by commerce that their origins are uncertain. Several species, including *Allopeas gracile*, *A. mauritanum* (Pfeiffer, 1852), and *A. clavulinum* (Potiez & Michaud, 1838) have been reported as introductions to the United States (Pilsbry, 1946; Dundee, 1970, 1971, 1974; Auffenberg & Stange, 1988). They have been intercepted in many kinds of cargo from tropical America, Asia, and Pacific islands including Hawaii.

Separation of *Allopeas* from *Lamellaxis* Strebel & Pfeffer, 1882, of which it was formerly considered a subgenus, is widespread in the recent literature (e.g., Naggs, 1992, and references cited therein; Cowie, 1997).

Allopeas gracile (Hutton, 1834)

(Figure 1)

Lamellaxis (Allopeas) gracilis (Hutton) Baker, 1945:88-89; Pilsbry, 1946:177-178, fig. 84(8-10), 85f-g; Bequaert & Miller, 1973:143.

Lamellaxis gracilis (Hutton), Dundee, 1970:101, 103, 106, 107-110, 112; Dundee, 1971:129, fig. 2 (as *Opeas gracile* on p. 130); Dundee, 1974:8-9; Auffenberg & Stange, 1988:[1-2], fig. 2; Smith et al., 1990:111.

Aclis californica Bartsch, 1927:4, pl. 1, fig. 2; Keen, 1937:28.

Aclis (Graphis) californica Bartsch, Oldroyd, 1927:578.

Shell lanceolate, 7-11.5 mm × 2.3-3.5 mm, with straight-sided or weakly convex spire and 6.5-10 more or less convex whorls. Apex blunt. Aperture 30% or less of total height. Peristome simple and delicate. Columella straight, reflected over the minute umbilicus, not truncat-



Figure 1

Allopeas gracile (Hutton, 1834). Holotype of *Aclis californica* Bartsch, 1927, USNM 362455. Length 5.0 mm. Photograph by J. H. McLean.

ed at base. Shell gray or yellowish to colorless, thin and translucent, glossy, with more or less distinct growth lines.

A complete synonymy for *A. gracile* would be very extensive. The above citations include chiefly the main references to North American occurrences.

The usual habitat is ground litter in moist places. Dundee (1970) observed the species in New Orleans, USA, on or within 1–2 cm of the ground in disturbed areas, under cover such as boards, bricks, or leaves, descending to a depth of 7–8 cm into the soil in cool weather. European and most United States records north of the southern tier of states appear to be in greenhouses.

Recent work by the author and others on the land snails of San Clemente Island has not recorded the species. Where it does occur, *A. gracile* often builds up dense populations, and it seems unlikely that these would go unnoticed by biologists working on the island. There is no way to know whether the specimen collected by R. H. Tremper was a single adventitious shell (dispersed through natural or human agency) or a shell from a population that had become established temporarily on the island. A locality labeling error is also a possibility.

There is an old record, without specific locality and not now verifiable, of the detection of *A. gracile* in California (Hill, 1951). The nearest established populations of *A. gracile* occur in Arizona, USA (Bequaert & Miller, 1973); Sonora, Mexico (Drake, 1953; Naranjo-García, 1991; author's collection); and the mainland of Baja California Sur, Mexico (Smith et al., 1990).

Acknowledgments

I thank J. H. McLean for calling the problem to my attention, reading a draft of the manuscript, and making helpful suggestions. The California Academy of Sciences curatorial staff gave access to comparative material in the CAS collection; F. Naggs confirmed the identification of *Allopeas gracile*; and F. G. Hochberg commented constructively on the manuscript.

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International Commission on Zoological Nomenclature

The following Applications were published on 26 March 1997 in Volume 54, Part 1 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., %The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2939—*Galba* Schrank, 1803 (Mollusca, Gastropoda): proposed designation of *Buccinum truncatulum* Müller, 1939 as the type species.

The following Opinions concerning mollusks were published on 26 March 1997 in volume 54, Part 1 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1860. *Acanthoteuthis* Wagner in Münster, 1839 and *Muensterella* Schevill, 1950 (Mollusca, Cephalopoda): placed on the Official List.

Opinion 1861. *Octopus vulgaris* Cuvier, [1797] and *Loligo vulgaris* Lamarck, 1798 (Mollusca, Cephalopoda): specific names conserved.

The following Application was published on 30 June 1997 in Volume 54, Part 2 of the *Bulletin of Zoological Nomenclature*.

Case 2996—*Pila* Röding, 1798 and *Pomacea* Perry, 1810 (Mollusca, Gastropoda): proposed placement on the Official List, and Ampullariidae Gray, 1824: proposed

confirmation as the nomenclaturally valid synonym of *Pilidae* Preston, 1915.

The following Opinion was published on 30 June 1997 in Volume 54, Part 2 of the *Bulletin of Zoological Nomenclature*.

Opinion 1868. *Patella longicosta* Lamarck, 1819 (Mollusca, Gastropoda): specific name conserved.

Manuscript Reviewers for Volume 40 of *The Veliger*

The following reviewers contributed their time, effort, and expertise to evaluate manuscripts submitted during the course of assembly of Volume 40. The quality of *The Veliger* depends strongly on the voluntary assistance of independent reviewers such as these, and we are grateful to them.

C. Avila, K. Bandel, M. C. Barnhart, D. W. Behrens, P. Beninger, H. Bertsch, R. Black, S. von Boletzky, K. J. Boss, J. C. Britton, T. H. Carefoot, K. B. Clark, E. V. Coan, R. H. Cowie, C. N. D'Asaro, R. T. Dillon, Jr., O. Domaneschi, D. J. Eernisse, W. P. Elder, K. C. Emberton, T. J. Frest, J. Geller, C. R. Givens, J. H. R. Goddard, G. A. Goodfriend, T. M. Gosliner, M. G. Harasewych, J. M. Healy, R. Hershler, C. S. Hickman, F. G. Hochberg, B. V. Holthuis, A. R. Holyoak, R. S. Houston, D. K. Jacobs, F. J. Janzen, M. J. Kennish, N. H. Landman, H. Lescinsky, D. R. Lindberg, M. deMaintenon, L. N. Marinovich, P. B. Marko, J. H. McLean, P. M. Mikkelsen, S. V. Millen, M. C. Miller, B. Morton, P. G. Oliver, L. R. Page, G. Pastorino, G. Paulay, W. F. Ponder, R. S. Prezant, T. A. Rawlings, R. L. Reeder, C. A. Richardson, R. Robertson, P. U. Rodda, G. Rosenberg, W. B. Rudman, A. S. M. Saleuddin, S. Sato, J. A. Schneider, P. Sharkey, F. Star-mühlner, G. Steiner, J. R. Stone, C. Thiriou-Quévieux, K. A. Thomas, R. Toll, M. Vecchione, G. J. Vermeij, J. Vol-tzow, S. E. Walker, T. R. Waller.

BOOKS, PERIODICALS & PAMPHLETS

Response to Review by Christopher Meyer and Robert Guralnick of *An Atlas of Cowrie Radulae* (Mollusca: Gastropoda: Cypraeoidea: Cypraeidae), Volume 40(3):280

We thank Meyer and Guralnick for their kind words about our *Atlas of Cowrie Radulae*. Although we appreciate the kind words, we are bewildered by the charges that "this volume is intended to be more than simply the description of the radulae of 202 species of cowries"; that there are "implicit but important statements about character-states and evolutionary patterns" in the work; and that those features are to be used in monographs of systematics and phylogeny.

The purpose of the volume was to illustrate the radular teeth of as many cowrie species as we could obtain. And that is precisely what we tried to do. There were essentially three choices we could make to present our work. We could have (1) arranged the cowrie radulae alphabetically by species; (2) organized the radulae by genera and arranged the genera either alphabetically or in Schilderian order; or (3) arranged the radulae in terms of patterns displayed by the teeth themselves. Kay (1960) introduced the notion of distinguishing cowrie radular teeth by pattern, identifying four patterns among the cypraeid radulae she then had available. It was obvious, however, with the radulae of 200 species in hand, that the original four patterns were inadequate. It did not seem to be an unreasonable step to recognize additional patterns, given that the concept of cowrie radular patterns has been available for more than 30 years. As we analyzed the illustrations, nine additional patterns seemed recognizable, and we arranged the radulae in terms of 13 patterns. We realize that our groupings are phenetic, but believed that it would be more useful to users to group species with similar patterns together.

It was not until all 202 species illustrations were compiled, however, that we thought to compare them with the currently recognized Schilderian scheme of classification. It was a complete surprise to find the remarkable consistency between Schilder's genera and our 13 radular patterns.

We clearly stated in the *Atlas* (p.7, col. 1, last paragraph) that "the features of the radulae illustrated here comprise but one component of an extensive data set of shell features, mantle characters, reproductive structures, nervous system pattern, larval shells, and fossil history now being assembled as a monograph of cowrie systematics and phylogeny (Kay, in preparation)." It is no secret that the second author is, and has been assembling such

a monograph for more than 40 years. Nor is it a secret that her work on cowrie systematics is designed for the new edition of the *Treatise of Invertebrate Paleontology*. Before either a systematic account and/or a phylogeny is completed, however, it is essential that the types of all the genera and species involved be reviewed. The Schilders provided an incomparable base on which to begin. Unfortunately, they were not able to either figure or even see many of the types of genera and species essential to a systematic review or a phylogeny. Until those types are critically determined, the systematics and phylogeny of the Cypraeidae are built on sand.

**Hugh Bradner
E. Alison Kay**

Revisión de las especies atlánticas de la familia Chromodorididae (Mollusca: Nudibranchia) del grupo cromático azul

by J. ORTEA, A. VALDÉS, and J. C. GARCÍA-GÓMEZ. 1996. *Avicennia*, Revista de Ecología, Oceanología y Biodiversidad Tropical, Suplemento 1 (Oviedo, 1996). 165 pp. Paperback, \$40 U.S. Available from Depto. de Biología de Organismos y Sistemas, Laboratorio de Zoología, Universidad de Oviedo, 33075 Oviedo, Asturias, España.

This work describes the taxonomy, anatomy, distribution, and aspects of the biology of the "blue chromatic group" of Atlantic Chromodorididae. Excellent color photographs and line drawings of the species depict the authors' ideas on the range of variation within each species. Scanning electron micrographs illustrate the radulae and jaw rodlets of the species; the reproductive organs are also diagrammatically shown. Numerous specimens of the species are dissected and analyzed, many from a wide range of localities throughout the Atlantic and Caribbean basins. The authors are to be congratulated for the extent of their collections and the huge amount of variation they illustrate for many of the species. We are presented with a great amount of useful biological information about species within five genera of Chromodorididae.

Any student of chromodorid nudibranchs must address and use this important manuscript.

However, I must point out a number of caveats that require discretionary consideration before any of the authors' conclusions are accepted. Researchers should be careful about the following:

1. There are several minor typographical errors and

textual inconsistencies. Most obvious is that the species lists in the Abstract and Summary Index are neither identical nor add up to the same number of species. Minor glitches include "Puesta con nuevos rojo naranja," which should have read "huevos," and *Risbecia nyalnya*, a frequent misspelling of *nyalya* (which is correctly spelled on page 147).

2. Synonymies are at times unsubstantiated, miss key references, or tax the credibility of even the most "variation-minded" biologist. For instance, on page 32, *Hypselodoris midatlantica* Gosliner, 1990, is synonymized (sin. nov.) with *H. tricolor*; however, not one word of explanation or discussion is given in the text. This is curiously juxtaposed with their paragraph (p. 42) that Schmekel & Portmann (1982) is "el mejor ejemplo de la mezcla de especies bajo el nombre de *H. tricolor*." The references (p. 58) to *Hypselodoris orsinii* omit the differing opinion of Schmekel & Portmann (1982). Figures 6 A–G and 51 and 52 are all purported to be *H. bilineata*(!).

3. Examples of radular variation (both meristic and morphological) are described. Graphs or regression analyses (*sensu* Bertsch, 1976) would have been most informative and supportive for their conclusions.

4. I found it difficult to match color variations with the different collecting localities. Maps of each species' distribution (rather than the single, universal Figure 3 indicating all collecting localities) correlated with radular or external color illustrations would have made this compendium more useful.

5. The authors' subspecies designations (after they have synonymized numerous nominal species) are biologically and philosophically suspect. Let me explain. In the past, studies of nudibranch biodiversity have been hampered by dissections of solitary dead slugs, resulting in the naming of multitudinous "new" species. Based on the contributions of Ernst Mayr and other evolutionary biologists, our understanding of the species has significantly changed from the Linnaean morphological typology that was rampant through the late 1800s and early 1900s. Today it is commonly known that variation exists within and between populations. The authors recognize the ranges of biological variation; this is one of the greatest strengths of their manuscript. However, their use of subspecies gives the appearance that they have slipped back into the typological denominating trap. Given oceanic currents, the mobility of larvae, and possibilities of genetic interchange, this reviewer believes that marine subspecies should be named only under exceptional circumstances.

Among the blue Atlantic chromodorids, the authors have convinced me of the existence of highly variable species. Their arguments for subspecies status of certain populations are not convincing. Synonymizing species and then re-erecting them as subspecies is not appropriate; they should not over-synonymize only to over-subspeciate! As I comment later, these groups may well be populations undergoing significant evolutionary

change, and should not be "fixed" with a nomenclatural (certainly not trinomial) status.

6. After carefully describing wide ranges of variation within the blue Atlantic chromodorids, the authors name several new species based on only one (*H. cimini*, *H. muniani*, *Mexichromis molloi*) or two (*H. gasconi*, *H. xicoi*, *Chromodoris goslineri*) specimens. One is even named *without any specimens*, giving a name to an animal studied by Malcolm Edmunds (1981) from Ghana. Naming new species based on other people's illustrations was commonplace among nineteenth century conchologists, but has no place today.

Let me present two comments in conclusion. First, the rampant variation and differing synonymies of the blue Atlantic chromodorids simply reflect a group of populations and species in significant evolutionary flux. I suspect that our attempts at codifying them too rigidly into distinct columbaria or "pigeonholes" is biologically premature. These may well be populations in crucial zoogeographical and evolutionary transition. Our taxonomy should reflect such dynamic realities. That is a challenge to those of us so used to the comfort of a "species name."

Second, I unequivocally state that any student of Atlantic (or worldwide) Chromodorididae species must refer to the issues and decisions raised in this work. Ortea, Valdés & García-Gómez have presented an excellent series of illustrations and descriptions of intraspecific variations in external coloration and radular morphology. These data are extremely useful and help fill in a major gap in our knowledge of the Atlantic "blue chromodorids."

Hans Bertsch

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Guamampa n.g. (Gastropoda, Pulmonata), a Bradybaenid Land Snail with Monadeniid Characters

by A. A. SCHILEYKO. 1996. *Bulletin du Muséum National d'Histoire Naturelle, Section A (Zoologie, Biologie et Ecologie Animales)* 18(3-4):401–408.

This paper consists of descriptions and figures of the shell and reproductive system of the Sulawesi land snail *Helix tuba* Albers, 1854, and the proposal of a new genus

(*Guamampa*) for it. The taxon is removed from Camaenidae and assigned to Aegistinae (of Bradybaenidae). Five other species are surmised to belong to the same genus but apparently were not dissected. Similarities are noted with reproductive characters of other Bradybaenidae, including the North American clade *Monadenia* Pilsbry, 1895. A HENNIG86 (Farris, 1988) cladistic analysis is performed on a small data set (four taxa and seven binary characters) and forms the basis for a far-ranging—and ultimately unjustified—suprageneric taxonomic change.

This work continues Schileyko's (1991) attempt to draw relationships among the taxa of Helicoidea *sensu lato*, criticized at length by Roth (1996) for its use of conjectural, non-analytical, and authoritarian taxonomy. In that work Schileyko presented a scenario based solely on characters of the lower reproductive tract, in which genera were derived sequentially from other contemporaneous genera (e.g., *Mohavelix* Berry, 1943, from *Sonorella* Pilsbry, 1900; *Sonorella* from *Sonorelix* Berry, 1943). His "family trees" used schematics emphasizing the characters that supported his scenario; other characters were selectively excluded from the discussion (e.g., the penial sheath of *Sonorella*). All genera, whether the monotypic *Eremariontoidea* Miller, 1981, or the speciose *Sonorella*, were treated as single entities—grades—along a few linear evolutionary paths; there was no representation of the diversity of side branches. Because many genera were considered to be derived directly from other genera (e.g., Schileyko, 1991:fig. 7), the system included numerous paraphyletic groups. Criteria of parsimony or independent characters supporting or falsifying these notions of ancestry and descent were not considered. Phylogenetic analysis by Roth (1996) falsified Schileyko's (1991) scenario as the most parsimonious account of helminthoglyptid evolution. The present paper is an improvement in that it includes a cladistic analysis, but as discussed below, that analysis presents problems of its own.

Like the Helicoidea paper, this one contains assertions without substantiation or analysis (e.g., p. 404: "*Aegista subchinensis* . . . is obviously very close to *A. chinensis* . . ."). It contains two-taxon statements ([Taxon A] is closely related to [Taxon B]), whereas the minimal form of such a statement that allows one to draw systematic conclusions is a three-taxon statement ([Taxon A] and [Taxon B] share derived character-state [X] which is not also shared by [Taxon C]). Other information is introduced without documentation. For example, the statement (p. 407) that mucus glands in the Mexican and Central American genera *Xanthonyx*, *Metostracon*, *Trichodiscina*, and *Miraverellia* are not alveolar internally but have anastomosing folds as in *Monadenia* should have been documented by reference to the author's own dissected specimens (if any) or to descriptions or figures elsewhere in the literature.

The sexual apparatus in Aegistinae is referred to as

plesiomorphic with respect to that in Bradybaeninae and Xanthonychinae (p. 401), but the cladistic data set (p. 407) lists two characters of which the state in *Aegista* is said to be derived with respect to that in other taxa in the analysis.

The statement (p. 405) that the anatomies of *Monadenia fidelis* (Gray, 1834), *M. infumata* (Gould, 1855), and *M. troglodytes* Hanna & Smith, 1933, do not differ significantly is unfortunate. This statement probably was intended to assert the generality within *Monadenia* of the characters being submitted to analysis, but as written it could be interpreted as dismissing species-specific (and in the case of *M. troglodytes*, subgeneric) differences among these taxa.

The HENNIG86 analysis is flawed in the following ways: (1) the character selection is limited to seven characters, all from organs of the lower reproductive tract. (2) The four taxa analyzed do not constitute a monophyletic group. *Aegista* and *Tricheulota* are only two among many genera in diverse subfamilies of Schileyko's (1991) taxonomy (Aegistinae and Bradybaeninae, respectively). No Xanthonychinae are analyzed, even though their similarities are brought into the discussion later (p. 407) and in terms of Schileyko's (1991:fig. 5) family tree they are derivative of bradybaenid taxa considered here. (3) Character-state polarities are based on non-explicit outgroup comparison with undefined "other helicoid taxa" (p. 406).

Schileyko gives neither the search algorithm used nor the tree statistics. When run as a four-taxon analysis (i.e., without an outgroup) using the implicit enumeration algorithm of HENNIG86, his data generate the tree (*Aegista*, *Monadenia*, (*Guamampa*, *Tricheulota*)) reported by him; the tree is nine steps long with consistency index (ci) 0.77 and retention index (ri) 0.60.¹ In spite of *Guamampa*'s clustering more closely with *Tricheulota* than with *Aegista*, the author continues to assign *Guamampa* to Aegistinae.

The starting point of the paper is the taxonomy of Schileyko (1991), as shown in Figure 1: Aegistinae (subfamily of Bradybaenidae) interpreted as ancestral, on the one hand, to Bradybaeninae and, on the other, to Xanthonychinae (of Xanthonychidae). The genital configuration in "Monadeniinae" (that is, *Monadenia*²) is seen as "immediately derived from the condition in Xanthonychinae" (p. 401).

Of course, because American helicoids were not in-

¹ When an outgroup with all characters in the plesiomorphic state is added, the following tree (10 steps long, with ci 0.70, ri 0.57) is produced: (outgroup, *Aegista*, (*Monadenia*, (*Guamampa*, *Tricheulota*))).

² Nordsieck (1987) proposed the redundant taxon Monadeniinae, containing only the genus *Monadenia* and exactly coextensive with it, as much for "bookkeeping" reasons as for its information content.

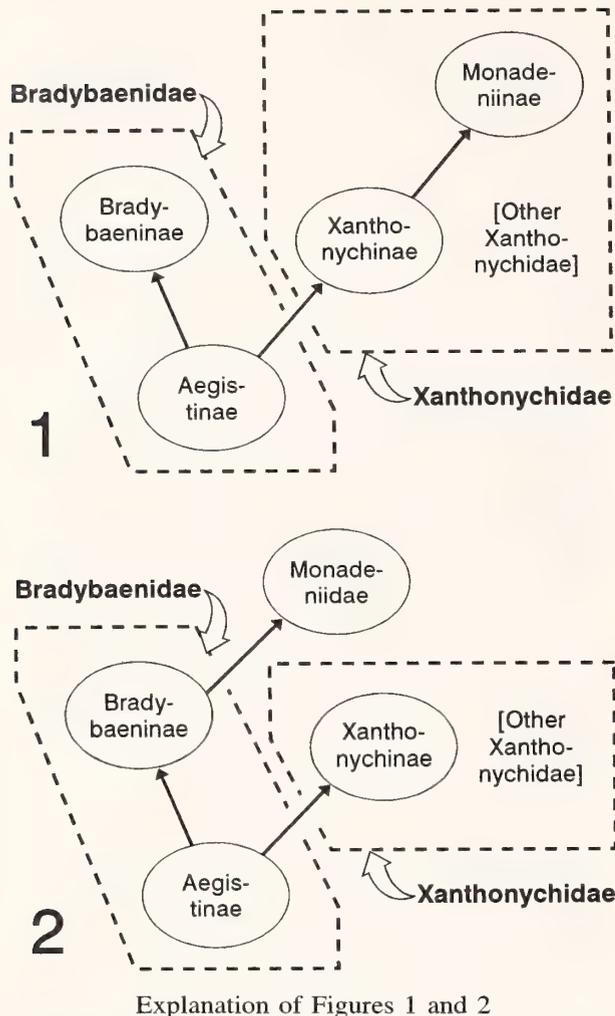


Figure 1 Relationships of family-group taxa according to Schileyko (1991). Straight arrows indicate "descent." Bradybaenidae is paraphyletic. "Other Xanthonychidae" includes the so-called "Sonorellinae" and "Micrariontinae," the members of which belong to Helminthoglyptidae (Roth, 1996); hence, Xanthonychidae *sensu* Schileyko (1991) is polyphyletic.

Figure 2 Relationships of taxa according to Schileyko (1996). Bradybaenidae is twice paraphyletic, Xanthonychidae polyphyletic.

cluded in the data set, the HENNIG86 analysis has no bearing on their relationship to *Monadenia*. But Schileyko's response to the results is to elevate *Monadenia* from genus to family rank (Figure 2). His stated reason is that "*Monadenia* was derived independently from ancestors other than those of the rest of American helicoids" (p. 407). This seems to be an argument for avoiding polyphyly of Xanthonychidae; but is that really a danger?

Xanthonychidae *sensu* Schileyko (1991:223) includes the so-called Sonorellinae and Micrariontinae. Both of

those are heterogeneous assemblages of taxa that fall out in disparate parts of the consensus tree for Helminthoglyptidae (Roth, 1996). The character-states that Schileyko (1991) used for grouping are widely homoplastic. Xanthonychidae *sensu* Schileyko (1991) is therefore already polyphyletic.

The author could have achieved the same goal merely by assigning *Monadenia* to Bradybaenidae, thereby endorsing Miller & Naranjo-García's (1991) and Roth's (1996) conclusions and avoiding the taxonomic mischief of the redundant name Monadeniidae. The point of this criticism, however, is not to argue over the rank at which the clade *Monadenia* is recognized—ultimately a sterile and subjective exercise. The solution is, instead, to discover monophyletic groups through wider cladistic analysis and express the results in a rank-free taxonomy (Gauthier et al., 1988; Roth, 1996).

It is to the author's credit that he attempted a cladistic analysis, which allows this paper to be criticized on specific points, rather than—as with his 1991 monograph—merely dismissed as irrelevant to future taxonomies. However, although the results have some limited interest in and of themselves, ultimately the phylogenetic analysis is not well integrated into the body of the work. It has the appearance of an afterthought or, worse, an attempt to justify conclusions previously reached by non-explicit means. Malacologists who value a rigorous, hypothesis-driven approach to molluscan systematics will file away the conclusions of this paper with a great big question mark and await a more knowledgeable treatment of the topic.

B. Roth

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Missouri Aquatic Snails

by SHI-KUEI WU, RONALD D. OESCH, and MARK E. GORDON. 1997. Missouri Department of Conservation, Natural History Series, No. 5. iv + 97 pp., 134 figs., 56 maps.

This well-organized, quarto-size manual reports the results of a statewide survey of aquatic snails initiated by author Oesch in 1982. Fifty-six species were recorded from Missouri; the identifications were made by Wu (pulmonates) and Gordon (operculates). The material is deposited in the University of Colorado Museum and is identified by museum lot numbers in the "records" section for each species. The work ends with a brief consideration of regional physiography and biogeography and a table assigning the species to a previously proposed system of aquatic community types.

The species are treated in a systematic order. Each species entry includes a common name, one or more sketch-like line drawings of the shell, a paragraph of diagnostic characters (although no explicit comparisons among species, and no identification key), a summary of distribution, a list of records from the Oesch survey, and a dot map plotting distribution on the drainage pattern of the state. Earlier historical collections from Missouri are not included in the distributional records, although former distribution is sometimes mentioned in a section of remarks.

The new taxon *Campeloma missouriensis* Gordon is proposed, necessitated by a recent neotype designation that left this upper Mississippi and lower Missouri River basin species without a valid name. *Campeloma missouriensis* is said to be a *nomen novum*, but it is actually the proposal of a new species, complete with holotype designation.

B. Roth

Advances in Trematode Biology

edited by BERNARD FRIED and THADDEUS K. GRACZYK. 1997. CRC Press, Boca Raton, Florida. 466 pp. ISBN 0-8493-2645-1.

The study of medically important trematode parasites has made significant advances over the past 10 years. *Advances in Trematode Biology* provides researchers and students with updates on immunology, biochemistry, physiology, and molecular biology. Malacologists concerned with snail-vectored trematode diseases in humans and animals or the relationships among mollusks and their parasites will find this book an important resource.

Atlante delle Conchiglie Marine del Mediterraneo. Atlas of the Mediterranean Seashells, vol. 2. (Caenogastropoda parte 1: Discopoda—Heteropoda)

by RICARDO GIANNUZZI-SAVELLI, FRANCESCO PUSATERI, ALBERTO PALMERI, and CLAUDIO EBREO. 1997. Published by "La Conchiglia," Rome. 258 pp., approximately 1000 figs. ISBN 88-86463-02-2.

Sometimes, the statement with the fewest words is the most eloquent. This handsome book says what it has to say through its thousand, more or less, colored illustrations. After a systematic catalog of the species contained, the supporting text is limited to the name and authorship of each species (often also with genus of original proposal), a brief statement of general distribution, and the locality and size of each figured specimen. The intention of this work is not to delve into "any deeper discussion of the various systematic, nomenclatural, and taxonomic problems due to insufficient knowledge or scarcity of available material" (p. 7), but rather to fully illustrate the shells of mollusks living in the Mediterranean Sea.

The photographs are of uniformly high quality, the gastropod shells posed in standard orientation against a black ground. SEM images are employed judiciously, mainly to show fine details such as protoconchs, but also for whole-shell illustrations of several smaller species.

A significant component of this volume is the Rissoidea. As P. Bouchet states in the preface, the most spectacular diversification among nearshore mollusks that has taken place in the Mediterranean is probably that in the Rissoidea: "Nowhere else in the world is it possible to encounter so many species of Rissoidea within one square meter of rocky bottom or seagrass bed" (p. 6). Although a critical review of Rissoidea—among other difficult-to-understand groups—is still needed, the identifications used in the Atlas are said largely to correspond to the most commonly held opinions of recent authors. The writers also have had the benefit of access to the collections and opinions of knowledgeable members of the Società Italiana di Malacologia.

I do not find a statement anywhere in this volume as to where and in what collections the illustrated specimens reside. (Perhaps the first volume in the series provided this information.) This simple fact, affecting the replicability of the experiment, as it were, means that persons wishing to consult the figured specimens would undoubtedly have to contact the authors to determine if such an examination were even possible.

That limitation, however, is not likely to mean much to lovers of fine illustrated books on mollusks, who should welcome this work as one of the best of its kind.

The volume is available at a cost of US \$130 from La Conchiglia, Via Focilide 31, 00125 Rome, Italy. Inquiries can be sent to M. A. Angioy, Editor, La Conchiglia, at conchiglia@pronet.it.

B. Roth

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c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

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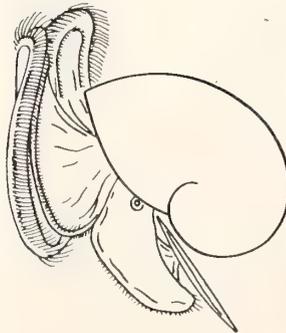
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