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CONTENTS

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ABSTRACT.—We studied seabird distribution beyond the continental shelf off eastern South America, between Tierra del Fuego (53°S) and southern Brazil (29°S) in the austral spring of 1975. Bird populations seemed low in this little studied area, but data from other seasons are too few to permit comparisons. Maximum numbers and diversity ocurred in the immediate vicinity of the Subtropical Convergence. The distribution of several species was largely restricted to zones of surface water (Subantarctic, Subtropical) on each side of the convergence. The occurrence of three immature Emperor Penguins *(Aptenodytes forsteri)* at 40°30'S, 54°34'W establishes the northernmost record for this Antarctic species.

Basic information on seabird distribution in the South Atlantic is surprisingly scanty. Most recent studies (e.g., Tickell and Woods, 1972; Cooke and Mills, 1972; Jehl, 1974; see also Watson et al., 1971 and references therein) have dealt largely with populations over the continental shelf or along the continental slope. This is not surprising as pelagic bird studies must usually be carried out incidental to other oceanographic or commercial activities. As a result, our knowledge is strongly biased in favor of those species that frequent near-shore waters or commercial shipping lanes.

An opportunity to obtain ornithological data from the little-studied area beyond the continental shelf of eastern South America was realized in the austral spring of 1975, when the R/V Hero was assigned to support studies on marine vertebrates in the South Atlantic (Cruise 75-5). This paper reports on the ornithological results of that cruise.

ITINERARY AND METHODS

Hero departed Ushuaia, Argentina, on 10 September, passing eastward through the Beagle Channel, and then northeastward through the Strait of Le Maire along a course parallel to but slightly beyond the edge of the continental shelf. On the morning of 16 September, Hero left the cold Subantarctic Zone of surface waters, passed through the Subtropical Convergence, and entered the warmer, less productive waters of the Subtropical Zone. At noon on 20 September Hero reached its northernmost station (28° 44'S) off southern Brazil and headed ESE to the Bromley Plateau (31° 30'S, 33° 30'W), arriving on 23 September. The route then turned southward and southwestward, and between 24-28 September generally followed or paralleled the edge of the Subtropical Convergence. On 29 September, Hero reentered subantarctic waters and continued southwestward, passing the Falkland Islands on 3 October and arriving in Ushuaia on 6 October (Fig. 1).

Shipboard observations and censuses were made by Rumboll with the assistance of R. L. Brownell, Jr. and other members of the scientific party and ship's crew. Censuses were made for a ten minute period during each two hour interval throughout the day. All birds seen were counted and the number of ship-following species was estimated (Table 1). Other observations and counts were made as often as possible, as work schedule and weather permitted. Censuses were not taken when the ship was stopped for studies of marine mammals. Surface water temperatures were taken at 0800, 1200 and 1800 hours. Distribution and densities of the commoner species are shown in Figures 2 - 11.

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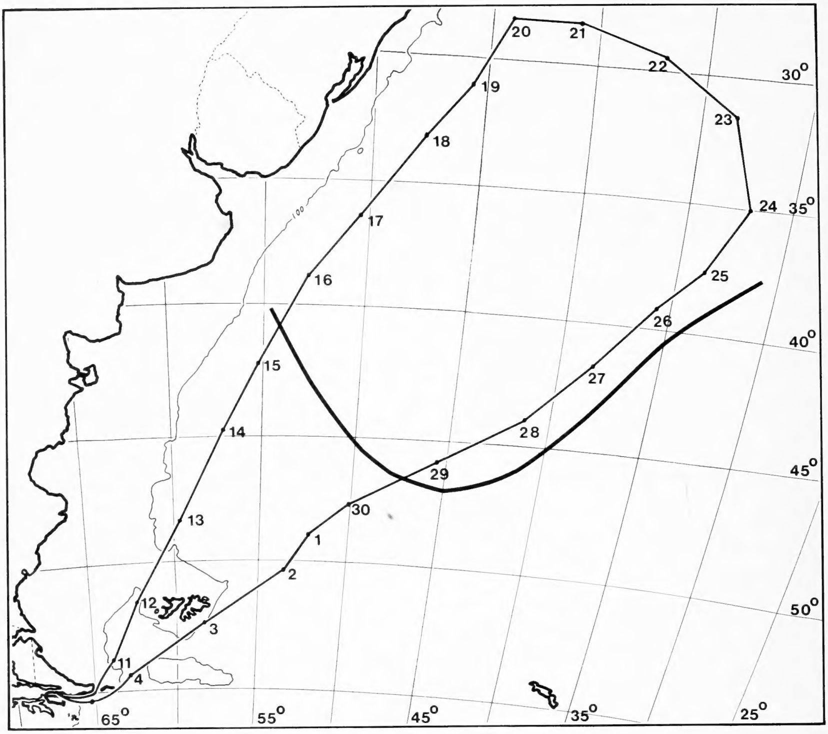

Figure 1. Cruise route of the R/V Hero (Cruise 75-5) in the South Atlantic Ocean, 11 September to 4 October 1975. Numbers indicate ship's noon position on each date from 11 September to 4 October. Heavy dark line marks the approximate location of the Subtropical Convergence. The light line marks the boundary of the continental shelf.

Weather conditions varied considerably but were, in general, suboptimal. Rough seas prevailed on many days, which seriously hampered observations, precluded collecting, and made sightings of birds flying close to or sitting on the water nearly impossible. A dense fog on 29 September virtually eliminated observations.

Collecting was done as opportunity presented. Specimens are deposited in the Natural History Museum, San Diego. Plankton samples were obtained daily; they have been deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires. Mallophaga were deposited at the University of Canterbury, Christchurch, New Zealand.

This study was supported by a grant from the National Science Foundation (NSF - OPP75 - 19724). The assistance of George E. Watson in identifying critical specimens is gratefully acknowledged.

ANNOTATED LIST OF SPECIES

Emperor Penguin *(Aptenodytes forsteri).*—The sighting of this species constitutes the most remarkable distributional record of the cruise. On 15 September, Rumboll saw two birds 100 m ahead of the Hero and watched them carefully until they dove when the ship was only 20 m distant; one hour later he saw a single bird. He noted that the color of the ear patch was washed out, which indicates that the birds were juveniles. Rumboll has had extensive experience with King Penguins *(A. patagonica)* on the Falkland Islands and is confident of his identification. The sightings were made at 40° 30′S, 54° 34′W, some 40 miles S of the Subtropical Convergence and over 400 miles off southern Buenos Aires Province, Argentina. This is by far the most northern record for either species of *Aptenodytes* (cf. Watson et al., 1971). The sighting of three birds in this ornithologically unexplored area—and hundreds of miles north of the pack ice—suggests that the winter range of juvenile or non-breeding Emperors may be far more extensive than is currently realized.

Gentoo Penguin *(Pygoscelis papua).*—One, 30 mi. SE Falkland Islands, 3 November.

Rockhopper Penguin *(Eudyptes crestatus).*—Small penguins, almost certainly of this species, were encountered, very uncommonly, in cold waters from west of the Falklands north to the latitude of the Valdes Peninsula (12-15 September), and on several days between 30 September and 5 October, as the ship approached and passed by the eastern edge of the Falklands. The largest flock was 7; most flocks comprised two or three individuals. This species probably winters fairly commonly in deep water beyond the continental shelf as far north as Uruguay (Jehl, 1974).

Magellanic Penguin *(Spheniscus magellanicus).*—This species is common over the continental shelf but rare over deeper waters (Jehl, 1974). The only sightings during this cruise were groups of 4 and 5 in the Beagle Channel on 10 September, 3 birds north of the Falklands on 13 September, and groups of 2, 2, and 3 far east of the Valdes Peninsula on 15 September.

Wandering Albatross *(Diomedea exulans).*—Widely distributed, though mostly uncommon, over entire route, with maximum numbers (18 on 25 September) in the vicinity of the Subtropical Convergence. No first-year birds were observed. Rumboll noted that most of the birds north of 35°S trailed their feet, whereas those farther south folded them forward into their belly feathers. This behavior may be related to thermoregulation and requires further substantiation. Rumboll did not identify any examples of *D. epomophora*, which seems to prefer shallower shelf waters (Jehl, 1974; Watson et al., 1971).

Black-browed Albatross *(Diomedea melanophris).*—Seen along the entire cruise route, though very uncommon in warm waters north of and remote from the Subtropical Convergence. The largest numbers (100-400 individuals) were encountered in the vicinity of the Falkland Islands, where the species nests. Rumboll noted the virtual absence of immatures, no more than 10 being recorded on the entire cruise. A concentration of 300 on 3 October near the Falklands was associated with a herd of Pilot Whales *(Globicephala melaena)* and Dusky Dolphins *(Lagenorhynchus australis).*

Yellow-nosed Albatross *(Diomedea chlororhynchos),* **Gray-headed Albatross** *(D. chrysostoma).*—On 23-25, and 27 September Rumboll saw small numbers of immature Yellow-nosed Albatrosses in warm waters north of the Subtropical Convergence. Gray-headed Albatrosses were recorded definitely on 26 September (1 bird) in the vicinity of the Convergence and were seen regularly but uncommonly thereafter to the vicinity of Staten Island (maximum 7 on 30 September). Fifteen "gray-headed" albatrosses were seen under poor conditions on 24 September. Rumboll felt that more than one species was present, but in view of the relatively high water temperatures (15.5°C) it seems likely that most were *chlororhynchos.*

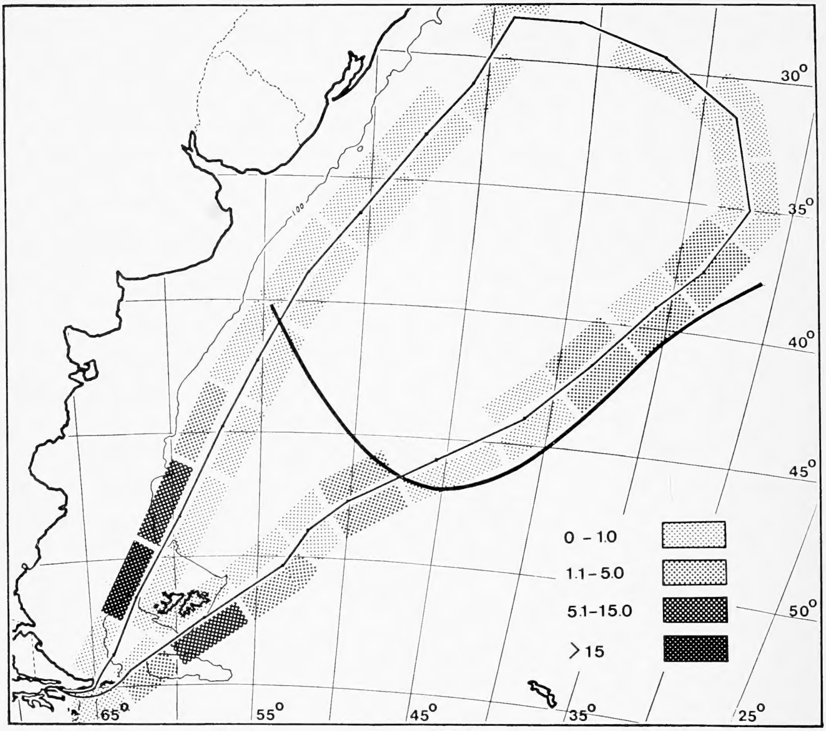

Figure 2. Distribution of *Diomedea melanophris* (outside of cruise track), and *Diomedea exulans* (inside of cruise track). Key to densities pertains to Figures 2-11.

The predilection of *chrysostoma* for colder waters is well known. An adult *chrysostoma* weighed 3700 g.

Sooty Albatrosses *(Phoebetria fusca, P. palpebrata).*—Both of these species were observed, *fusca* much more commonly (21 vs. 6 sightings). Records of *palpebrata* were made along or south of the Subtropical Convergence, whereas *fusca* preferred warmer waters.

Giant Petrel *(Macronectes giganteus).*—Giant Petrels (all presumably *M. giganteus)* were common in Subantarctic waters, uncommon along the Subtropical Convergence, and almost unrecorded in the Subtropical zone. With the exception of a white-phased bird near Staten Island on 4 October, all sightings were of dark-plumaged individuals.

Southern Fulmar *(Fulmarus glacialoides).*—Regular and fairly common south of the Subtropical Convergence, but most abundant in the vicinity of land (Tierra del Fuego, Falklands). Only two individuals were sighted north of the Convergence.

Cape Pigeon *(Daption capensis).*—This was the species encountered most commonly. It occurred throughout the entire cruise area, though it was much less common north of the Subtropical Convergence. Cape Pigeons are well known scavengers and immediately investigate floating scientific specimens or garbage. Rumboll saw several using their wings to dive after jellyfish. On 17 September, he saw two birds with bright pink patches on the belly, perhaps marked by other researchers.

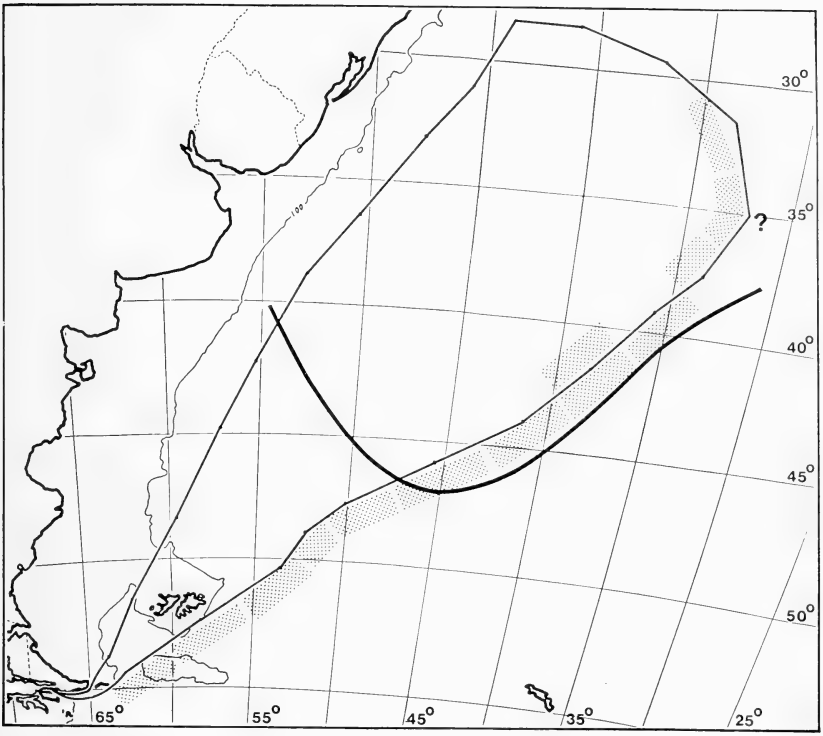

Figure 3. Distribution of *Diomedea chrysostoma* (outside) and *Diomedea chlororhynchos* (inside).

Prions *(Pachyptila* spp.).—Packs of prions were fairly common over the southern half of the cruise route, except in the vicinity of land, and were particularly common along the Subtropical Convergence. One possible *P. belcheri* was identified among many prions seen on 16 September. On 27 September, along the Subtropical Convergence, Rumboll collected 3 prions and on 30 September, south of the Convergence, 4 more. Although these show considerable variation in bill shape, all seem referable to *salvini,* and are presumed to have originated on Tristan da Cunha (G. E. Watson, pers. comm.). These records considerably extend the western range of *salvini* (cf. Watson et al., 1971).

Blue Petrel *(Halobaena caerulea).*—A single bird NE of the Falklands on 2 October, and three birds probably of this species on 16-17 September. The latter records, if correct, seem far north for this predominantly cold-water species.

Atlantic Petrel *(Pterodroma incerta).*—This was the commonest and most easily identified species of *Pterodroma.* Although it was regular along the northern part of the route, it was most abundant in the immediate vicinity of the Subtropical Convergence. A male weighed 650 g.

Soft-plumaged Petrel *(Pterodroma mollis).*—Encountered daily between 17 and 26 September, in Subtropical waters. Only a few were seen each day; the highest count, 21, was made on 20 September.

Pterodroma spp.—Between 21 and 25 September, north of the Convergence, Rumboll observed a few individuals of two or more species of *Pterodroma.* His descriptions suggest *Pt. arminjoniana* (mainly) and *Pt. lessoni* (one record).

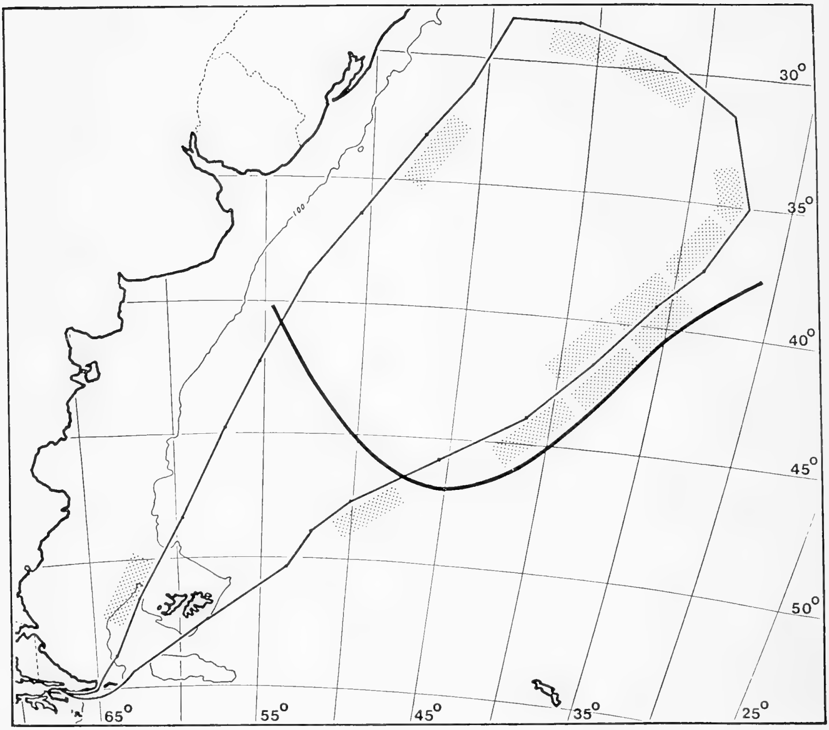

Figure 4. Distribution of *Phoebetria palpebrata* (outside) and *Phoebetria fusca* (inside).

Shoemaker *(Procellaria aequinoctialis)*.—This species, which prefers deep, offshore waters (Jehl, 1973, 1974) was sighted throughout the entire cruise, but was rare in the Subtropical zone. No significant concentrations were observed. Two individuals of *P. a. conspicillata* were seen along the Convergence on 24-25 September. A specimen of *P. a. aequinoctialis* weighed 1100 g.

Pediunker *(Procellaria cinerea)*.—The Pediunker, or Gray Petrel, was widely distributed over deep waters, most records being made near the Subtropical Convergence. On most days no more than one bird was reported. The largest concentration, 13 in an afternoon, was found in the vicinity of a herd of Pilot Whales well off Golfo San Jorge on 14 September. A male collected on 28 September weighed 1050 g. Distribution maps in Watson et al., (1971) suggest that the Pediunker and Shoemaker are commoner over the Continental Shelf than farther offshore. This is an artifact, resulting from the fact that most seabird observations in the South Atlantic have been made near the coast. Actually, both species prefer deep waters, and the Pediunker is extremely rare over the shelf (Jehl, 1974, Cooke and Mills, 1972).

Cory's Shearwater *(Calonectris diomedea)*.—An unidentified shearwater at the Bromley Plateau on 23 September was probably this species, which has recently been reported wintering in fair numbers off the coast of northern Argentina (Cooke and Mills, 1972).

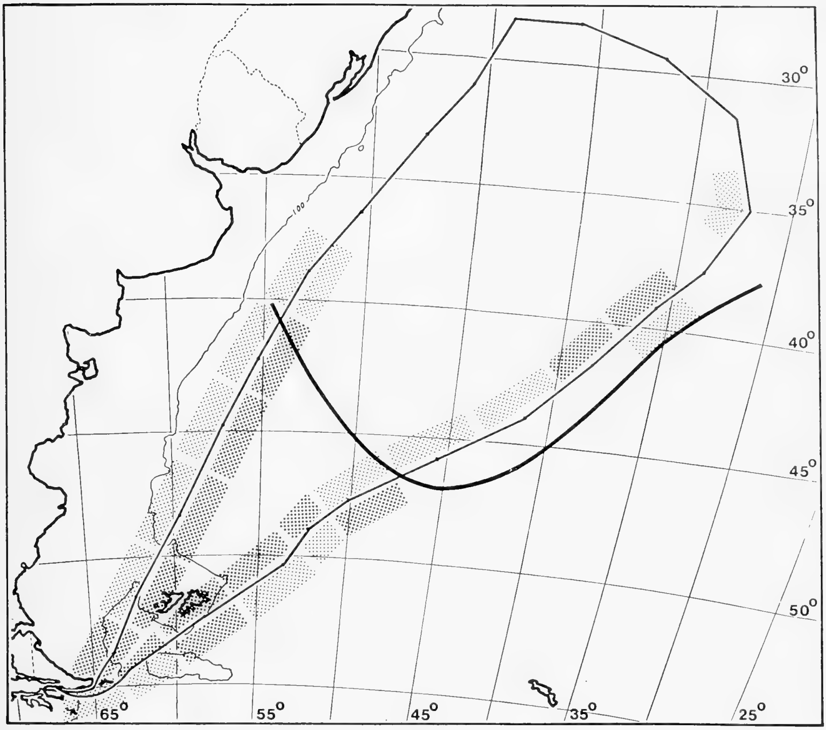

Figure 5. Distribution of *Fulmarus glacialoides* (outside) and *Macronectes giganteus* (inside).

Sooty Shearwater *(Puffinus griseus).*—Seen along most of the cruise route, but common only in cool waters; very rare or absent in warm waters. Areas of local abundance, principally near Staten Island and in the Strait of Le Maire, are near presumed nesting localities. A flock of 3000 along the south shore of Staten Island in the early evening of 4 October may have been flying toward a staging area.

Greater Shearwater *(Puffinus gravis).*—Watson (1975) considers this a species of "cool waters near the Subtropical Convergence." During this cruise it was found almost exclusively in warm waters north of the Convergence, where it was fairly common. Its distribution paralleled that of *Pterodroma mollis* and largely complemented that of *Puffinus griseus,* which occurred mainly in cooler waters.

Manx Shearwater *(Puffinus puffinus).*—Three individuals near 37° 30′S, 34°W were the only sighting of this species, which winters commonly off the South American coast between Brazil and northern Argentina.

Small shearwaters *(Puffinus* spp.).—On 26 September, near 39°S, 35°S 33′W, Rumboll saw a single small shearwater with an extremely fast and shallow wing beat, a brownish back, and with the white of the undertail coverts extending upward onto the sides of the rump. These characters suggest the Fluttering Shearwater *(P. gavia),* which is only known to occur in the New Zealand region. On 20 September he saw another small shearwater, but with a pale grayish back. This observation may refer to the Allied Shearwater *(P. assimilis),* which has been reported from the general area.

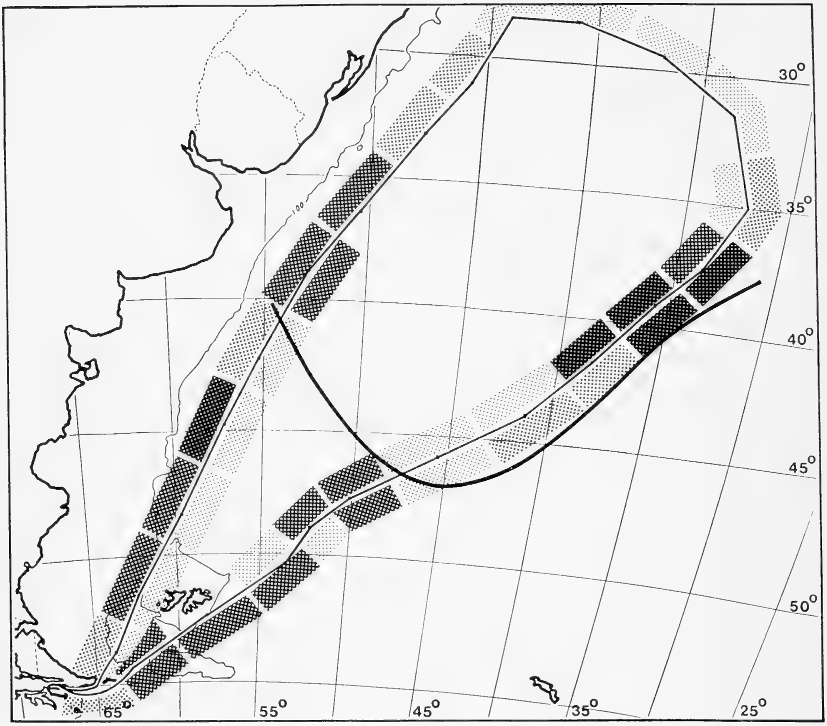

Figure 6. Distribution of *Daption capensis* (outside) and *Pachyptila* sp. (inside).

Wilson's Storm-Petrel *(Oceanites oceanicus).*—Uncommon though scattered along the entire route; seemingly commonest near the Subtropical Convergence and rarest in waters warmer than 17°C. Rumboll noted that it was most frequently seen near patches of floating kelp. A specimen taken 46° 24′S, 56° 55′W is referable to *O. o. oceanicus.*

Gray-backed Storm-Petrel *(Garrodia nereis).*—Rare, a total of 11 birds seen on 6 dates. All observations were made south of the Subtropical Convergence and beyond the continental shelf.

Black-bellied Storm-Petrel *(Fregetta grallaria).*—Rare, a total of 13 birds observed on 10 dates. Except for a tendency to remain far offshore, the species exhibited no obvious distributional pattern, occurring in very cold as well as in very warm waters. Many observations were made north of the range shown by Watson et al., (1971).

Diving-Petrels *(Pelecanoides* spp.).—Diving petrels were fairly common in the vicinity of the Beagle Channel and Strait of Le Maire (10-11 September, maximum 150) and in the vicinity of the Falklands and Staten Island (3-5 October). Two specimens of *P. urinatrix* were taken aboard ship on 4, 5, October; presumably all records pertain to that species. Several diving-petrels were seen beyond the continental shelf off Buenos Aires Province on 26-27 September (maximum, 14 on the 27th); from previous records (Jehl, 1974) it seems probable that these were *urinatrix.*

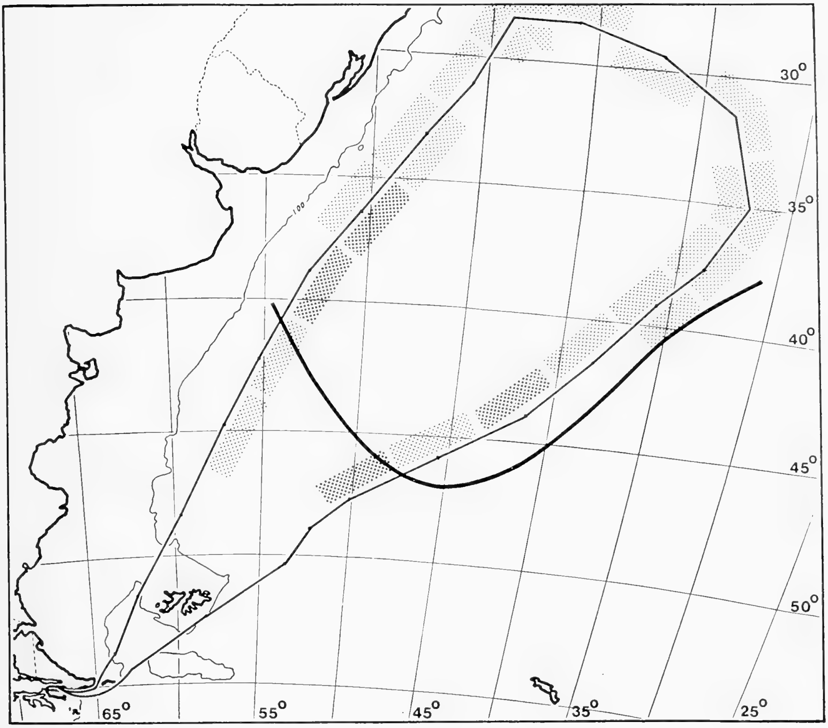

Figure 7. Distribution of *Pterodroma mollis* (outside) and *Pterodroma incerta* (inside).

Skuas *(Catharacta* spp.).—Skuas were seen occasionally, though rarely more than one per day, with most records from north of 47°S. The birds rarely approached the ship and Rumboll made no attempt to determine which form(s) was present.

Jaegers *(Stercorarius* spp.).—Three unidentified jaegers were seen off the coast of Brazil on 19-20 September.

Kelp Gull *(Larus dominicanus).*—Uncommon but regular south of 48°S. All observations were made within 300 miles of land.

Terns *(Sterna* spp.).—Scattered terns, usually individuals but occasionally small flocks, were seen between 48°S and 29°S. There was no obvious pattern; maximum concentrations (14, 9 birds) were observed near the Subtropical Convergence on 16 and 29 September, respectively. Terns rarely approached the ship and specific identification was impossible, although most observations presumably refer to *S. hirundinacea.*

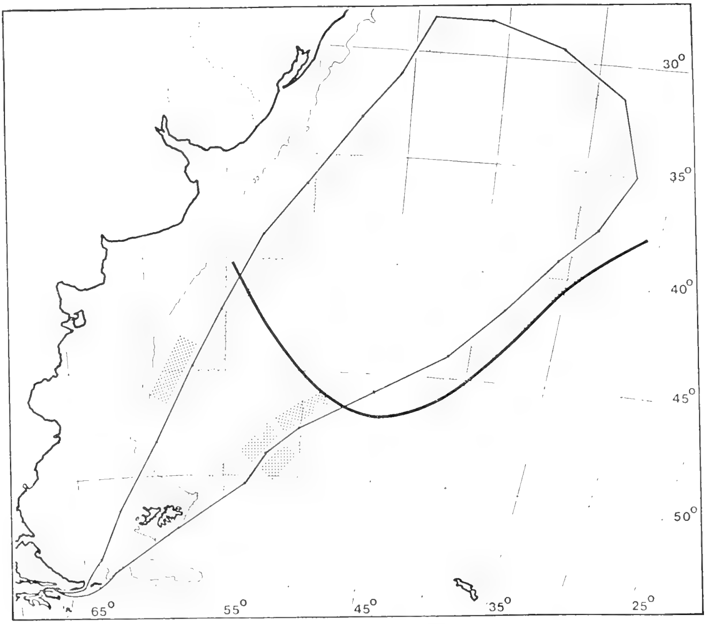

Figure 8. Distribution of *Procellaria cinerea* (outside) and *Procellaria aequinoctialis* (inside).

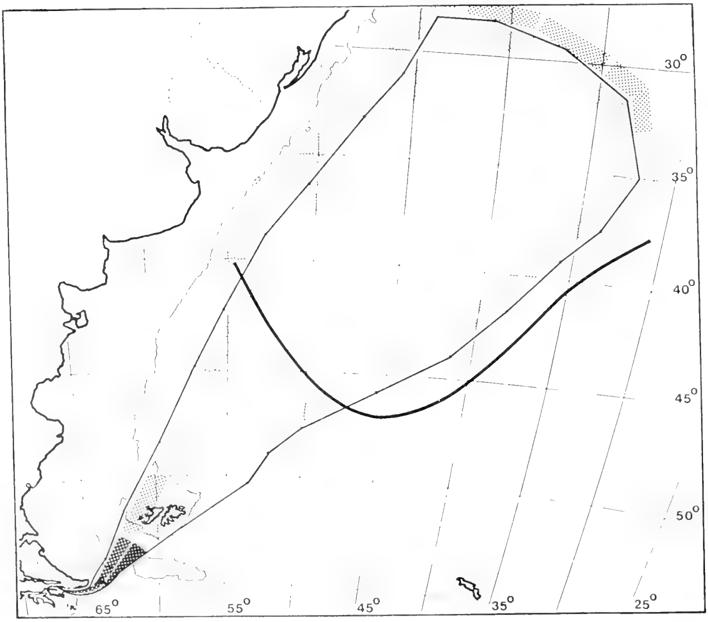

Figure 9. Distribution of *Puffinus gravis* (outside) and *Puffinus griseus* (inside).

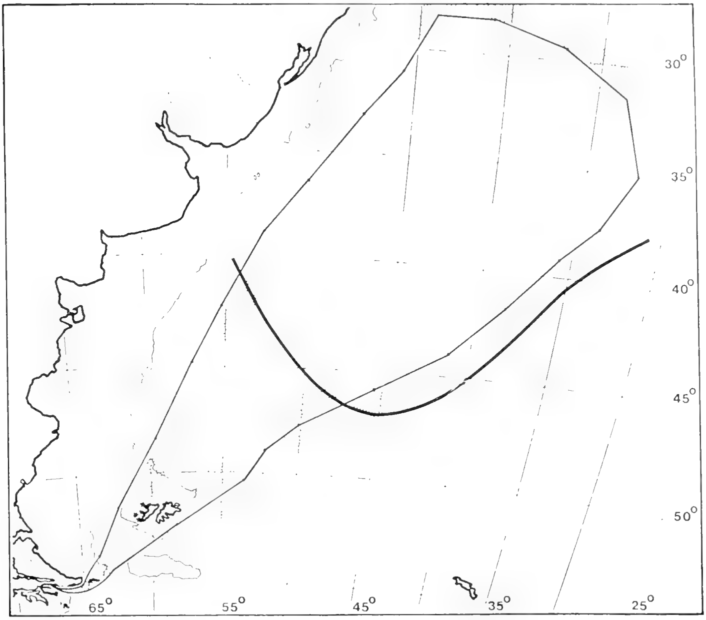

Figure 10. Distribution of *Fregetta tropica* (outside) and *Garrodia nereis* (inside).

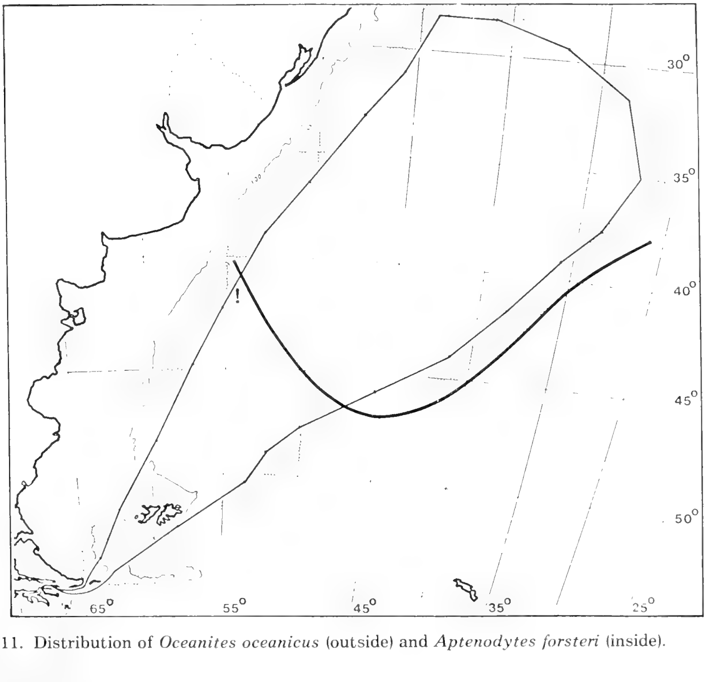

Figure 11. Distribution of *Oceanites oceanicus* (outside) and *Aptenodytes forsteri* (inside).

TABLE 1. Summary of daily censuses. Abundance indicated is average number of birds per ten minute census are omitted.

	September										
	11	12	13	14	15	16	17	18	19	20	21
Eudyptes sp		+	+	+	0.2						
Diomedea exulans		0.7	0.3	+	+	0.6	0.7	0.2	0.3		
Diomedea melanophris	1.0	15.5	5.3	4.2	0.5	0.6	0.7	0.2		0.2	
Diomedea chlororhynchos											
Diomedea chrysostoma											
Phoebetria fusca								+			+
Phoebetria palpebrata		+									
Macronectes giganteus	4.0	4.0	3.8	4.3	1.3	0.2					
Fulmarus glacialoides	2.2	0.2	0.5	+	0.8	0.2					
Daption capensis	3.5	9.2	11.0	15.7	2.8	8.4	5.7	2.8	2.6	0.2	0.4
Pachyptila sp.	0.5	+	1.0	+	+	7.4					
Procellaria aequinoctialis				0.2	+	+	0.3	0.2		0.2	
Procellaria cinerea				1.8	+						
Puffinus gravis						0.4	0.3	0.2	0.2	0.4	3.0
Puffinus griseus	10.5	1.5	0.2	0.2	+		+		0.3		0.2
Pterodroma incerta				0.5	0.3	4.4	2.0	0.2		0.2	
Pterodroma mollis							0.2	1.0	1.0	0.6	0.6
Pterodroma sp.											0.2
Oceanites oceanicus	0.2			0.7	0.7	0.6	0.8		0.3	+	0.2
Fregetta tropica										+	+
Garrodia nereis		0.2	+		0.7						
Storm-petrel sp.							1.2	0.8	0.3		
Pelecanoides sp.	3.0										
Catharacta skua					0.2	+	+		+	+	
Larus dominicanus	+	+	0.2								
Sterna sp.			+	0.2	+	0.8					
Periods of observation	4	6	6	6	6	5	6	5	6	5	5
Latitude °S	53°50′S	51°17′S	48°05′S	44°45′S	41°50′S	38°53′S	36°32′S	33°22′S	31°14′S	28°44′S	28°45′S
Longitude °W	64°10′W	62°19′W	59°42′W	57°11′W	54°50′W	52°52′W	50°23′W	47°41′W	45°51′W	44°05′W	41°02′W
Sea temperature °C	8.9	6.4	6.6	7.5	7.8	16.7	16.1	18.3	17.7	20.0	20.5
No. species	9	11	11	13	17	13	12	9	8	9	8

period. Birds seen during the day, but not in census period, are indicated by + . Species seen on fewer than four dates

									October				
22	23	24	25	26	27	28	29	30	1	2	3	4	5
								+			+		+
0.8	0.2	0.1	3.0	0.4	1.5	+		1.2	0.2	0.7	0.5	0.5	0.2
	0.2	0.2	3.0	2.0	2.0	1.0	0.2	3.3	0.8	1.7	13.5	3.5	0.4
	+	0.8	1.0		0.2								
		?		+	0.2	0.4	0.2	1.0	0.2	0.3	+	+	
+		+	0.6	0.6	0.2								
				0.2	+	+		0.2					
		+		1.6	2.0	0.2	+	0.3	1.8	5.0	1.2	3.5	1.0
				+				1.7	0.8	0.8	3.2	0.3	0.8
+	1.0	1.6	17.4	30.4	4.5	3.2	+	8.7	0.8	12.3	11.0	10.8	4.4
		+	11.4	40.8	37.5	0.6	1.0	14.0	10.8	0.3		8.3	
	0.2	+	1.0					1.2	1.2	0.2	0.2	0.3	
			+	+	+	+		0.2	1.2				
2.0	1.4	+	0.6										
	+	+	+	+	+	0.2		0.2	+		0.2	83.8	+
+		+	+	0.2	0.8	3.2	0.5	1.8					
	+	0.2	2.0	+									
0.2	0.4		+	0.4									
	+	1.0	1.0		+	+		1.0	+	+		+	
+	+				+		0.2	0.5		+			
								0.5		0.2		+	
			0.4										
					0.2						+	+	+
				+	+		0.2	+					
										+		0.3	+
+	+	+				+	+						
5	5	5	5	5	4	5	4	6	4	6	6	6	5
29°44'S	31°42'S	35°04'S	37°32'S	39°18'S	—	43°58'S	45°44'S	47°29'S	48°42'S	50°11'S	52°20'S	54°12'S	50°00'S
37°19'W	33°47'W	32°20'W	33°55'W	35°54'W	—	41°31'W	45°49'W	50°10'W	52°28'W	53°32'W	58°06'W	62°32'W	64°55'W
20.0	17.1	15.5	14.4	11.5	—	8.5	9.0	5.8	5.0	3.9	5.0	5.5	6.5
8	13	15	17	17	16	13	10	17	10	13	11	14	9

DISCUSSION

The sparseness of seabirds over the open ocean was impressive. In the Subantarctic Zone birds were uncommon and diversity was moderate, 12-13 species being recorded on most days. In the Subtropical Zone birds were rare, only 8-9 species being seen each day. The greatest numbers and diversity (16-17 species daily) occurred near the Subtropical Convergence, where warm- and cold-water faunas intermingled. But even there numbers were low. Lacking quantitative data from other years or other seasons, we are unable to advance any firm interpretation for these data. (Data obtained by Tickell and Woods [1972, Table 5] during a cruise between the Equator and South Georgia are not strictly comparable.)

The low numbers of Southern Hemisphere residents encountered may be a seasonal phenomenon, adults having already retreated southward to the vicinity of nesting islands. The low numbers of trans-equatorial migrants (Sooty and Greater shearwater, Wilson's Petrels) may indicate that birds summering in the Northern Hemisphere had not yet returned. Similarly, we are unable to compare deep water vs. continental shelf avifaunas, as the only available quantitative data from the shelf pertain to winter (Jehl, 1974) or mid-summer (Cooke and Mills, 1972) transects, except to point out the absence or rarity of species that prefer nearshore waters (Magellanic Penguin, Royal Albatross, Sooty Shearwater, Magellanic Diving-Petrel).

Very few concentrations were encountered. Local pockets of diving-petrels and Sooty Shearwaters in the Strait of Le Maire on 11 September and larger flocks of sooties at Staten Island on 4 October seem attributable to the proximity of nesting colonies, as do concentrations of Black-browed Albatrosses near the Falklands. A local concentration, 17 species off the Valdes Peninsula on 15 September, may have been related to upwelling, as numbers of Pilot Whales were also feeding in the area. A small assemblage of 50 prions, 30 Cape Pigeons, 10 Black-browed Albatrosses and a scattering of other species near 47° 29′S, 50° 10′W on 30 September could not be attributed to any particular oceanographic conditions. Rumboll noted that storm-petrels were often found near masses of floating kelp and suggested that these mats may "filter" planktonic organisms and thus enrich local feeding conditions.

Temperature preferences.—It is well established that the distribution of many seabirds is related to sea surface temperatures. Temperature preferences are not always precise and may shift seasonally, be affected by the proximity of breeding colonies, or change in response to exceptional feeding opportunities, such as may occur in the vicinity of convergences. The temperature preferences of species observed in this cruise (Figure 12) are largely in accord with those found by previous workers (e.g., Murphy, 1936; Biermann and Voous, 1950; Jehl, 1973, 1974; Watson, 1975). Thus, many common species (e.g., *Daption capensis, Diomedea melanophris)* occurred over a broad range. *Eudyptes* sp., *Diomedea chrysostoma, Phoebetria palpebrata, Macronectes giganteus, Fulmarus glacialoides, Pterodroma incerta, Procellaria cinerea, Puffinus griseus, Garrodia nereis,* and *Larus dominicanus,* were largely or entirely restricted to Subantarctic waters (15°C), whereas *Diomedea chlororhynchos, Phoebetria fusca, Pterodroma mollis,* and *Puffinus gravis,* occupied the Subtropical Zone (18°C). The occurrence of *Puffinus gravis* in the Subtropical Zone is somewhat surprising, as this species typically prefers colder waters. This species is absent from shelf waters in winter (Jehl, 1974); presumably birds seen on this cruise were migrants returning from the Northern Hemisphere that had not yet reached cooler waters near the breeding grounds. The apparent preference of *Larus dominicanus* for cold waters is an artifact due to the proximity of land in the more southern part of the cruise route; this species rarely wanders more than 50 miles to sea.

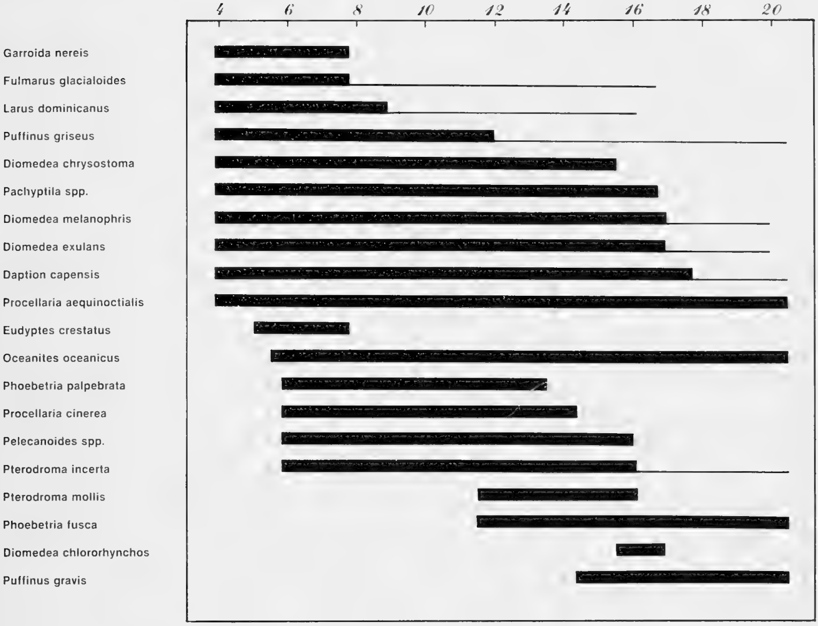

Figure 12. Temperature distribution of marine species encountered in this study. The major distribution is indicated by a solid bar, scattered records by a thin line.

Oiling.—Elsewhere Jehl (1974) has commented on the high frequency of oiling among procellariiform birds and penguins over the continental shelf of Argentina, particularly in the vicinity of major shipping lanes. Thus, it is interesting that over the open ocean, far from commercial traffic, Rumboll saw only one oiled bird, a Cape Pigeon 200 miles N of the Falklands.

Seabirds and marine mammals.—Seabirds have often been noted in the vicinity of marine mammals, particularly baleen whales, but the reports are usually anecdotal and provide little insight into the basis for the association. Opportunities to study such interactions are few and dwindling, as commercial harvesting continues to deplete whale populations.

We observed whales on 8 occasions: *Globicephala melaena* – 3 occasions; *Balaenoptera physalus* – 1; *Hyperoodon planifrons* –1; *Physeter catodon* –1 (2?), and unidentified – 1. In four cases, bird numbers increased in the vicinity of whales. In order not to disturb the whales we did not attempt to collect in the area. However, the species composition of these seabird flocks did not differ from those encountered elsewhere, suggesting that the birds and whales were responding independently to favorable feeding conditions.

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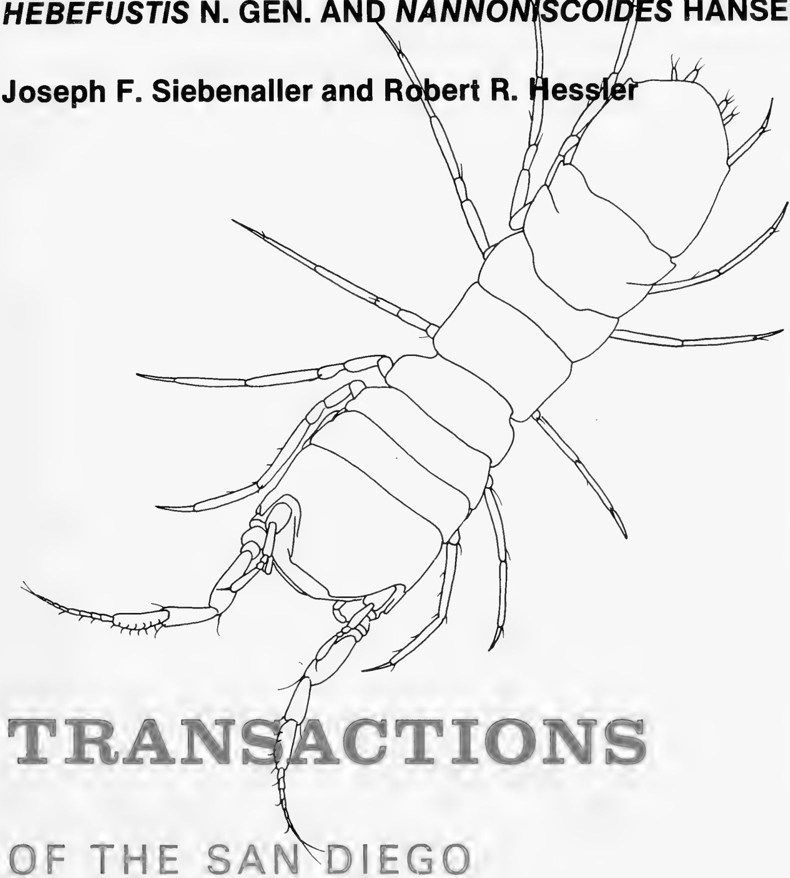
THE NANNONISCIDAE (ISOPODA, ASELLOTA): *HEBEFUSTIS* N. GEN. AND *NANNONISCOIDES* HANSEN

Joseph F. Siebenaller and Robert R. Hessler



TRANSACTIONS

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The Nannoniscidae (Isopoda, Asellota): *Hebefustis* n. gen. and *Nannoniscoides* Hansen

Joseph F. Siebenaller and Robert R. Hessler

ABSTRACT.—The morphologically diverse asellote isopod family Nannoniscidae Hansen 1916 is redefined and contrasted with the other major families of the superfamily Janiroidea. The bulbous fifth article of antenna I and the medial fusion of pereonites 6 and 7 are generally useful in distinguishing a nannoniscid. Where these features are absent, other characters must be employed: the single major dactylar claw on pereopods II-VII, the flat triangular molar process of the mandible, uropodal shape, and the presence of major setae on the tergites of pereonites 2-4.

The desmosomatid genus *Thaumastoma* Hessler is referred to the Nannoniscidae. *Sugoniscus* Menzies and George is placed in family *incertae sedis* pending further study. Features of *Desmosoma coalescum* Menzies and George are redrawn and the species is referred to *Nannoniscus.*

The definition of the genus *Nannoniscoides* Hansen is clarified and four new species are described. *Nannoniscus excavatifrons* Birstein is transferred to *Nannoniscoides.* A morphologically similar new genus, *Hebefustis,* is described with seven new species. *Nannoniscus primitivus* Menzies, *N. robustus* Birstein and *Nannoniscoides hirsutus* Menzies are referred to *Hebefustis.*

These new descriptions are based on materials taken from benthic samples encompassing a depth range of 587-5223 m in the North and South Atlantic Ocean. The bathymetric range of *Nannoniscoides* is 180-4833 m; the range of *Hebefustis* is 587-5223 m. A list of the described species of the family is given.

The isopod superfamily Janiroidea (= Paraselloidea Wolff, 1962) is found throughout the benthic marine environment (Kussakin, 1973). Although its representatives are reasonably abundant in many shallow-water habitats, it achieves its greatest diversity in the deep sea (Wolff, 1962; Menzies et al., 1973; Hessler and Thistle, 1975). Here the superfamily has undergone a major radiation, both in terms of species richness and variety of supraspecific taxa, such that it is one of the most diverse elements in any deep-sea community (Hessler and Sanders, 1967).

The Janiroidea contains approximately 20 family in current usage. About 12 of these are to be regarded as significant. For the most part these families are easily recognized and distinctly well defined. However, the Nannoniscidae is unusual in that while there is seldom any question about which species should be included within it, there are no key features which are universally possessed by all of its members. Thus, the Nannoniscidae displays a range of morphologies (e.g., *Nannoniscoides angulatus* Hansen, 1916; *Nannoniscus hanseni* Just, 1970; and *Nannonisconus latipleonus* Schultz, 1966) that causes considerable difficulty in constructing an adequate familial diagnosis.

This paper treats two genera [*Hebefustis* n. gen. with seven new species and *Nannoniscoides* Hansen (1916) with four new species] which highlight this problem in that both lack the distinctive bulbosity of the distal article of the first antenna and some lack the medial fusion of the sixth and seventh pereonites. These have generally been used as the hallmarks of the family. In order to clarify why we, and others in the past, feel these genera belong in the family, the paper redefines the Nannoniscidae and compares it to the other families.

The present study is based primarily on the extensive collections accumulated by the deep-sea sampling program of the Woods Hole Oceanographic Institution (Sanders et al., 1965; Hessler and Sanders, 1967; Sanders and Hessler, 1969). This program has made a series of sampling transects throughout the Atlantic Ocean, running out from shallow coastal waters into the abyss. Such transects are located off the northeastern United States (Gay Head–Bermuda transect), Surinam,

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northern Brazil, Argentina, Southwest Africa, Angola, Senegal, and Ireland. Additional samples have come from the Bay of Biscay (J. Allen, University of Newcastle upon Tyne), the Canary Islands (J. Allen), and the Weddell Sea (J. Rankin, University of Connecticut). A list of stations is given in Table 1.

Institutional abbreviations used in this study follow: WHOI, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA; SIO, Scripps Institution of Oceanography, La Jolla, California, USA; ZMUC, Zoological Musem, University of Copenhagen, Copenhagen, Denmark; USNM, United States National Museum, Washington, D.C., USA.

SYSTEMATICS

Nannoniscidae Hansen, 1916 (Nannoniscini *auctoris*)

Diagnosis.—Body usually slender, less commonly broad and flat. Cephalon not fused with thorax; pereonites 5-7 not enlarged; 1-5 free, 6 and 7 frequently fused medially *(Nannonisconus* has pereonite 7 fused to pleon instead); often a recurved ventral medial spine present on pereonite 7 or female operculum. Eyes absent. Antenna I often 5-segmented with bulbous distal article, or unmodified and with 6 or rarely 7 segments. Antennae well separated; frons with interantennal ridges, varying from slightly to massively developed, or with rostral crest. Antenna II of male generally more robust and setose than that of female. Mandibular molar process flattened, triangular lobe with setiferous apex; palp generally present and well developed. Maxilliped with second and third segments of palp broad, approximately width of endite, segments 4 and 5 much more slender. Pereopods of normal length, with one major terminal claw; epimeres of I-IV rarely project markedly anteriorly; major anterolateral seta of pereonites 2-4 stems from tergite, not coxa of limb; pereopods V-VII not exceptionally flattened for swimming, but may have plumose natatory setae. Uropods insert ventrally, almost universally biramous, with well-developed protopod.

Type species.—Nannoniscus oblongus G. O. Sars, 1870.

References.—Nannoniscini Hansen, 1916:83; Gurjanova, 1932:50; 1933:413; Nordenstam, 1933:251; Menzies, 1962a:29; 1962b:133; Wolff, 1962:31; Menzies and George 1972:95.

Remarks.—This definition is lengthy in contrast to some of those in the past (Hansen, 1916; Gurjanova, 1932, 1933; Nordenstam, 1933; Menzies, 1962a, 1962b; Wolff, 1962; Menzies and George, 1972), but such detail is necessary in view of the fact that no single feature uniformly diagnoses the family. The definition retains the essential features of Hansen's definition of the group Nannoniscini (1916), while accommodating the new morphologies that have been discovered since his work.

Two features are commonly useful in distinguishing a nannoniscid—the bulbous distal article on the first antenna and the medial fusion of pereonites 6 and 7. However, not uncommonly one and rarely both of these features are absent *(Austroniscus, Nannoniscoides biscutatus, N. coronarius).* In such cases other characters must be utilized.

Nannoniscid pereopods II-VII have only one major dactylar claw, which separates them from the Janiridae,[1], Jaeropsidae, Acanthaspididae, Microparasellidae, and Antiasidae.

A yet more useful feature is the flat, triangular molar process, which is found in only three other families: Macrostylidae, Pseudomesidae, and Desmosomatidae. Even the Thambematidae, which are similar to nannoniscids in so many ways, can be differentiated in this respect.

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[1] *Janthura abyssicola* Wolff, 1962 is a janirid that blurs the distinction between the two families in two ways. The pereopodal dactyli have only one major claw, and the mandibular molar process is triangular. As Wolff pointed out, these features are quite aberrant within the Janiridae, but the species shows other features that document its inclusion. Important in the present context are the bifid lateral margins of pereonites 1-3, relatively slender maxillipedal palp articles (segments) 2 and 3, large biramous uropod, and typical janirid body shape.

TABLE 1. Station data.

Station	Depth (m)	Latitude	Longitude
WHOI 95	3753	38°33′ N	68°32′ W
122	4833	35°51′ N	65°32′ W
126	3806	39°37′ N	66°47′ W
142	1624-1796	10°30′ N	17°52′ W
155	3730-3783	00°03.5′ S	27°48′ W
156	3459	00°45′ S	29°26′ W
159	834-939	07°58′ S	34°22′ W
162	1493	07°59′ S	34°06′ W
167	943-1007	07°54′ S	34°17′ W
169	587	08°03′ S	34°24′ W
202	1427-1643	09°05′ S	12°17′ E
		08°56′ S	12°15′ E
245	2707	36°55.7′ S	53°01.4′ W
247	5208-5223	43°33′ S	48°58.1′ W
256	3906-3917	37°40.9′ S	52°19.3′ W
328	4426-4435	50°04.7′ N	15°44.8′ W
Chain 35, Dredge 12	769-805	07°09′ S	34°25′ W
ALLEN S33	1784	43°40.8′ N	03°36′ W

Macrostylids are easily distinguished by several special features, including distinctive body form, extensive elaboration of sensory setae on the first antenna of mature males, close packing of pereonites 1-3, unique adaptation of pereopods I-III for living beneath the sediment surface, and styliform uropods.

The Pseudomesidae can be differentiated on the basis of their compact, uniramous uropod and lack of both squama on the second antenna and palp on the mandible. *Micromesus,* which Birstein (1963a) placed in the Pseudomesidae, does have a bulbous first antenna, but is similar in no other way.

Differentiation from the Desmosomatidae is a difficult problem. There is nothing in the diagnosis of this family (Hessler, 1970) to exclude *Austroniscus* or the two above-mentioned species of *Nannoniscoides.* Unquestionably, the two families are very closely related, yet viewing all the species as a whole, they do fall into two subgroups. It is not surprising that it is the species which should be regarded as relatively primitive within the Nannoniscidae that blur the distinctions (the secondary amplification of swimming morphology in *Austroniscus* notwithstanding).

Our diagnosis of the Nannoniscidae does include one feature that objectively discriminates the two families. The major seta on the anterolateral corner of pereonites 2-4 stems from the tergite as opposed to the coxa. Two exceptions to this are *Nannoniscus muscarius* and *N. perunis* Menzies and George, 1972. Here the seta arises from the coxa of pereopod II. In both species the coxa of this limb projects well forward, whereas in nannoniscids in general the coxae do not extend much beyond the tergite. In desmosomatids the coxae of pereopods II-IV always project in front of the tergite. Thus, the positioning of this seta may reflect the general development of the coxal epimere.

Generic composition.—Nannoniscus Sars, 1870; *Austroniscus* Vanhöffen, 1914 (partim); *Nannoniscoides* Hansen, 1916; *Nannonisconus* Schultz, 1966; *Thaumastosoma* Hessler, 1970; *Hebefustis* n. gen.

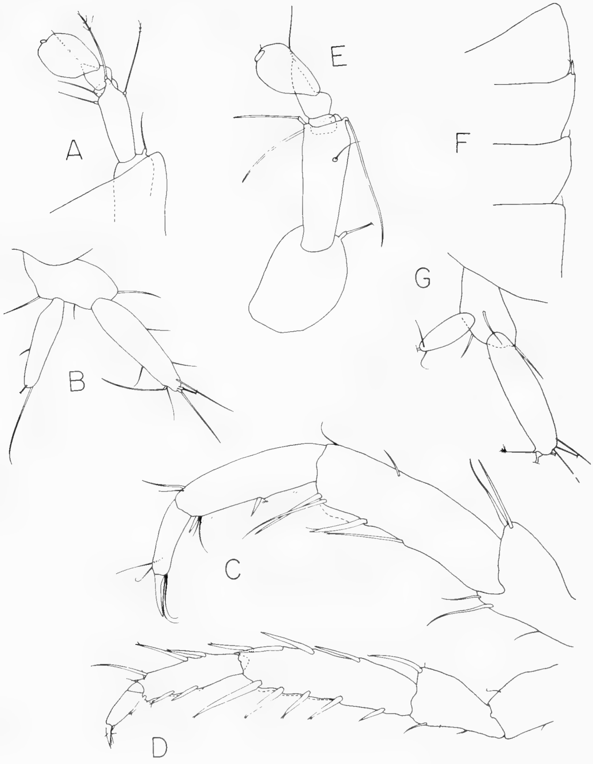

Figure 1. *Nannoniscus* sp., Anton Bruun 11 Sta. 108, brooding female (USNM 120965, identified as *Desmosoma coalescum* Menzies and George, 1972). A. right antenna I, lateral view; B. left uropod, *in situ;* C. right pereopod I, *in situ;* D. right pereopod II, *in situ. Nannoniscus coalescus,* Anton Bruun 11 Sta. 179 (holotype, *Desmosoma coalescum* Menzies and George, 1972, USNM 120964). E. right antenna I, dorsal view; F. pereonites 1-4; G. right uropod, *in situ,* exopod somewhat foreshortened in this perspective.

Synonomy.—Nannoniscella Hansen, 1916, with *N. groenlandica* Hansen, 1916, and *N. vinogradovi* Gurjanova, 1950 is a synonym of *Austroniscus* Vanhöffen, 1914 (by Birstein, 1962:33-34). The monotypic *Austroniscoides* Birstein, 1963b *(A. bougainvillei* Birstein, 1963b) is a synonym of *Janthura* (by Menzies and George, 1972:95). *Austrofilius* Hodgson, 1910, is a synonym of *Neojaera* Nordenstam, 1933 (by Menzies, 1962a:74-75).

We concur with Menzies and George (1972) in the transfer of *Austroniscoides* Birstein, 1963b from the Nannoniscidae to the Janiridae, and the synonomy of *Austroniscoides* with *Janthura* Wolff, 1962. Birstein (1962, 1963a) included *Austrofilius* Hodgson, 1910 in the Nannoniscidae. However, we follow Menzies (1962a:74-75) and Wolff (1962:206) in the removal of *Austrofilius* from the family, and its synonomy with *Neojaera* Nordenstam, 1933.

The monotypic genus *Sugoniscus* Menzies and George, 1972 was placed by them in the Nannoniscidae, requiring them to broaden the familial diagnosis in order to accommodate it. However, *Sugoniscus* does not show even superficial resemblance to any nannoniscid; it bears no features that ally it to this family in particular. In *Sugoniscus* the cephalon and mouthpart appendages are highly modified to accommodate a possibly parasitic mode of existence. The genus lacks interantennal ridges, and the antennae are much more laterally placed than is typical of the Nannoniscidae. The first antenna is unmodified. Pereonites 6 and 7 are unfused, and there are no ventral spines. The high degree of fringing ornamentation is unknown in the Nannoniscidae. Its inclusion renders the concept of the family useless. Therefore, we relegate *Sugoniscus* to family *incertae sedis* pending further study.

By the criterion of the seta on the anterolateral corner of pereonites 2-4, the genus *Thaumastosoma*, which Hessler (1970) placed in the Desmosomatidae, should be removed to the Nannoniscidae. This genus also possesses midventral spines on pereonite 7 and the female operculum. Such a feature is common in the Nannoniscidae, but is otherwise unknown among the Desmosomatidae.

Species realignment.—Nannoniscus primitivus Menzies, 1962b, *Nannoniscus robustus* Birstein, 1963a, and *Nannoniscoides hirsutus* Menzies, 1962b are referred to *Hebefustis* (see below). *Nannoniscus excavatifrons* Birstein, 1970 is referred to *Nannoniscoides* (see below).

Previously, two species have been removed from the family: *Nannoniscus bicuspis* Sars, 1885 to *Haploniscus* by Richardson (1908:75); and *Austroniscus ectiformis* Vanhöffen, 1914 to *Caecianiropsis* by Menzies and Pettit (1956:442).

Desmosoma coalescum Menzies and George, 1972 should also be placed in the Nannoniscidae, because it has pereonites 6 and 7 fused, and a 5-segmented first antenna having a bulbous fifth article. Menzies and George's original illustration (Menzies and George, 1972, fig. 31B) is incorrect regarding antenna I, based on our examination of the holotype. The fifth article in their drawing is in reality a lateral projection of the fourth, and the bulbous fifth was omitted (Fig. 1E). In addition, their fig. 31A erroneously shows epimeres on the anterior four pereonites. Other aspects of this species morphology are consistent with the diagnosis of the Nannoniscidae as given here, and should be considered as *Nannoniscus coalescus*. The additional two specimens designated *D. coalescum* (USNM 120965) by Menzies and George are also nannoniscids, but they differ from the holotype *inter alia* in the structure of the first pereopod and in having a large recurved ventral medial spine anterior to the operculum, and therefore are not this species, but are an undescribed species of *Nannoniscus*. Table 2 gives the names of species referable to Nannoniscidae.

Nannoniscoides Hansen, 1916

Type species.—Nannoniscoides angulatus Hansen, 1916.

Diagnosis.—Antenna I unspecialized, 6- (or rarely 7-) segmented; segments 3-5 well developed; penultimate segment lacking lateral projection; distal segment with simple, unmodified terminal aesthetasc. Pleon with posterolateral spines. Operculum (female pleopod II) elongate, with concavity and calcareous fringe at midline of distal edge; operculum approximately 0.85 or more dorsal length of pleon. Pereopods I-III lack epimeres. Pereopod I of medium robustness; ventral surface of carpus and propodus with thin setae, except for distal robust seta on carpus. Cephalon with pointed lateral lappets. Pereonites 6 and 7 may be free or fused. Pereonite 2 with robust seta on anterolateral corners. Medial lobes of male pleopods I taper distally. Uropod length averages 0.3 length of pleon. Body depressed; length roughly three times tergal width of pereonite 2.

Remarks.—The only other nannoniscid genera with a 6-segmented, unmodified antenna I are *Austroniscus* and *Thaumastosoma*. *Nannoniscoides* differs in having pleonal posterolateral spines, and in lacking an epimere on the coxa of pereopod I. *Thaumastosoma* displays a sexual dimorphism of pleonar shape not seen in *Nannoniscoides*. In addition the female operculum of *Austroniscus* is much smaller in

TABLE 2. A compilation of the nannoniscid species (* indicates generic type species).

Genus	Species
Nannoniscus	*acanthurus* Birstein, 1963a; *aequiremis* Hansen, 1916; *affinis* Hansen, 1916; *analis* Hansen, 1916; *arcticus* Hansen, 1916; *armatus* Hansen, 1916; *australis* Vanhöffen, 1914; *bidens* Vanhöffen, 1914; *camayae* Menzies, 1962b; *caspius* Sars, 1897; *coalescus* (Menzies and George, 1972); *crassipes* Hansen, 1916; *detrimentus* Menzies and George, 1972; *hanseni* Just, 1970; *inermis* Hansen, 1916; *laevis* Menzies, 1962b; *laticeps* Hansen, 1916; *minutus* Hansen, 1916; *muscarius* Menzies and George, 1972; *oblongus** Sars, 1870 (figured 1899); *ovatus* Menzies and George, 1972; *perunis* Menzies and George, 1972; *plebejus* Hansen, 1916; *reticulatus* Hansen, 1916; *simplex* Hansen, 1916; *spinicornis* Hansen, 1916; *tenellus* Birstein, 1963a
Nannonisconus	*latipleonus** Schultz, 1966
Austroniscus	*acutus* Birstein, 1970; *groenlandicus* (Hansen, 1916); *karamani* Birstein, 1962; *ovalis** Vanhöffen, 1914; *rotundatus* Vanhöffen, 1914; *vinogradovi* (Gurjanova, 1950)
Nannoniscoides	*angulatus** Hansen, 1916; *biscutatus* n. sp.; *coronarius* n. sp.; *excavatifrons* (Birstein, 1970); *gigas* n. sp.; *latediffusus* n. sp.
Hebefustis	*alleni* n. sp.; *cornutus* n. sp.; *dispar* n. sp.; *hexadentium* n. sp.; *hirsutus* (Menzies, 1962b); *mollicellus* n. sp.; *par* n. sp.; *primitivus* (Menzies, 1962b); *robustus* (Birstein, 1963a); *vafer** n. sp.
Thaumastosoma	*distinctum* (Birstein, 1963a); *platycarpus** Hessler, 1970; *tenue* Hessler, 1970

relation to the size of the pleon, a reflection of the broadened swimming morphology of this genus. The insertions of the posterior pereopods in *Austroniscus* become more medial as one moves posteriorly, whereas in *Nannoniscoides* the posterior insertions are all equally far from the midline.

Nannoniscoides females closely resemble *Hebefustis* n. gen. in general body shape, particularly in the shape of the pleon. They may be easily distinguished by the number of segments in the first antenna, the robustness of the setae on the propodus and carpus of pereopod I, the form of the cephalic lappets, and the shape of the operculum.

This genus contains the following species: *Nannoniscoides latediffusus,* n. sp.; *N. biscutatus,* n. sp.; *N. coronarius,* n. sp.; *N. gigas,* n. sp.; *N. angulatus* Hansen, 1916, type species; *N. excavatifrons (= Nannoniscus excavatifrons* Birstein, 1970). *Nannoniscoides hirsutus* Menzies, 1962b is transferred to *Hebefustis* (see discussion in that section). The reassignment of *Nannoniscus excavatifrons* Birstein, 1970 to *Nannoniscoides* is based on its obvious similarity to the type species. Its inclusion provides a continuum of morphological features from the extreme of the type species, described from only male specimens (Hansen, 1916; Just, 1970; Gurbunov, 1946 mentions the occurrence of *N. angulatus* in the Kara Sea, but provides only biogeographic information) to the species described here from females and immature males.

The type species, *Nannoniscoides angulatus,* is distinct in several respects, including length-width ratios, the ventral medial projection of pereonite 7 and the shape of the pleon. *Nannoniscoides excavatifrons* and a male of *N. latediffusus* n. sp. closely resemble *N. angulatus* in head structure and the lengthening of the lateral lobes of pereonite 2. *Nannoniscoides excavatifrons* has a 6-segmented unmodified antenna I; *N. latediffusus* has an unmodified antenna I which is unique in being 7-segmented in the male. The shape of the pleon, the length-width ratios, and the type of setation on the propodus and carpus of pereopod I of *N. excavatifrons* clearly link the new species described here with *N. angulatus.* These features strengthen the case for the assignment of these species to *Nannoniscoides,* a decision based principally on the 6-segmented structure of antenna I (Just, 1970),

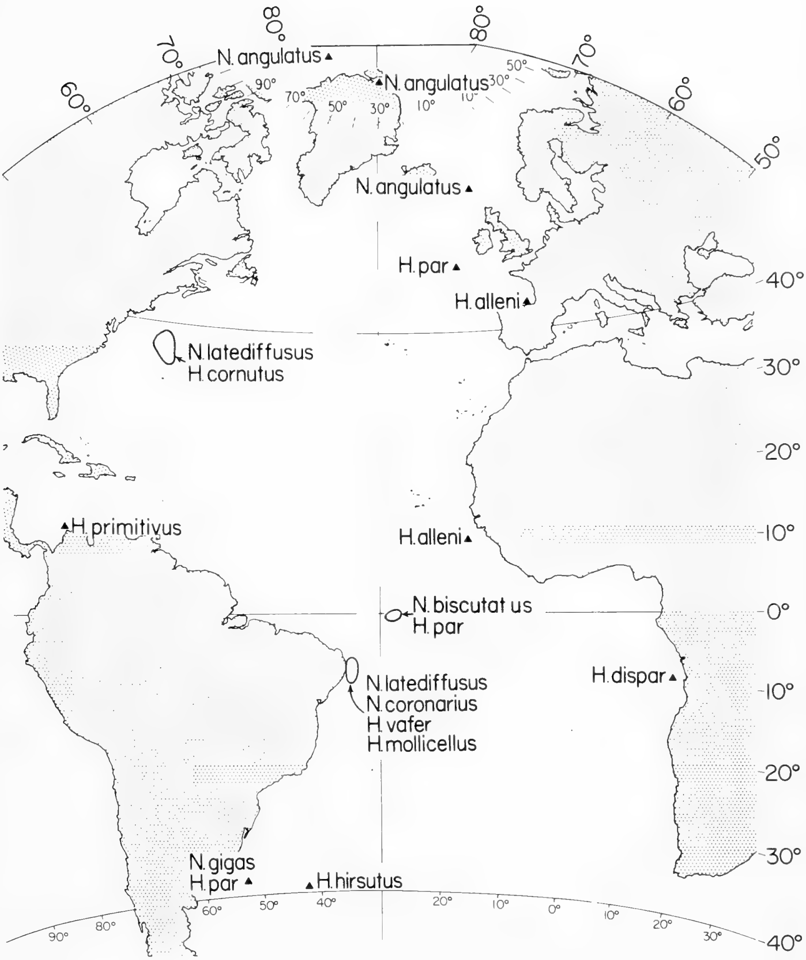

Figure 2. *Nannoniscoides* and *Hebefustis:* geographical distribution of species in the Atlantic Ocean.

the shape of the pleon, and the pointed cephalic lappets.

Sexual dimorphism.—The sexual dimorphism exhibited in this genus is the most extreme seen in the Nannoniscidae. Mature, or nearly mature males may have a more massively developed cephalon than females (cf. male and female of *N. latediffusus)*, and more strongly produced lateral lobes of pereonite 2. Typically, the primary sexual differences in nannoniscids (aside from the pleopod differences) are merely the more robust male second antenna and differences in overall body and pleonar dimensions and ratios.

In *Nannoniscoides* there is also an indication of sexual differences in the first antenna, unique in the Nannoniscidae. These differences may be manifest in the number of aesthetascs and relative lengths of segments 5 and 6 (cf. *N. biscutatus).* (The number of segments varies between the male and female of *N. latediffusus.)*

However, the occurrence of extreme sexual dimorphism within the genus appears to be variable; one finds species in which sexual dimorphism is expressed mainly in the robustness of the second antennae, as is commonly the case in other genera (see drawing of undescribed male, *Nannoniscoides* No. 5, Fig. 6).

Distribution.—Nannoniscoides angulatus: North Atlantic, north of the Faroes, 1284 m (Hansen, 1916); northernmost part of the Kara Sea, 698 m (Gurbunov, 1946); Jørgen Brønlund Fjord, Greenland, 160-180 m (Just, 1970). *Nannoniscoides excavatifrons:* northwest Pacific, in the Kurile-Kamchatka area, 1440-1540 m (Birstein, 1970). *Nannoniscoides latediffusus:* northwest Atlantic, equatorial southwest Atlantic, 587-4833 m. *Nannoniscoides biscutatus:* equatorial southwest Atlantic, 3459-3783 m. *Nannoniscoides coronarius:* equatorial southwest Atlantic, 1493 m. *Nannoniscoides gigas:* South Atlantic, Argentine Basin, 3909-3917 m. *Nannoniscoides* No. 5: South Atlantic, Argentine Basin, 2707 m. The map in Fig. 2 shows the distribution of species of *Nannoniscoides* in the Atlantic Ocean.

Nannoniscoides biscutatus n. sp.

Figure 3

Holotype.—WHOI 156, brooding female, 1.7 mm long, USNM 169386.

Paratype.—WHOI 155, male, 2.0 mm long, USNM 169387; WHOI 156, 1 preparatory female, 1 juvenile female, WHOI 155, 2 brooding females, SIO.

Distribution.—Equatorial Atlantic Ocean, 3459-3783 m.

Etymology.—bis, Latin, in two ways, twice; *scutatus,* Latin, armed with a shield.

Diagnosis.—Antenna I terminal segment elongate, not inflated, length to width ratio (1/w) 5.0 (holotype), 3.6 (allotype). Segment 6, 0.5 (holotype), 0.4 (allotype) times length of segment 2. Combined length of segments 3-6, 1.4 (holotype), 1.89 (allotype) times length of segment 2. Segment 5 of male much longer than segment 6; segment 5 with two distal aesthetascs, segment 6 with one. (Differs from female which has single aesthetasc on segment 6 and segment 6 longer than segment 5.)

Pereonites 6 and 7 free.

Pleon with posterolateral processes (teeth), 0.67 (holotype and allotype) removed from anterior edge. Width of pleon between midpoints of concavities formed by teeth 0.79 (holotype), 0.84 (allotype) width of pleon; pleon 1/w 1.06 (holotype), 1.10 (allotype). Pleon 0.67 (holotype), 0.69 (allotype) times width of pereonite 2.

Female operculum 1/w 1.6; 1.0 times length of pleon (excluding pleonal somite 1).

Male pleopod I sides from proximal end to lateral lobes relatively straight. Lateral lobes forming posteriorly projecting spines. Outer margins of medial lobes convex, tapering to broad points distally. Pleopod I 1/w 5.6; 0.8 length of pleon.

Uropod length 0.4 (holotype and allotype) length of pleon. Endopod 1/w 4.0 (holotype and allotype). Exopod 1/w 4.0 (holotype and allotype). Endopod length 1.8 (holotype and allotype) times length of protopod.

Cephalic keels (on inner margins bordering antennae) not strongly developed. Cephalic width 0.8 times that of pereonite 2.

Body length 3.3 (holotype), 3.7 (allotype) times tergal width of pereonite 2.

Remarks.—Nannoniscoides biscutatus n. sp. may be distinguished from *N. coronarius* n. sp., the other member of the genus which lacks medial fusion of pereonites 6 and 7, by the less developed and more widely separated cephalic keels of *N. biscutatus,* as well as by its more elongate uropodal rami, the narrower, more elongate form of the articles of antenna I and the somewhat more elongate body form.

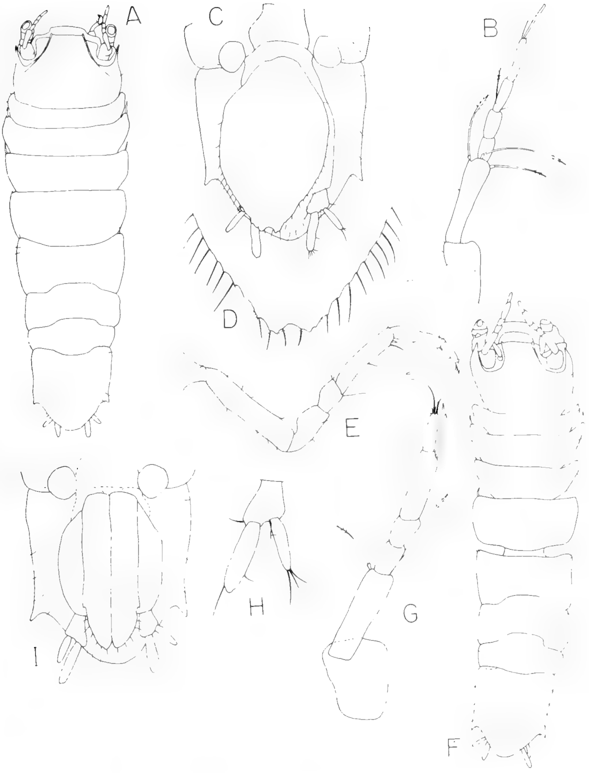

Figure 3. *Nannoniscoides biscutatus* n. sp., WHOI 156. A. brooding female (holotype), dorsal view; B. brooding female (holotype) right antenna I, lateral view; C. brooding female (holotype) operculum; D. posterior margin of operculum; E. juvenile female right pereopod I. WHOI 155. F. male (paratype) dorsal view; G. male (paratype) left antenna I, dorsal view; H. male (paratype) left uropod, *in situ;* I. male (paratype) pleon, ventral view.

Nannoniscoides gigas n. sp.

Figure 4

Holotype.—WHOI 256, preparatory female, 2.8 mm long, USNM 169388.

Paratype.—WHOI 256, 1 additional preparatory female, SIO.

Distribution.—Argentine Basin, South Atlantic Ocean, 3909-3917 m.

Etymology.—Latin, giant.

Diagnosis.—Antenna I terminal segment inflated, length to width ratio (l/w) 2.0; length of segment 6, 0.5 times length of segment 2; combined length of segments 3-6, 0.3 times length of segment 2.

Pereonites 6 and 7 fused.

Pleon with posterolateral processes (teeth) 0.71 removed from anterior edge. Width of pleon between midpoints of concavities formed by teeth 0.76 width of pleon; pleon l/w 0.93; pleon width 0.74 times width of pereonite 2.

Female operculum l/w 1.3; 0.8 times length of pleon.

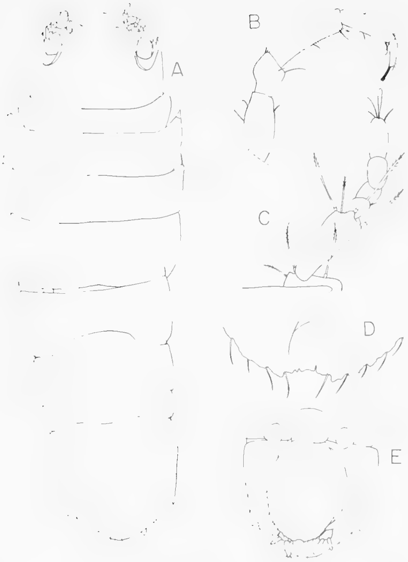

Figure 4. *Nannoniscoides gigas* n. sp., WHOI 256, preparatory female (holotype). A. dorsal view; B. right pereopod I; C. right antenna I, lateral view; D. posterior margin of operculum; E. pleon, ventral view.

Uropod 0.2 times length of pleon. Endopod 1/w 2.6; exopod 1/w 3.5; endopod length 1.6 protopod length.

Cephalic keels not well developed. Cephalic width 0.7 times that of pereonite 2.

Body length 3.0 times tergal width of pereonite 2.

Remarks.—Of the species with fused pereonites 6 and 7, *N. gigas* is only similar to *N. latediffusus. Nannoniscoides gigas* differs in having the pleonal posterolateral teeth positioned much more posteriorly, less elongate distal segments on antenna I and a somewhat shorter and broader female operculum.

Nannoniscoides coronarius n. sp.

Figure 5

Holotype.—WHOI 162, brooding female, 1.4 mm long, USNM 169389.

Other material.—Holotype female only.

Distribution.—Equatorial southwest Atlantic Ocean, 1493 m.

Etymology.—Latin, relating to a crown or garland.

Diagnosis.—Antenna I terminal segment relatively narrow, not inflated, length to width ratio (1/w) 2.6; segment 6, 0.3 times length of segment 2. Combined length of segments 3-6, 1.3 times length of segment 2.

Pereonites 6 and 7 free.

Pleon with posterolateral processes (teeth) 0.73 removed from anterior edge. Width of pleon between midpoints of concavities formed by teeth 0.68 width of pleon. Pleon 1/w 0.81; width 0.79 times width of pereonite 2.

Female operculum 1/w 1.6; approximately as long as pleon.

Uropod length 0.3 length of pleon; endopod 1/w 2.8; exopod 1/w 2.1. Endopod length 1.6 times protopod length.

Distinct cephalic keels, located on surface of frons rather than on its lateral margins. Cephalic width 0.9 times that of pereonite 2.

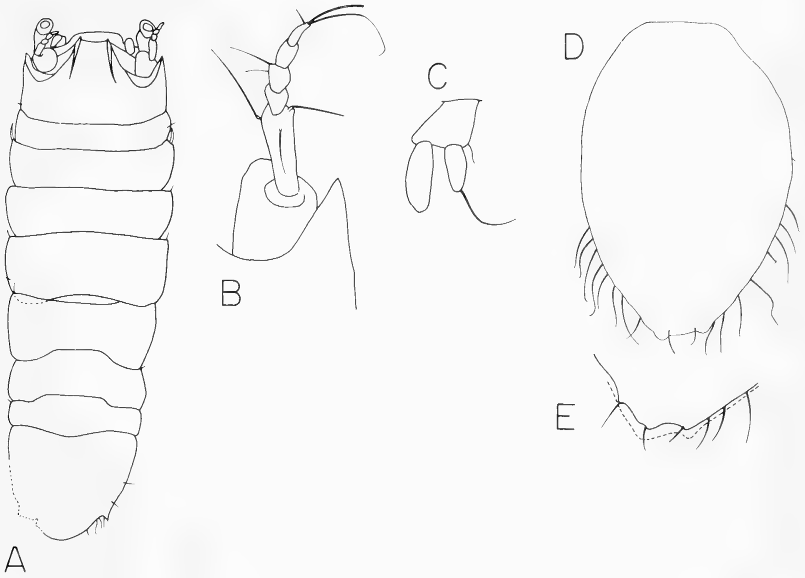

Figure 5. *Nannoniscoides coronarius* n. sp., WHOI 162. A. brooding female (holotype), dorsal view; B. brooding female (holotype) right antenna I; C. brooding female (holotype) left uropod, *in situ;* D. brooding female (holotype) operculum; E. posterior margin of operculum.

Body length 3.1 times tergal width of pereonite 2.

Remarks.—The medially positioned paired keels on the surface of the frons are thus far unique to this species. It and *N. biscutatus* n. sp. may be readily distinguished from all others of the genus by the lack of medial fusion of pereonites 6 and 7. *Nannoniscoides coronarius* differs from *N. biscutatus* in having more closely spaced cephalic keels, more compact uropodal rami and articles of antenna I, and a less elongate body form.

Nannoniscoides latediffusus n. sp.

Figure 6

Holotype.—WHOI 169, brooding female, 2.0 mm long, USNM 169390.

Paratype.—WHOI 169, male, 1.7 mm long, USNM 169391, and preparatory female, USNM 169404; WHOI 169, 10 spec., SIO.

Other material.—WHOI 122, 1 spec.; WHOI 126, 1 spec.; WHOI 159, 1 spec.; WHOI 167, 2 spec.; WHOI Chain 35, Dredge 12, 1 spec., SIO.

Distribution.—Northwest Atlantic Ocean, 587-4833 m.

Etymology.—*late,* Latin, broadly or widely; *diffusus,* Latin, distributed or spread out.

Diagnosis.—Antenna I 6-segmented (holotype), 7-segmented in adult male (see Remarks); length to width ratio (l/w) of terminal segment 3.1 (holotype). Segment 6, 0.7 times length of segment 2. Combined length of segments 3-6, 1.4 times length of segment 2.

Pereonites 6 and 7 fused.

Pleon with posterolateral processes (teeth) 0.55 (holotype), 0.59 (allotype) removed from anterior edge. Width of pleon between midpoints of concavities formed by teeth 0.79 (holotype), 0.90 (allotype) times width of pleon; pleon l/w 0.93

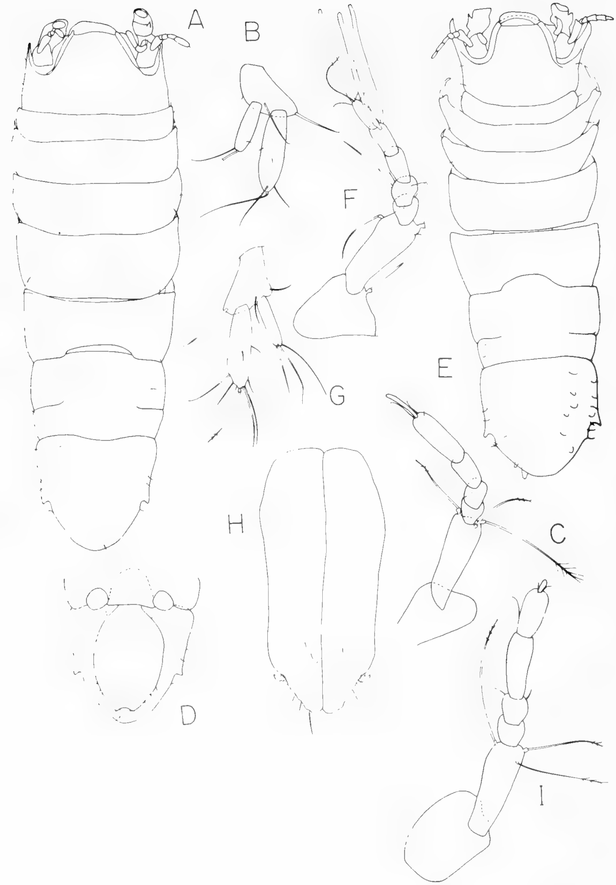

Figure 6. *Nannoniscoides latediffusus* n. sp., WHOI 169. A. brooding female (holotype), dorsal view; B. preparatory female (paratype) right uropod, *in situ;* C. brooding female (holotype) right antenna I, dorsolateral view; D. brooding female (holotype) pleon, ventral view; E. male (paratype), dorsal view; F. male (paratype) right antenna I, dorsal view; G. male (paratype) left uropod, *in situ;* H. male (paratype) pleopods I, *in situ;* I. WHOI 167 juvenile male, right antenna I, dorsal view.

(holotype), 1.0 (allotype). Pleon 0.73 (holotype and allotype) times width of pereonite 2.

Female operculum l/w 1.6; 0.9 length of pleon.

Male pleopods I narrowly rounded distally; lateral lobes with hook-like process; l/w 4.4; pleopod 0.8 times length of pleon.

Uropod length 0.3 (paratype female and paratype male) times length of pleon. Endopod l/w 3.4 (paratype female), 3.8 (paratype male). Exopod l/w 3.2 (paratype female), 4.3 (paratype male). Endopod length 1.5 (paratype female and male) times protopod length.

Cephalic keels (on inner margins bordering antennae) well developed (see Remarks). Cephalic lappets of male highly developed. Cephalic width 0.9 times that of pereonite 2 (holotype and allotype).

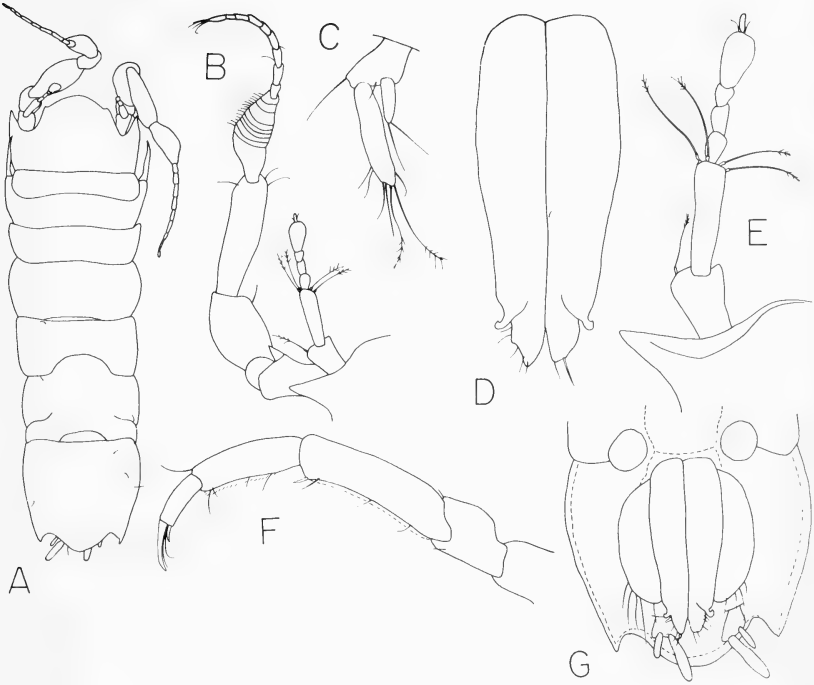

Figure 7. *Nannoniscoides* No. 5, WHOI 245, undescribed male. A. dorsal view; B. left antennae I and II, dorsolateral view; C. left uropod; D. pleopods I; E. left antenna I, dorsolateral view; F. left pereopod I, *in situ;* G. pleon, ventral view.

Body length 3.2 (holotype), 2.9 (allotype) times tergal width of pereonite 2.

Remarks.—The uropods are broken off the holotype female. The male differs markedly from the female in its well-developed cephalon (keels and lappets), antenna I (7-segmented with 3 aesthetascs, one from segment 7 and two from segment 6, rather than 6-segmented with 1 aesthetasc in the female) and in the development of pereonites 2 and 3 (the projecting lobes and setae). This dimorphism of the first antenna is unusual in the Nannoniscidae. In other nannoniscid genera the only antennal dimorphism is expressed in the robustness and setation of antenna II.

The male specimens of this species (WHOI 169 and WHOI 167) are of particular note. They display a continuum of body form from that of the female to that characteristic of the adult male of the generic type species (a single male), *N. angulatus.* Pleopods I also show a transition to more highly developed lateral lobes and hook-like processes in the mature male of *N. latediffusus.* There is also a transition from the 6-segmented female antenna to the 7-segmented copulatory male antenna through the 6-segmented antenna of the juvenile male of WHOI 167.

This species has an exceptionally broad geographic and bathymetric range. The possibility remains that *N. latediffusus* consists of sibling species possessing more restricted depth ranges; however, no clear-cut morphological evidence permits such a differentiation.

Hebefustis n. gen.

Diagnosis.—First antenna 5-segmented, distal segment elongate and somewhat inflated; segment 4 lacks a lateral projection, segments 3 and 4 well developed, not hidden.

Pleon with posterolateral spines.

Operculum (female pleopod II) ovoid to pear-shaped; length about 0.66 of length of pleon (measured in dorsal view); distal margin straight without calcareous fringing margin.

Anterior three pereopods lack epimeres; pereopods of medium robustness. Pereopod I: ventral surface of carpus and propodus have robust setae.

Rounded cephalic lappets.

Male pleopod I widest proximally; sides convex proximally, concave to straight distally; limb often flared distally.

Uropods relatively short; uropod length about 0.25 length of pleon.

Pereonites 6 and 7 fused medially.

Body depressed; length about 3.8 tergal width of pereonite 2.

Type species.—Hebefustis vafer n. sp.

Etymology.—Hebes, Latin, meaning blunt; *fustis,* Latin, meaning club. The name is masculine, and was suggested by the shape of the terminal articles of the first antenna.

Remarks.—One cannot tell from Menzies' (1962b) descriptions whether *H. hirsutus* and *H. primitivus* have pointed or rounded cephalic lappets. The holotype (sole specimen) of *H. hirsutus* cannot be found (R. J. Menzies, pers. comm.). The condition of the sole specimen of *H. primitivus* does not allow a judgment as to the shape of the cephalic lappets.

The females of this genus are similar to those of *Nannoniscoides,* particularly in the overall body shape, the posterolateral processes on the pleon, and the general robustness of the first pereopods. The two genera may be distinguished on the basis of the structure of the first antenna (6-segmented in *Nannoniscoides,* 5-segmented in *Hebefustis),* the type of setae on the propodus and carpus of pereopod I (thin in *Nannoniscoides,* robust in *Hebefustis),* the shape of the female operculum (elongate, with a distal concavity at the midline in *Nannoniscoides;* pear-shaped to ovoid in *Hebefustis,* with a straight distal margin), and the shape of the lateral lappets of the cephalon (pointed in *Nannoniscoides,* rounded in *Hebefustis).*

Several species of *Nannoniscus* also closely resemble *Hebefustis (N. bidens* Vanhöffen, 1914, *N. camayae* Menzies, 1962b, and *N. minutus* Hansen, 1916). These species have acute posterolateral pleonal processes and a 5-segmented antenna I. However, the first antennae of these species differ from *Hebefustis* in that the fourth segment of the *Nannoniscus* species has a large lateral projection. In addition, *N. minutus* bears a large recurved ventral medial spine anterior to the operculum.

This genus contains the following species: *Hebefustis vafer* n. sp., type species; *H. primitivus (= Nannoniscus primitivus* Menzies, 1962b); *H. robustus (= Nannoniscus robustus* Birstein, 1963a); *H. mollicellus* n. sp.; *H. par* n. sp.; *H. alleni* n. sp.; *H. hirsutus (= Nannoniscoides hirsutus* Menzies, 1962b); *H. cornutus* n. sp.; *H. dispar* n. sp.; *H. hexadentium* n. sp.

These species can be subdivided into two groups, one comprised of the first six species, and the other of the remaining four.

The cluster containing *H. cornutus, H. dispar, H. hexadentium,* and *H. hirsutus* has acute processes on the posterolateral margins of pereonites 6 and 7. These species differ from one another in the following ways: *H. hexadentium* lacks a robust seta on the corners of pereonite 2; the other species have a robust seta. They also differ in the shape of segment 5 of antenna I, and in the ratios formed describing the pleonal features.

The remaining species (*H. vafer, H. primitivus, H. robustus, H. mollicellus, H. par,* and *H. alleni)* do not have acute posterolateral processes on the corners of pereonites 6 and 7. Within this group the species display a high degree of similarity. Where pereopod I is available on the specimens, differences often occur in the setation patterns of the propodus and carpus between species. However, there may be differences in the number of setae between the right and left pereopods of the same individual, as well as intraspecific differences. For this reason, the setation pattern is not a reliable diagnostic character for specific differences. Differentiation among these species must be made on the somewhat subtle basis of ratios of the dimensions of body parts, particularly of the antenna I and the pleon.

Nannoniscus primitivus Menzies (1962b), *N. robustus* Birstein (1963a), and *Nannoniscoides hirsutus* Menzies (1962b) should be transferred to *Hebefustis.*

Nannoniscus robustus: The complete set of drawings given by Birstein allows unambiguous placement in *Hebefustis. Inter alia,* the structure of the 5-segmented antenna I, the robust setae of the carpus and propodus of pereopod I, and the shapes of the pleon and the female pleopod II match precisely the diagnostic characters of the genus.

Nannoniscus primitivus: The structure of the 5-segmented antenna I and the shape of the male pleopod I are clearly characteristic of *Hebefustis.* The pleon is somewhat unusual in having two pairs of acute processes. However, this feature is similar to the double vertices on the pleon of the male of *H. cornutus.*

Nannoniscoides hirsutus: The type specimen cannot be found (R. J. Menzies, pers. comm.), and hence, certain difficulties arise in placing this species in *Hebefustis.* The primary difficulty is the number of segments in antenna I. In Menzies' figure (1962b, fig. 30c), a dorsal view of the holotype, the first antenna is drawn 5-segmented, the condition in *Hebefustis.* Supporting evidence for the placement of this species in *Hebefustis* is found in the robust setae of the propodus of pereopod I, the acute posterolateral processes on pereonites 6 and 7 (similar to *H. cornutus, H. dispar,* and *H. hexadentium),* and the structure of the distal end of the male pleopod I, which is somewhat squared-off.

Distribution.—Hebefustis alleni: Bay of Biscay and northeast Atlantic, 1623-1796 m. *Hebefustis cornutus:* northwest Atlantic, 3753-3806 m. *Hebefustis dispar:* southeast Atlantic, 1427-1643 m. *Hebefustis hexadentium:* Argentine Basin, South Atlantic Ocean, 5024 m (Menzies, 1962b). *Hebefustis hirsutus:* South Atlantic Ocean, 5024 m (Menzies, 1962b). *Hebefustis mollicellus:* equatorial South Atlantic, 943-1007 m. *Hebefustis par:* northeast, equatorial and South Atlantic, 3459-4435 m. *Hebefustis primitivus:* Caribbean, North Atlantic, 2868-2875 m (Menzies, 1962b). *Hebefustis robustus:* northwest Pacific, 5461-5690 m (Birstein, 1963a). *Hebefustis vafer:* equatorial southwest Atlantic, 587 m.

The map in Fig. 2 shows the distribution of the species of *Hebefustis* occurring in the Atlantic Ocean.

Hebefustis vafer n. sp.

Figures 8 and 9

Holotype.—WHOI 169 (type locality), preparatory female, 2.3 mm long, USNM 169392.

Paratype.—WHOI 169, copulatory (?) male, 1.8 mm long, USNM 169393; WHOI 169, 18 other spec., ZMUC, SIO.

Distribution.—Equatorial southwest Atlantic Ocean, 587 m.

Etymology.—Latin, artful, sly or crafty.

Diagnosis.—Antenna I segment 5 thin and elongate; length to width ratio (l/w) 4.1 (holotype), 4.0 (allotype); length segment 5, 0.8 (holotype), 0.9 (allotype) length segment 2. Pereonites 6 and 7 with no posterolateral projection. Pereonite 4 l/w 0.6

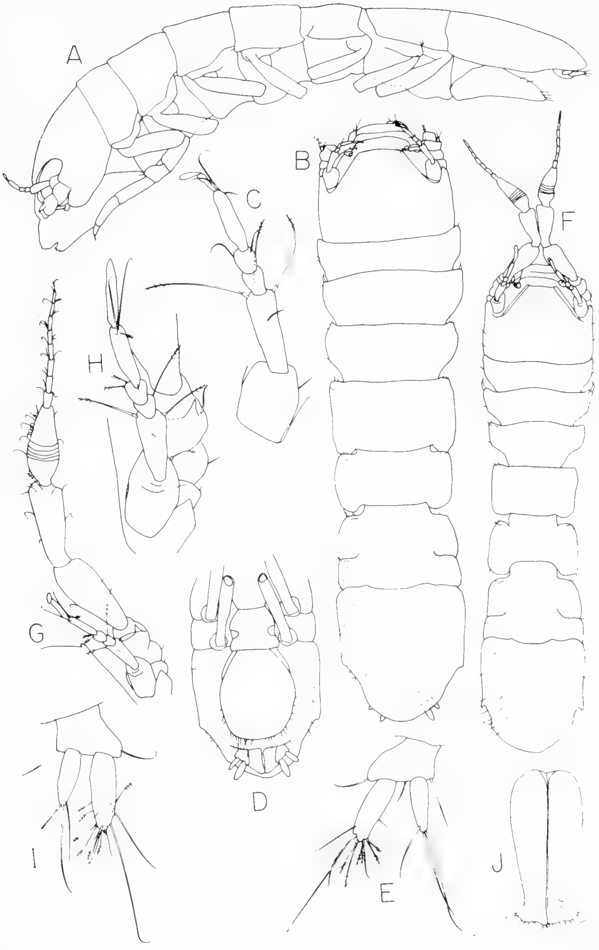

Figure 8. *Hebefustis vafer* n. sp., WHOI 169. A. preparatory female (holotype), lateral view; B. preparatory female (holotype), dorsal view; C. preparatory female (holotype) right antenna I, dorsal view; D. preparatory female (holotype) pleon, ventral view; E. preparatory female (holotype) right uropod, *in situ;* F. male (paratype), dorsal view; G. male (paratype) right antennae I and II, dorsal view; H. male (paratype) right antenna I, dorsal view; I. male (paratype) left uropod, *in situ;* J. male (paratype) pleopods I.

(holotype), 0.5 (allotype); width 0.9 (holotype), 0.8 (allotype) times tergal width of pereonite 2; sides approximately straight. Pereonite 2 with robust seta on anterolateral corners.

Pleon with acute posterolateral processes (teeth) approximately 0.6 (holotype and allotype) distant from anterior edge; sides of pleon anterior to teeth relatively straight (straight with slight concavity before teeth in male). Pleon width between midpoints of concavities formed by teeth 0.9 (holotype), 1.0 (allotype) pleon width. Pleon l/w 1.1 (holotype and allotype). Pleon width 0.9 (holotype and allotype) times width of pereonite 2.

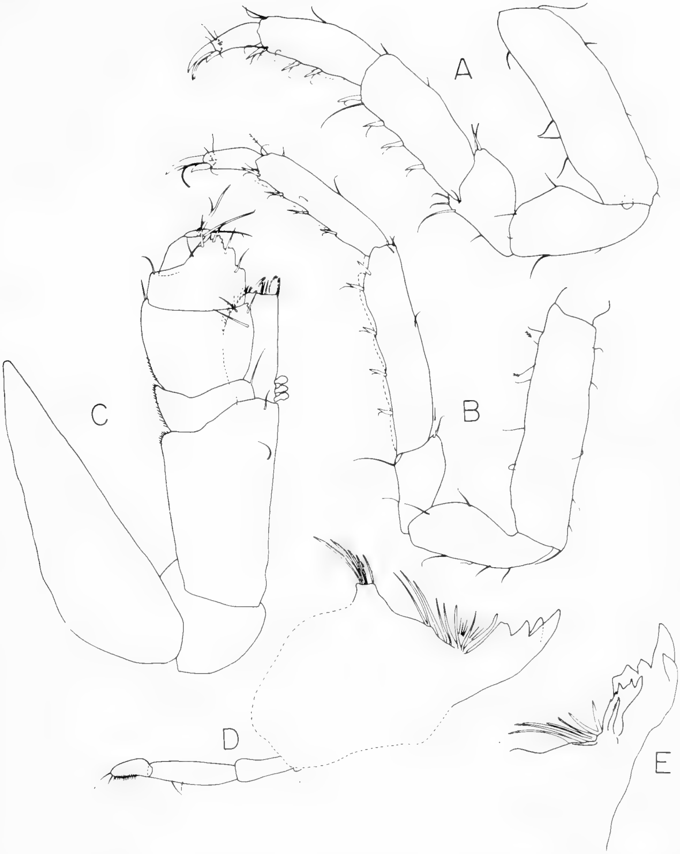

Figure 9. *Hebefustis vafer* n. sp., WHOI 169, brooding female. A. left pereopod I; B. left pereopod II; C. right maxilliped; D. right mandible; E. distal portion of left mandible.

Female operculum somewhat ovoid; l/w 1.2; 0.7 length of pleon (measured in dorsal view).

Male pleopod I l/w 4.3; 0.7 length of pleon; sides constricted proximal to lateral lobes, which are broadly flared.

Body length 4.2 (holotype), 4.3 (allotype) times tergal width of pereonite 2.

Remarks.—Of the species which lack posterolateral spines on pereonites 6 and 7, *H. vafer* n. sp. is most similar to *H. mollicellus* n. sp. The bodies of these two species are somewhat more elongate than those of *H. par* n. sp. and *H. alleni* n. sp. *Hebefustis vafer* differs from *H. mollicellus* in having a more elongate article 5 of antenna I; the pleonal posterolateral teeth are more anteriorly placed in the female and the posterior portion of the pleon does not taper as sharply. The male of *H. vafer* is much narrower in pereonites 4-5 relative to the female and the male pleopods differ between the two species in length-width ratios. The distal margin of pleopods I are broadly flared in *H. vafer*.

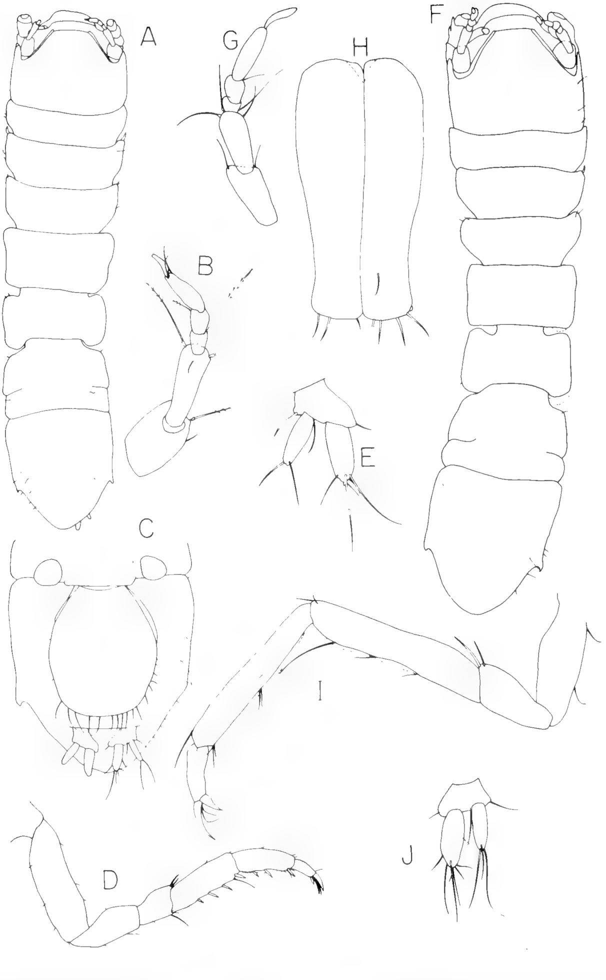

Figure 10. *Hebefustis mollicellus* n. sp., WHOI 167. A. brooding female (holotype), dorsal view; B. brooding female (holotype) right antenna I, dorsal view; C. brooding female (holotype) pleon, ventral view; D. preparatory female right pereopod I; E. brooding female (holotype) right uropod, *in situ;* F. male (paratype), dorsal view; G. male (paratype) left antenna I, lateral view; H. immature male (paratype) pleopods I; I. male (paratype) right pereopod VI, *in situ;* J. male (paratype) left uropod, *in situ.*

Hebefustis mollicellus n. sp.

Figure 10

Holotype.—WHOI 167, brooding female, 2.0 mm long, USNM 169394.

Paratype.—WHOI 167, immature male, 1.5 mm long, USNM 169395; WHOI 167, 2 spec. and 1 frag., SIO.

Distribution.—Equatorial South Atlantic Ocean, 943-1007 m.

Etymology.—Latin, dainty or little.

Diagnosis.—Antenna I segment 5 length to width ratio (l/w) 3.2 (holotype), 3.3 (allotype); 0.7 (holotype), 0.9 (allotype) times length of segment 2.

Pereonites 6 and 7 without acute posterolateral processes. Pereonite 4 l/w 0.55 (holotype and allotype); sides gently concave; slightly broader anteriorly. Width 0.9 (holotype), 0.85 (allotype) width of pereonite 2. Pereonite 2 with robust seta on anterolateral corners.

Pleon with acute posterolateral processes (teeth) 0.7 (holotype), 0.6 (allotype) removed from anterior edge. Sides of pleon anterior to teeth straight, nearly parallel. Pleonal width between midpoints of concavities formed by teeth 0.85 (holotype), 0.87 (allotype) times width of pleon. Pleon l/w 1.2 (holotype), 1.1 (allotype). Width of pleon 0.9 (holotype), 1.0 (allotype) times width of pereonite 2.

Female operculum l/w 1.2; 0.6 length of pleon (measured in dorsal view).

Male pleopod I l/w 3.9; 0.7 length of pleon. Distal corner of limb with slight bulbous process (immature male).

Body length 4.3 (holotype), 4.7 (allotype) times tergal width of pereonite 2.

Remarks.—This species is most similar to *H. vafer* n. sp. These two species differ in the shape of the distal article of antenna I, and the positioning of the pleonal posterolateral processes. The males of the two species differ in the degree of narrowing of pereonites 4 and 5 relative to the female and in the morphology of pleopods I.

Hebefustis par n. sp.

Figure 11

Holotype.—WHOI 328, preparatory female, 2.4 mm long, USNM 169396.

Paratype.—WHOI 328, male, 1.8 mm long, USNM 169397.

Other material.—WHOI 156, 21 spec.; WHOI 256, 8 spec., SIO, ZMUC.

Distribution.—Northeast, equatorial, and South Atlantic Ocean, 3459-4435 m.

Etymology.—Latin, equal, a match.

Diagnosis.—Antenna I segment 5 elongate and bulbous, widest distally; length 3.3 (holotype), 3.2 (allotype) times greater than width (l/w). Segment 5 (holotype and allotype) length approximately equal to length of segment 2.

Pereonites 6 and 7 without posterolateral processes. Pereonite 4 l/w 0.5. Width 0.9 (holotype), 0.7 (allotype) times width of pereonite 2. Pereonite 2 with robust seta on anterolateral corner.

Pleon with acute processes (teeth) 0.8 (holotype), 0.9 (allotype) distant from anterior edge. Anterior to teeth, sides of pleon slightly convex, tapering inward in front of teeth. Pleon width between midpoints of concavities formed by teeth 0.7 times width of pleon. Pleon width 0.8 (holotype), 0.9 (allotype) times width of pereonite 2. Pleon l/w 1.0 (holotype and allotype).

Female operculum length approximately equal to width; 0.66 length of pleon.

Male pleopod I l/w 4.2; 0.8 times length of pleon. Lateral lobes with oblique ridge.

Body length 3.7 (holotype), 3.0 (allotype) times tergal width of pereonite 2.

Remarks.—This species has a rather broad geographic range. There are subtle differences among individuals of the three stations in the first antennae and in the shape of pereonite 4. However, the range of this variability is not appreciably greater than that within any one population. The paucity of copulatory males at these stations may preclude recognition of specific differences among the populations. Of the species lacking posterolateral projections on pereonites 6 and 7, *H. par* n. sp. is most similar to *H. alleni* n. sp. These two differ from the other species of this cluster in having more robust bodies relative to their length. *Hebefustis par* differs from *H. alleni* in having a more elongate distal segment of antenna I,

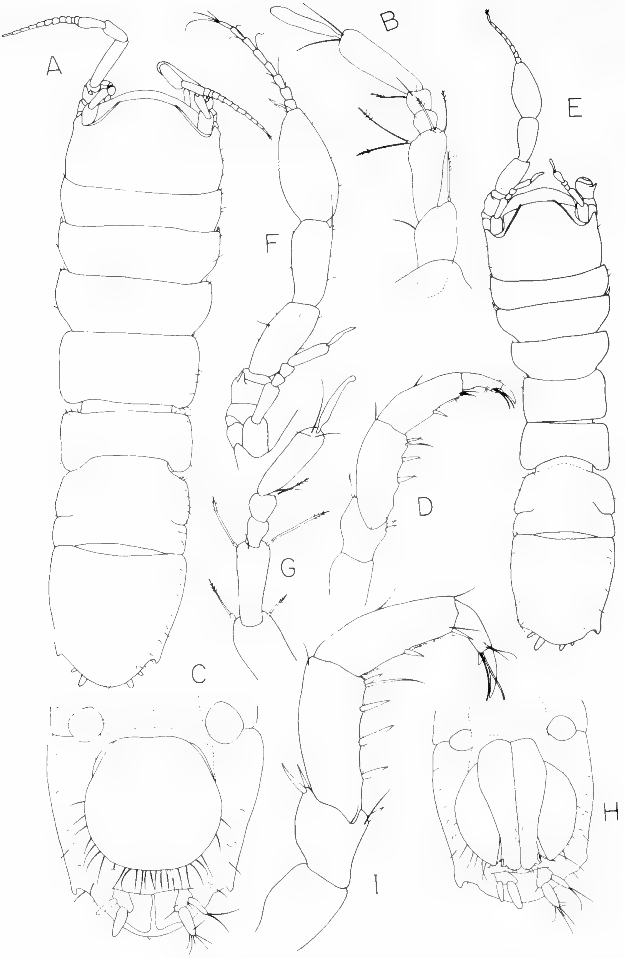

Figure 11. *Hebefustis par* n. sp., WHOI 328. A. preparatory female (holotype), dorsal view; B. preparatory female (holotype) right antenna I, lateral view; C. preparatory female (holotype) pleon, ventral view; D. preparatory female right pereopod I, *in situ;* E. male (paratype), dorsal view; F. male (paratype) left antennae I and II, dorsal view; G. male (paratype) left antenna I, dorsal view; H. male (paratype) pleon, ventral view; I. male (paratype) right pereopod I, *in situ.*

approximately equal in length to article 2, and in the more anterior placement of the pleonal posterolateral teeth.

The setation of the merus may differ between the right and left first pereopods of the same individual. In Figure 11, the differences in setation of the right first pereopods of the female and male are shown. The setation on the ventral surface of the merus of the left female first pereopod is the same as that on the merus of the right male first pereopod.

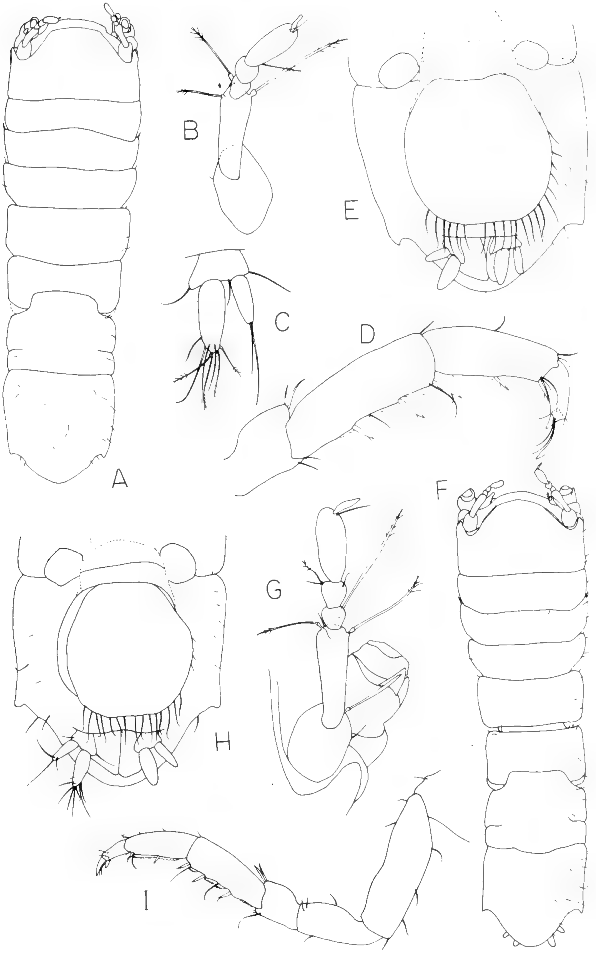

Figure 12. *Hebefustis alleni* n. sp., Allen S33. A. preparatory female (holotype), dorsal view; B. preparatory female (holotype) left antenna I, dorsal view; C. preparatory female (holotype) left uropod, *in situ;* D. preparatory female (holotype) right pereopod I, *in situ;* E. preparatory female (holotype) pleon, ventral view. WHOI 142. F. female, dorsal view; G. female right antenna I; H. female pleon, ventral view; I. female left pereopod I.

Hebefustis alleni n. sp.

Figure 12

Holotype.—Allen S33, preparatory female, 1.8 mm long, USNM 169398.

Other material.—WHOI 142, 6 spec., 1 frag.

Distribution.—Bay of Biscay and northeast Atlantic Ocean, 1623-1796 m.

Etymology.—After John Allen.

Diagnosis.—Antenna I segment 5, 2.4 times longer than wide (1/w); 0.6 times length of segment 2.

Pereonites 6 and 7 without posterolateral processes. Pereonite 4 l/w 0.5. Sides relatively straight; width 0.9 times width of pereonite 2. Pereonite 2 with robust seta on anterolateral corners.

Pleon with acute processes (teeth) 0.7 removed from anterior edge. Sides anterior to acute processes gently convex. Pleon width between midpoints of concavities formed by teeth 0.8 times width of pleon; length approximately equal to width.

Female opercular length approximately equal to width. Length of pleopod II 0.6 times length of pleon.

Body length 3.4 times tergal width of pereonite 2.

Remarks.—There are subtle differences in the shape of the pleon in specimens taken from the two localities (see Fig. 12E and 12H). *Hebefustis alleni* n. sp. can be differentiated from other species of the genus, which lack posterolateral projections on pereonites 6 and 7, on the basis of the robust body form, the relatively compact distal article of antenna I and the more posterior placement of the pleonal processes.

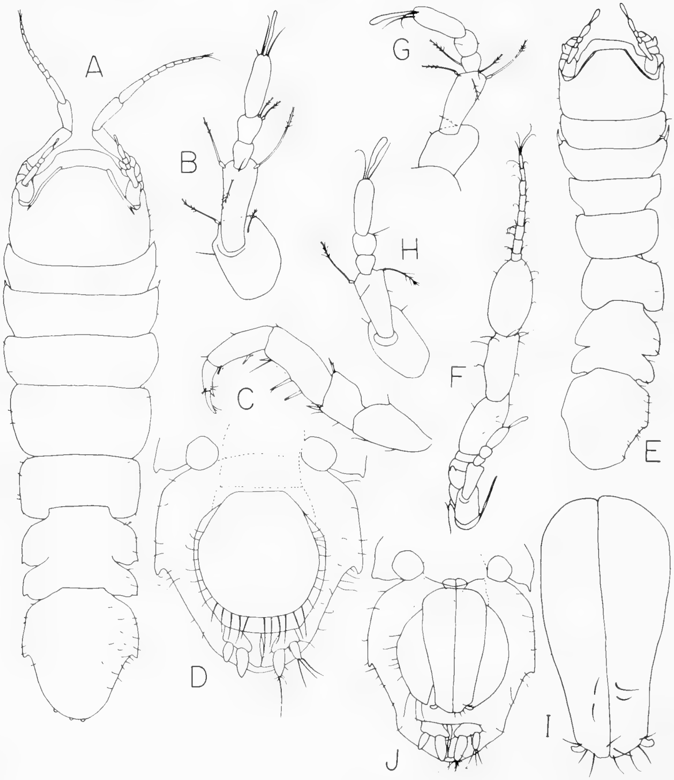

Figure 13. *Hebefustis cornutus* n. sp., WHOI 126. A. preparatory female (holotype), dorsal view; B. preparatory female (holotype) left antenna I, dorsal view; C. preparatory female (holotype) left pereopod I; D. preparatory female (holotype) pleon, ventral view; E. male (paratype), dorsal view; F. male (paratype) left antennae I and II, dorsal view; G. male (paratype) right antenna I, lateral view; H. male (paratype) left antenna I, dorsal view; I. immature male (paratype) pleopods I; J. male (paratype) pleon, ventral view.

Hebefustis cornutus n. sp.

Figure 13

Holotype.—WHOI 126, preparatory female, 2.0 mm long. USNM 169399.

Paratype.—WHOI 126, immature male, 1.5 mm long, USNM 169400; WHOI 126, 5 spec., SIO.

Other material.—WHOI 95, 1 spec.

Distribution.—Northwest Atlantic Ocean, 3753-3608 m.

Etymology.—Latin, horned.

Diagnosis.—Antenna I segment 5 somewhat bulbous; length to width ratio (1/w) 3.1 (holotype), 2.8 (allotype); sides nearly parallel; length 0.8 (holotype and allotype) times length of segment 2.

Pereonites 6 and 7 with acute processes on posterolateral corners. Pereonite 4 1/w 0.6 (holotype), 0.5 (allotype); sides convex, broadest anteriorly. Width 0.8 (holotype and allotype) times width of pereonite 2. Pereonite 2 with robust setae on anterolateral corners.

Pleon with acute processes (teeth) approximately 0.5 (holotype and allotype) way back from anterior edge. Sides of pleon just anterior to teeth parallel. Width of pleon between concavities formed by teeth 0.9 (holotype and allotype) times width of pleon; 1/w 1.2 (holotype and allotype), 0.8 times width of pereonite 2 (holotype and allotype). Male pleon with angular margin posterior to posterolateral teeth.

Female operculum 1/w 1.1; 0.6 times length of pleon (measured in dorsal view).

Male pleopod I 1/w 4.0; 0.6 times length of pleon (measured in dorsal view); limb tapers distally, without lateral oblique ridge.

Body length 3.6 (holotype), 4.0 (allotype) times tergal width of pereonite 2.

Remarks.—Note the double angles of the male pleon, somewhat similar to the pleon of *H. primitivus. Hebefustis cornutus* belongs to the cluster of species having acute processes on the posterolateral corners of pereonites 6 and 7. *Hebefustis cornutus* is readily discriminated on the basis of rather anterior placement of the posterolateral spines on the pleon; the pleon is distinctly longer than wide, and pereonite 4 narrow.

Hebefustis hexadentium n. sp.

Figure 14

Holotype.—WHOI 247, preparatory female, 2.2 mm long, USNM 169401.

Paratype.—WHOI 247, male, 1.7 mm long, USNM 169402; WHOI 247, 1 brooding female, SIO.

Distribution.—Argentine Basin, South Atlantic Ocean, 5208-5223 m.

Etymology.—*hexa,* Latin, six; *dens,* Latin, tooth.

Diagnosis.—Antenna I segment 5 broadest proximally, tapering distally. Length to width ratio (1/w) 3.1 (holotype), 2.6 (allotype); length 0.6 (holotype), 0.8 (allotype) length of segment 2.

Pereonites 6 and 7 with posterolateral spines on posterior corners. Pereonite 4 1/w 0.5 (holotype and allotype); broader anteriorly; width 1.0 (holotype), 0.8 (allotype) times width of pereonite 2. Pereonite 2 lacks robust seta on anterolateral corner.

Pleon with acute processes (teeth) 0.6 (holotype and allotype) removed from anterior edge. Sides of pleon parallel anterior to teeth. Width of pleon between midpoints of concavities formed by teeth 0.9 (holotype and allotype) times width of pleon. Pleonal width 0.8 (holotype), 0.9 (allotype) times width of pereonite 2. Pleon 1/w 1.05 (holotype and allotype).

Female operculum 1/w 1.1; 0.6 length of pleon.

Male pleopod I 1/w 3.6, 0.7 length of pleon; not flaring distally; without oblique ridge.

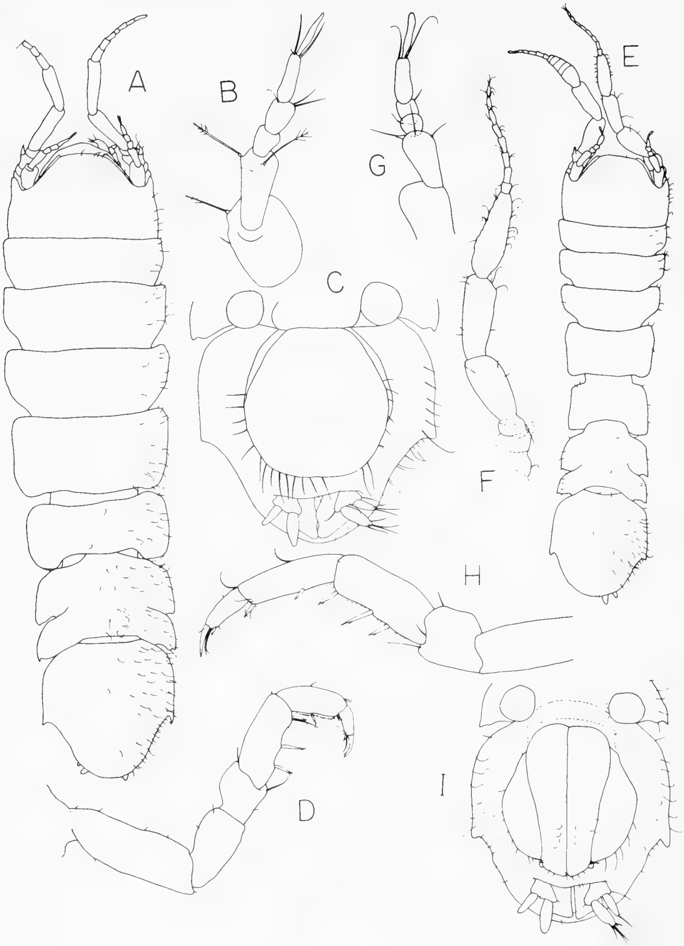

Figure 14. *Hebefustis hexadentium* n. sp., WHOI 247. A. preparatory female (holotype), dorsal view; B. preparatory female (holotype) left antenna I, dorsal view; C. preparatory female (holotype) pleon, ventral view; D. brooding female right pereopod I; E. male (paratype), dorsal view; F. male (paratype) right antenna II, dorsal view; G. male (paratype) left antenna I, lateral view; H. male (paratype) left pereopod I, *in situ;* I. male (paratype) pleon, ventral view.

Body length 3.9 (holotype), 4.2 (allotype) times tergal width of pereonite 2.

Remarks.—The lack of a robust seta on the anterolateral corner of pereonite 2 is unique among the species of this genus.

Hebefustis hexadentium n. sp. is strikingly similar to *H. hirsutus* (Menzies, 1962b). It differs in lacking a robust seta on the anterolateral corner of pereonite 2, in having a less rounded pleon anterior to the teeth, and in having a uropodal endopod that is somewhat longer relative to its width. Because the holotype of *H. hirsutus* is lost, the relationships of these two species cannot be explored.

Hebefustis hexadentium differs from the other new species possessing acute

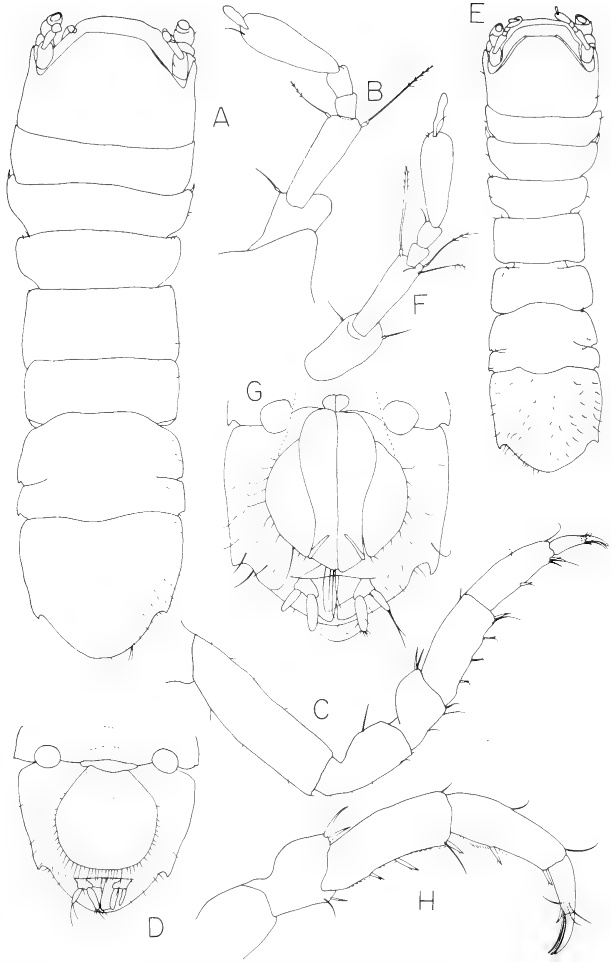

Figure 15. *Hebefustis dispar* n. sp., WHOI 202. A. preparatory female (holotype), dorsal view; B. preparatory female (holotype) right antenna I, lateral view; C. brooding female right pereopod I; D. preparatory female (holotype) pleon, ventral view; E. male (paratype), dorsal view; F. male (paratype) right antenna I, lateral view; G. male (paratype) pleon, ventral view; H. male (paratype) right pereopod I.

processes on pereonites 6 and 7 in the intermediate placement of the pleonal posterolateral spines and the relative shortness of the second article of antenna I.

Hebefustis dispar n. sp.

Figure 15

Holotype.—WHOI 202, preparatory female, 2.4 mm long, USNM 169403.

Paratype.—WHOI 202, male, 1.8 mm long, USNM 169405; WHOI 202, 103 spec. and frag., SIO, ZMUC.

Distribution.—Southeast Atlantic Ocean, 1427-1643 m.

Etymology.—Latin, unequal, dissimilar.

Diagnosis.—Antenna I segment 5 increases in width distally, length to width ratio (l/w) 2.8 (holotype), 3.0 (allotype); 1.1 (holotype and allotype) times longer than segment 2.

Pereonites 6 and 7 with posterolateral acute processes on posterior corners. Pereonite 4 l/w 0.4 (holotype), 0.5 (allotype); segment broadest posteriorly or with parallel sides; width 0.8 (holotype and allotype) times width of pereonite 2. Pereonite 2 with robust seta on anterolateral corners.

Pleon with acute posterolateral processes (teeth) 0.7 (holotype and allotype) removed from anterior edge. Sides of pleon anterior to teeth converge posteriorly; width of pleon between midpoints of concavities formed by teeth 0.7 (holotype), 0.8 (allotype) times pleonal width. Pleonal width 0.9 (holotype), 1.0 (allotype) times width of pereonite 2. Pleon l/w 0.84 (holotype), 0.89 (allotype).

Female operculum l/w approximately 1.0; 0.7 times length of pleon (measured in dorsal view).

Male pleopod I l/w 4.2, 0.8 length of pleon; somewhat flared distally, with oblique ridge on surface, terminating at lateral lobe.

Body length 3.4 (holotype), 3.9 (allotype) times tergal width of pereonite 2.

Remarks.—This species belongs to that cluster possessing acute processes on the posterolateral margins of pereonites 6 and 7. *Hebefustis dispar* is readily distinguished by its distinctive first antenna, and the converging sides of the pleon anterior to the teeth. Male pleopods I possess distinctive ridges on the distal surface.

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First records of Risso's dolphin (*Grampus griseus*) from the Gulf of California with detailed notes on a mass stranding

Stephen Leatherwood, Carl L. Hubbs, and Matilda Fisher

Abstract. *Grampus griseus* has been reported in the northeastern Pacific (near the coast) from southern British Columbia, Canada, to Acapulco, México, and near 2 oceanic islands, Isla de Guadalupe, off Baja California, México, and Clipperton Island, west of Costa Rica. On the basis of 2 sightings from an aircraft and of observations in detail on a mass stranding, penetration into the Gulf of California is herein recorded.

Resumen. *Grampus griseus* se extiende en la región nordeste del Pacífico desde cerca de las costas meridonales de la Columbia Británica (Canadá) hasta Acapulco (México) y en las inmediaciones de 2 islas oceanicas, Guadalupe (frente a Baja California) y Clipperton (al oeste de Costa Rica). Se incluye información sobre la penetración de esta especie en el Golfo de California, al considerar 2 observaciones desde un avión y los datos detallados obtenidos al vararse y morir cinco individuos en las costas del Golfo.

INTRODUCTION

The wide-ranging, nearly cosmopolitan delphinid *Grampus griseus* (Cuvier), often called "Risso's dolphin" (Fig. 1), has been reliably reported in the northeastern Pacific Ocean: inshore, from southern British Columbia (Guiguet and Pike 1965) southward to Acapulco, México, and offshore, not only of the mainland coast, but also near oceanic islands, including Isla de Guadalupe, off the Mexican state of Baja California (Hubbs 1961:145), and from Clipperton Island, west of Costa Rica (Leatherwood et al. 1972:92). These records, and many others, from the northeastern Pacific, are being documented by Stephen Leatherwood and colleagues.

This paper presents observations that document the penetration of *Grampus griseus* into the Gulf of California, on the basis of 2 well-separated sightings from an airplane on a marine-mammal survey, and of detailed observations along the northwestern shore of the Gulf, by Matilda Fisher and family, of a mass stranding of 5 individuals, all of which died overnight. Some plausible causes of such lethal strandings are discussed.

Because this species was not seen by 2 of us (Leatherwood and Hubbs), on numerous research trips around the Gulf, by ship, automobile, and airplane, we believe that Risso's dolphin is not common anywhere in the Gulf of California.

AERIAL OBSERVATIONS

During an aerial survey of marine mammals in the tropical eastern Pacific Ocean, National Marine Fisheries Service observers Eric G. Barham, William E. Evans, and James M. Coe encountered herds of *Grampus griseus* at 2 well-separated locations in the Gulf of California, México (Fig. 2). At 0958 h, 13 February 1974, they observed a herd estimated to contain 50 ± 10 individuals at ≈ 24°52′N, 108°58′W, in the

FIG. 1. *Grampus griseus*, 1 of several collected on northeastern shore of Florida and exhibited in Marineland of Florida.

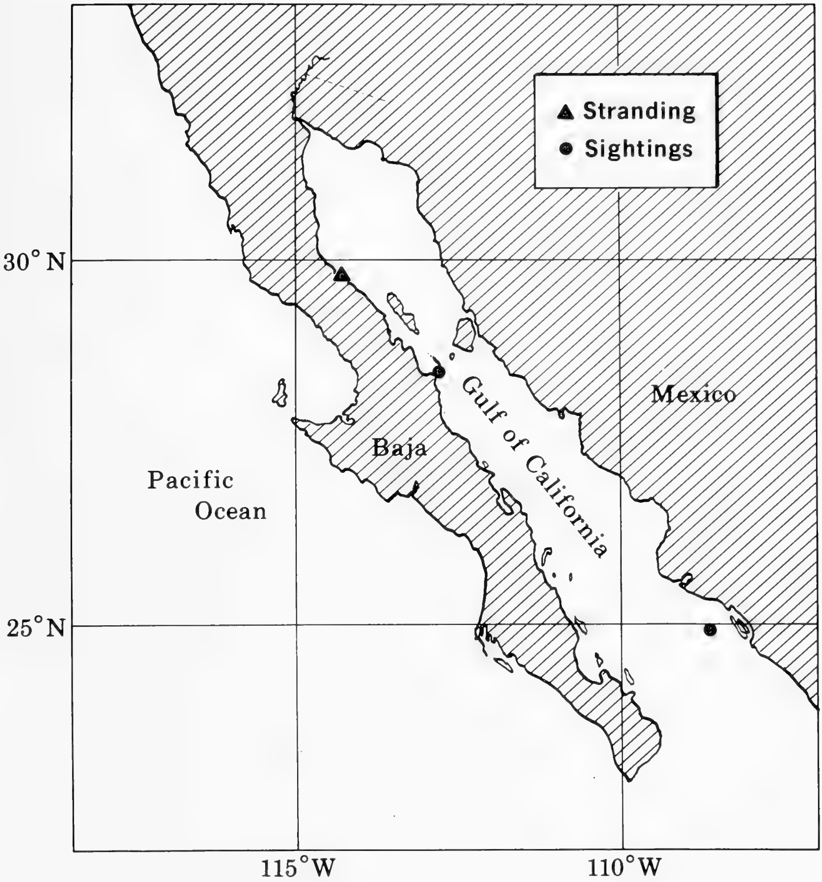

FIG. 2. Location of records for *Grampus griseus* in the Gulf of California.

southern and eastern part of the Gulf, some distance west of Isla Altamura, Sinaloa. At 1216 h on the same day they saw 2 more individuals of the species much farther north, at ≈ 28°21′N, 112°30′W, close to the northern and western shore of the Gulf, southwest of Isla San Lorenzo, and off the far-southern part of the State of Baja California (which occupies the northern half of the peninsula of the same name). Each of these locations is close to, if not partly within, one of the deep basins that occupy much of the southern two thirds of the Gulf (Shepard 1950, Rusnak et al. 1964). Because this delphinid seems to be largely an offshore species wherever it occurs, it may well be assumed that in the Gulf it occurs chiefly in the deeper areas, where the water is relatively clear.

The stranding here recounted, however, lies in the transitional area approaching the northern part of the Gulf, where the water is relatively shallow, and often rendered more or less turbid by the upwelling of deep deposits of varved sediment that have stemmed from past discharges of the sediment-rich Colorado River.

THE LETHAL MASS STRANDING

On 18 June 1973, the vacationing family of Ernest G. Fisher, of Brea, California, while camping on the northwestern shores of the Gulf of California, encountered the stranding of 5 cetaceans that were later identified, from their photographs (Fig. 3), as Risso's dolphins. The Fisher camp was at Punta Buféo, "about 5 miles" [≈ 8 km] north of the establishment of "Papa Fernández," on Bahía San Luis Gonzaga, in the state of Baja California (Fig. 2). At ≈ 1700 h they watched several large dolphins seemingly chasing a large school of fish, thought to be mullet, and apparently taking some at the surface, in the presence of numerous gulls. The dolphins were relatively close to the beach, usually within 100 m. At times they approached the shoreline, where a broad shallow shelf was being created by the receding tide (Fig. 3a).

At ≈ 1730 h the dolphins ceased their apparent feeding activity and headed toward the beach. One of them (in the foreground in Fig. 3b) suddenly outstripped the other 4 and continued alone up the gradually sloping beach, at first separately, until it was in no more than "one foot" [≈ 0.3 m] of water (not enough to cover it). Here, for ≈ 10 minutes, it began rooting in the sand. By then breathing seemed to have become labored, and the animal appeared to be unable to maintain an upright position. Not long after this individual had moved shoreward, the 4 other dolphins slowly proceeded into shallow water, where they remained with the first that stranded and kept nudging at it; at times they gave the impression of trying to force it back toward deeper water (Fig. 3c). For some time, the 4 remained near the obviously incapacitated individual, even when members of the observing party entered the rapidly shoaling water and touched them. To the observers, the breathing of the other animals seemed to remain more normal than that of the first to strand, and their actions seemed to be more coordinated. They appeared to avoid complete stranding, even when they ventured into water < "one foot" [≈ 0.3 m] deep. They extricated themselves from the beach and negotiated the tidal change. The observers got the impression that the 4 may have merely followed the "leader" to the point of death.

By ≈ 1800 h the dolphin that first approached the shore had definitely stranded. As the tide continued to ebb, during the large tidal movements characteristic of the upper Gulf, the 4 still-mobile animals gradually moved farther from the beach, but continued to stay close inshore. By midnight, the first grampus that stranded had died, and was being carried up the beach by the incoming tide. The 4 pod-mates were still in attendance, remaining within "about 100 feet" [≈ 30 m], swimming back and forth along the beach. At ≈ 0200 h the following morning (19 June), the situation had not changed, except that the first animal to strand and die was being tossed about in the surfline of the still-incoming tide, while the other 4 still stayed within "100 feet" [≈ 30 m], seemingly patrolling.

At dawn, ≈ 0530 h, the dead animal was high and dry (Fig. 3d). Its length was estimated at the site to be "12–13 feet" [nearly 4 m] and its weight to be "600 lbs" [≈ 270 kg]. No major recent external injuries were apparent, though the body was covered by numerous healed scars (as is characteristic of the species). Subsequent examination of the photographs showed that it was a female. At 0600 hr the other 4 pod-mates were found to be stranded about "300 ft" [≈ 100 m] southward, but were still alive. By 0800 h they too had perished. All 4 were estimated to be of about the same size, about "12 ft" [4 m] and to weigh "500 to 600 lbs" [≈ 227–272 kg]. They also were heavily scarred, but none showed any obvious recent external injury. Examination of the photographs (Fig. 3e) showed that at least 3 were females: at least 4 of the 5 animals were of that sex.

Although all of the dolphins were of similar size, they varied considerably in coloration. One was nearly white all over; the others ranged from dark gray to light gray (another characteristic of the species), with white areas of varying size on the belly. All 5 carcasses were towed offshore and released in the Gulf.

These detailed observations of the stranding of a pod of *Grampus griseus* apparently constitute the first known sighting of the genus and species in the Gulf of Cali-

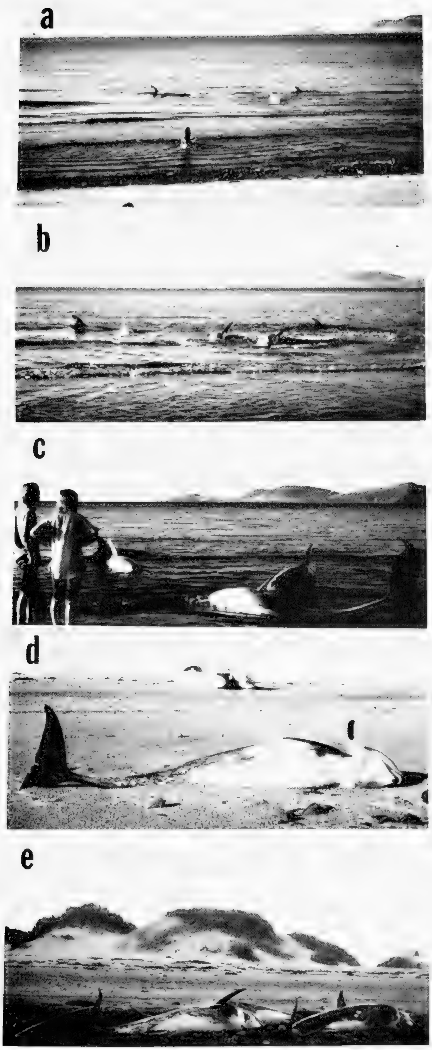

FIG. 3. Sequential views of the reported stranding of *Grampus griseus*. a. The 5 *Grampus* dolphins are in the shallows where they had been feeding on mullet (≈1700 h, 18 June 1973). b. The animals approaching the shallows (≈1730 h). c. The first animal in the process of stranding (≈1740 h). The other 4 continue to remain close by, despite the rapidly ebbing tide, at times nudging the "distressed" one. d. The following morning (≈0530 h, 19 June 1973) the first one to strand is now high and dry. e. The remaining 4 stranded animals alive ≈10 m farther down the beach (≈0600 h, 19 June 1973).

fornia. The observed details of this stranding follow in various respects the sequences described for some other almost continuously watched cetacean strandings, including one involving ≈ 20 pilot whales (*Globicephala* sp.) recounted by Hubbs (in Norris 1966:605). In a rather major aspect, however, this *Grampus* mass stranding seems to differ, in that just before starting to strand, the 5 individuals appeared to be feeding actively, whereas it has generally been thought that stranded cetaceans have little or no recently ingested food in their stomachs. One noted exception to this generalization involved an adult female pilot whale found on 20 August 1952 freshly stranded at Encinitas, San Diego County, California, with flesh so flaccid that a depression formed by slight pressure on the surface remained, although the stomach and even the throat were strangely crammed with freshly ingested giant kelp, *Macrocystis,* calling to mind the propensity of sick dogs to devour grass.

The behavior of a single member of the grampus group here reported suddenly changed, its respiration seemed labored and its equilibrium appeared unstable. For some time, the 4 others appeared to function normally, while staying close to the one first stranded.

Why cetaceans, such as those comprising this pod of *Grampus,* at times rather suddenly strand and then die, as individuals or in groups of varying size, for no readily perceptible reason, has long been a topic of discussion, probably largely because thorough postmortem studies are often lacking. Some postmorten examinations have revealed that at least some strandings result from sickness or injury. Alternatively, some mass strandings seem to have involved apparently healthy and uninjured animals. Those stranded, individually or in groups, frequently seem to make little or no effort to head back seaward, often even resisting efforts of sympathetic persons to lead them to safety.

The observations recounted here, although contributing some data on events in a cetacean stranding, seem to have no critical bearing on the cause or causes of the lethal phenomenon. Theories regarding causes of cetacean strandings have been many and diverse. A recent summary (Leatherwood et al. 1976) states:

> Strandings of lone individuals usually involve an animal which is sick or injured. Mass strandings, involving from several to several hundred individuals, appear to be far more complex and may result from herd-wide disease conditions, from fear reactions, or from failure of the echolocation system due to physiological problems or environmental conditions which combine to reduce its effectiveness, to mention only a few.

Reysenbach de Haan (1957), Fraser (in Norris 1966:602), Caldwell and Caldwell (1971), and Ridgway and Dailey (1972), among others, have discussed the probable role of parasitism in strandings of cetaceans. James G. Mead (*personal communication*) found that all members of a herd of short-finned pilot whales *(Globicephala macrorhynchus)* that stranded in North Carolina in 1974 were heavily infested by parasites in the ear canals, implicating possible mass infection in whole-herd strandings. Incidence of such infestation of the middle ear was found to be relatively low in samples of presumably healthy spotted and spinner dolphins *(Stenella* spp.) incidentally captured in tuna seines, but changes in incidence with age suggest that the parasite or parasites involved may be a factor in natural mortality (Dailey and Perrin 1973). It is hoped that such evidence of the association of parasitism with stranding will be further tested, along with additional determination of such parasitism in nonstranded cetaceans.

ACKNOWLEDGMENTS

The authors thank Eric G. Barham, James M. Coe, and William E. Evans for providing the sight records from the Gulf of California, and William E. Evans, James G. Mead, Kenneth S. Norris, William F. Perrin, Sam H. Ridgway, and Forrest G. Wood for helpfully reviewing the manuscript. David K. Caldwell kindly provided the photograph reproduced as Fig. 1.

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TRANSACTIONS
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JOANELLIA LUNDI SP. NOV. (CRUSTACEA: MALACOSTRACA) FROM THE MISSISSIPPIAN HEATH SHALE OF CENTRAL MONTANA

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Abstract. **Joanellia lundi** is described from the Heath Shale of Montana. The material represents a poorly sclerotized aenigmacarid associated with the syncaridan *Squillites spinosus*. It is the first occurrence of the genus *Joanellia* in North America.

Schram and Schram (1974) redescribed the syncarid malacostracan, *Squillites spinosus* Scott, 1938, from a black paper shale near the top of the Heath Shale, based on material found by Dr. Richard Lund of Adelphi University. Associated with *Squillites* in the Heath is a biota of leaf fragments encrusted with *Spirorbis*, conchostracan crustaceans, an aenigmacarid aeschronectidan (Malacostraca: Hoplocarida), and vertebrates (xenacanth sharks, acanthodian, and paleoniscoids). The associated fauna and stratigraphy of the Heath Shale are related in detail in Schram and Schram (1974).

The aenigmacarid aeschronectidan of the Heath Shale is described here. The material is plentiful but poorly preserved and comes from two localities in Fergus County, Montana: most specimens from sec. 28, T. 14 N, R 20 E, 1.2 km [=2 miles] south and 3.7 km [=6 miles] east of Heath; and some from T. 14 N, R. 19 E, 1.4 km [=2¼ miles] south of Heath. The material is deposited in the Field Museum of Natural History, Chicago (numbers prefixed PE) and the Carnegie Museum of Natural History, Pittsburg (numbers prefixed CM).

Discussion

The association of the aenigmacarid, *Joanellia lundi*, with the syncaridan, *Squillites spinosus*, is noteworthy. The associated faunas of the Heath Shale and general regional lithology indicate the Heath represents a lagoonal setting (R. D. Norby, *personal communication*). This is another instance in the Paleozoic when an aenigmacarid–syncaridan association in a lagoonal setting is recorded. The other is in the Upper Pennsylvanian, Madera Formation, of New Mexico (Schram and Schram, 1979) where *Aenigmacaris minima* is found with the syncarid *Uronectes kinniensis*. Thus, there seems to be a distinctive Late Paleozoic lagoonal fauna of crustaceans akin to what is seen in nearshore marine and coal measure chronofaunas (Schram, *in press*).

This is also the first occurrence of the genus *Joanellia* in North America. It was previously only known from the Lower Viséan of Britain (Schram, 1979). Interestingly, the earlier occurrence is in the entirely different faunal setting of a nearshore marine habitat.

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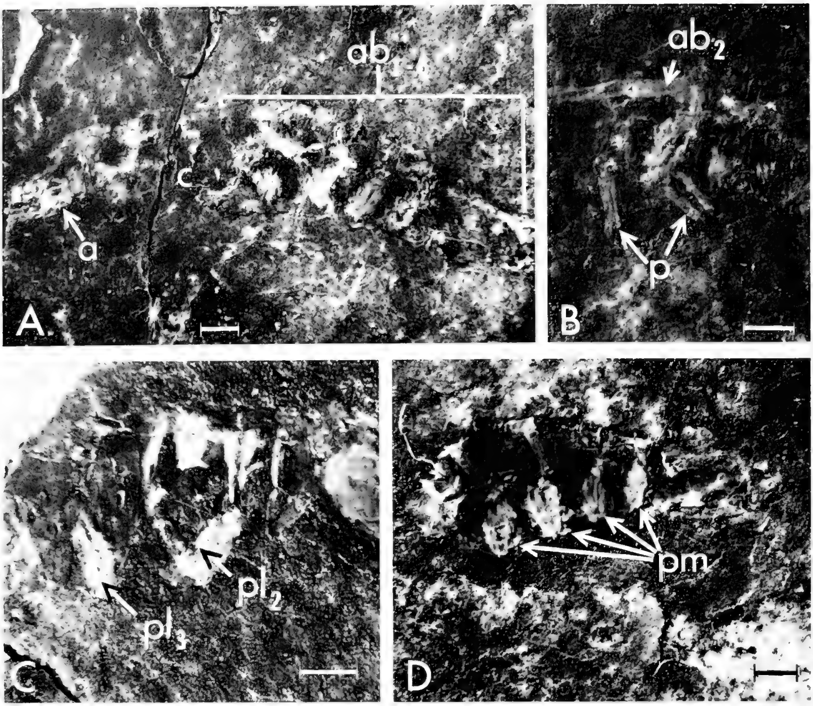

FIG. 1. ***Joanellia lundi*** sp. nov. (A) PE 18383, holotype. (B) PE 18382, anterior abdomen with stenopodous pleopods. (C) PE 18384, anterior of abdomen with pleomere pleura. (D) PE 18373, preserved remnants of pleopod muscles. a—antenna, ab—abdominal segments, p—pleopods, pl—pleomere pleura, pm—pleopod muscles, PE—specimens deposited at the Field Museum of Natural History, Chicago. Scales = 1 mm.

SYSTEMATICS

Class MALACOSTRACA Latreille 1806
Subclass HOPLOCARIDA Calman 1904
Order AESCHRONECTIDA Schram 1969
Family AENIGMACARIDIDAE Schram and Horner 1978
Genus *JOANELLIA* Schram 1979

Diagnosis.—Small aenigmacarid. Carapace subtrapezoidal in lateral outline. Second pleomere longer than any of the other first 5 pleomeres. Uropods terminal on 6th pleomere and directed posteriorly (probably flap-like).

Range.—Dinantian (Viséan) to Middle Namurian (Upper Mississippian).

Remarks.—The genus *Joanellia* was described by Schram (1979) based on Viséan material from Scotland and northern England. Schram and Horner (1978) suggested allying *Joanellia* with the genus *Aenigmacaris.* This assignment was based on both genera having very elongate and poorly sclerotized tailfans, and stenopodous pleopods.

JOANELLIA LUNDI sp. nov.

Figs. 1 and 2, Table 1

Diagnosis.—Carapace subtrapezoidal with short rounded branchiostegal lobes. Cuticle poorly sclerotized. Abdominal pleurites 1 through 4 with posterior extension and triangular ventral margins.

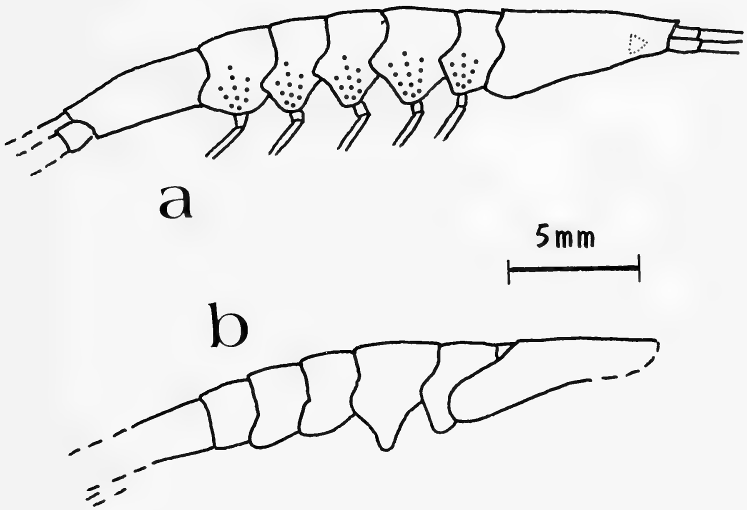

FIG. 2. ***Joanellia lundi*** sp. nov. from the Heath Shale, Upper Mississippian, Montana (dots indicate location of mandible and pleopod muscles). (B) *Joanellia elegans* (Peach) 1908, Dinantian, Lower Carboniferous, Great Britain.

Holotype.—PE 18383 (Fig. 1a).

Type locality.—As described in the introduction (collected specimens not separated as to locality).

Derivation of name.—Named in honor of Dr. Richard Lund, the collector of the material, who over the years has generously made this and other Paleozoic crustacean material available to us for study.

Description.—The entire cuticle of the animal is poorly sclerotized. The carapace has a blunt anterior end with a faint optic notch (PE 18383, Fig. 1a, CM 33893). The posterior carapace margin is gently curved or bowed anteriad and the branchiostegal lobe is rounded (PE 18384, CM 33898). Only the proximal segments of antennae have been preserved, and several specimens (e.g., PE 18383, Fig. 1a, PE 18384, CM 33893) reveal the proximal segment was moderate in size and the next most distal segments were of longer but undetermined length. The mandible (PE 18383, 18384) is relatively large but apparently not highly sclerotized nor mineralized.

The first 4 pleomeres are all similar, except for the 2nd being larger than any of the others (PE 18384, Fig. 1c). The first 4 abdominal segments have triangular ventral margins and a posteriorly directed extension on the pleuron (PE 18317, 18384, Fig. 1c). The 5th pleomere pleura is broadly rounded (PE 18375). Pleomeres 1 through 5 have stenopodous pleopods (PE 18323, 18375, 18382, Fig. 1b), with only the proximal short segments, and part of the long, next most distal segment being preserved.

TABLE 1. Measurements (in millimetres) for some specimens of ***Joanellia lundi*** sp. nov. * denotes the holotype.

Specimen	Carapace length	Abdominal length (pleomeres 1–6)
PE 18317	3.7	7.5
PE 18373		7.3
PE 18380		11.0
PE 18382		9.4
PE 18383*	4.1	7.4
PE 18384	3.2	
CM 33893		7.8

These 5 pleopods were also equipped with a well-developed musculature (PE 18308, 18309a, 18371, 18373, Fig. 1d, 18380, 18383) which took origin on the sides of the abdominal segments. The 6th pleomere is very long (PE 18380). The uropods are apparently flap-like, situated terminally, and directed markedly posteriad (PE 18314, 18383), but further details of their exact form are obscure. Nothing can be discerned concerning the telson.

A partial reconstruction is presented in Fig. 2a.

Remarks.—Because the cuticle was so poorly sclerotized the specimens of *Joanellia lundi* are poorly preserved. As a result really pertinent descriptive features of the antennae, thoracopods, and tailfan are lacking.

Several differences of *Joanellia lundi* with *Joanellia elegans* (Fig. 2b) of the Scottish Viséan can be delineated. *Joanellia elegans* has a sharp posterior extension to the branchiostegite lobe of the carapace, no marked posterior extensions on the abdominal pleura, only pleomere pleura 1 and 2 with triangular ventral margins, and pleomere pleura 3 through 5 broadly rounded.

Some representative measures of *Joanellia lundi* are given in Table 1.

Acknowledgments

The authors thank Dr. Richard Lund, Adelphi University, for generously allowing us to study the material, and Dr. Rodney Norby, Illinois State Geological Survey, for helpful discussions concerning the Heath Shale. Drs. Richard Lund and Niles Eldredge, American Museum of Natural History read the manuscript and offered constructive comments.

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TRANSACTIONS
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THE GENUS *ARCHAEOCARIS,* AND A GENERAL REVIEW OF THE PALAEOSTOMATOPODA (HOPLOCARIDA: MALACOSTRACA)

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Abstract. Newly discovered material of *Archaeocaris graffhami* Brooks, 1962, allows a more complete description and reconstruction of that animal. Reexamination of all specimens of *Archaeocaris* results in some modifications in the reconstruction of *Archaeocaris vermiformis* Meek, 1872, as well. All Paleozoic palaeostomatopod species are reviewed.

Introduction

Dr. Charles Sandburg of the United States Geological Survey in Denver, Colorado, referred some crustacean fossils to me for identification which proved to be *Archaeocaris graffhami* Brooks, 1962. The specimens were collected from the upper Pilot Shale at Bactrian Mountain in the Pahranagat Range, Nevada, and effectively extend the stratigraphic range of this species from the Upper Mississippian, Chesteran, back into the Lower Mississippian, Kinderhookian.

This new material and my study of the British palaeostomatopods prompted a reexamination of all specimens of *Archaeocaris.* A general summary review of the entire order is presented, with a clarification of the relationships of *Archaeocaris* to the rest of the Palaeostomatopods.

Systematic Paleontology

Phylum Crustacea, Pennant, 1777
Class Malacostraca, Latreille, 1806
Subclass Hoplocarida, Calman, 1904
Order Palaeostomatopoda, Brooks, 1962
Family Perimecturidae, Peach, 1908
Genus *Archaeocaris,* Meek, 1872

Diagnosis.—Carapace smooth with posterodorsal margin deeply excavated to expose dorsum of posterior thoracomeres; mandible well sclerotized; uropods lobate; telson ovoid; body cross section circular to oval.

Archaeocaris graffhami Brooks 1962. (Figs. 1–3, 4b, 5a)

Brooks 1962, p. 214, Pls. 8 and 47; Schram 1969*a,* p. 217, Table 1.

Diagnosis.—Body moderate to large; weak development of mandible in relation to overall body size; abdominal pleura simple and undecorated; carapace thin and poorly sclerotized.

Remarks.—The holotype (part, Museum of Comparative Zoology at Harvard, 5849, and counterpart, University of Oklahoma, 4411) is poorly preserved (Fig. 5a).

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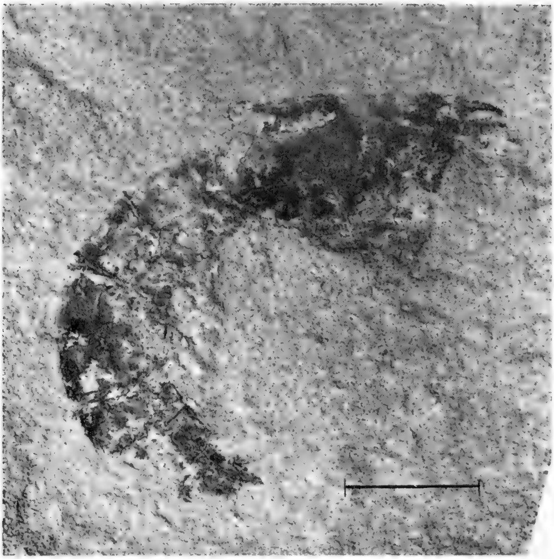

FIG. 1. *Archaeocaris graffhami* Brooks, 1962; USNM 220967; scale 1 cm.

Most of the tail is missing and there is no carapace. Indeed, as Brooks (1962) pointed out, only the ratio of the width of the mandible to body length, .023 (0.8 mm:35 mm) allowed these specimens to be distinguished from *Archaeocaris vermiformis*.

Additional material.—The new material from Bactrian Mountain consists of 3 specimens of more or less complete animals. USNM 220967 (Fig. 1), the largest and best preserved specimen, has a mandible width of 0.7 mm and an approximate body length of 41 mm, i.e., ratio of .017, somewhat smaller than for the types of *A. graffhami*. The body is generally poorly sclerotized, but the carapace is especially so, as seen on USNM 220967 and 220968 (Fig. 2). The tail fan, parts of which are seen on all 3 specimens, appears to consist of an ovoid telson and large lobate uropods, but again, unfortunately the preservation leaves something to be desired. USNM 220969 (Fig. 3) has pleopods preserved, and USNM 220967 and 220968 bear traces of cephalic and thoracic appendages, though little can be definitely determined for any of these except that the anterior thoracopods were subchelate. The deep excavation of the dorsal posterior margin of the carapace is evident on USNM 220967. Although the holotype counterparts are so poorly preserved that comparison with the Nevada specimens is difficult, the trapezoidal form and relative size of the mandible, the rounded shape of the abdominal pleurites, and the subchelate appendages seem to relate the entire group of specimens.

The associated fauna at Bactrian Mountain (Sandberg and Poole 1970) is an open marine, relatively deep water fauna of phosphatic brachiopods, *Chonetes*, sponge spicules, and ostracodes. Elias and Branson (1959) report a marine fauna in the Delaware Creek member of the Caney Shale in Oklahoma with the holotype of *A. graffhami*, including *Linoproductus*, the clam *Caneyella*, a snail *Macrocheilus*, several cephalopods, and abundant conodonts. Such a deep water, open marine association is unusual for Late Paleozoic malacostracans, which are more typically found in near-shoreline situations of shallow marine or brackish–freshwater habitats.

The range of *A. graffhami* is extended by inclusion of the material from Nevada. The lower and middle units of the Pilot Shale are dated on the basis of conodonts as

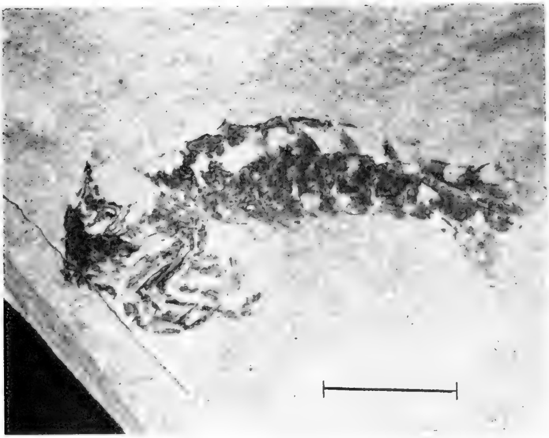

FIG. 2. *Archaeocaris graffhami* Brooks, 1962; USNM 220968; scale 1 cm.

latest Devonian; the upper Pilot Shale, which contains the shrimp, is lowermost Kinderhookian in age. The holotype comes from the Caney Shale, uppermost Meremecian or lowermost Chesteran in Pontotoc County, Oklahoma, USA.

Archaeocaris vermiformis Meek, 1872 (Figs. 4a, 5b, 5c)

Meek 1872, p. 335; 1875, p. 321, Pl. 18, Fig. 7; Ortmann 1897, p. 283; Van Straelen 1931, p. 71; Brooks 1962, p. 211, Pls. 8, 45, and 46; 1969, vol. R, p. R535, Fig. 341; Schram 1969*a*, p. 217, Table 1.

Diagnosis.—Body small; cuticle well sclerotized; relatively strong development of the mandible in relation to overall body size; abdominal pleura sculptured and marked with furrows.

Remarks.—The holotype and paratype series in the National Museum are not as well preserved as the series of specimens at Princeton University (Fig. 5b, 5c), 1597 d/1 to 1597 d/14. The treatment of Brooks (1962) remains substantially unchanged by me except for a few points resulting from preparation of the Princeton material.

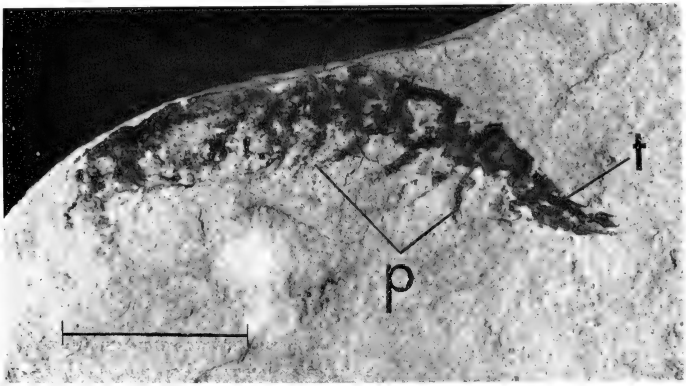

FIG. 3. *Archaeocaris graffhami* Brooks, 1962; USNM 220969; scale 1 cm. p = pleopods, t = telson.

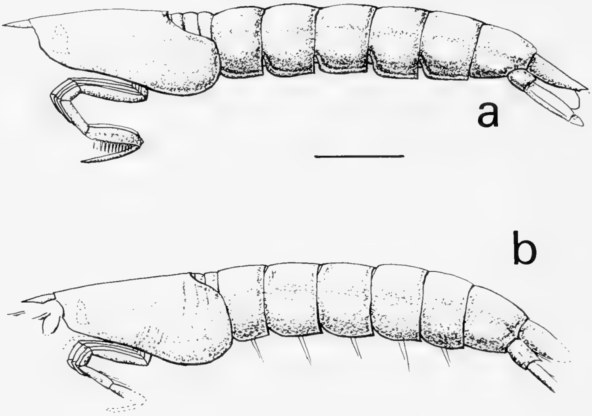

FIG. 4. Reconstructions of the species of *Archaeocaris*, scale 1 cm. (a) *Archaeocaris vermiformis* Meek, 1872. (b) *Archaeocaris graffhami* Brooks, 1962.

Additional material.—The counterpart of 1597 d/1 to that illustrated in Brooks (1962, Pl. 46, Fig. 2) shows more clearly that the carapace extended along the midline to about the 6th thoracomere and the lateral wings of the carapace extended posteriad to cover the pleurae of the last 3 thoracomeres, thus leaving the 3 posteriormost thoracomeres exposed dorsally. This arrangement of the carapace is also observable on 1597 d/7. In addition, 1597 d/1 also clearly preserved a series of large spines on the propodus segments of the anterior thoracic appendages opposed to the subchelate dactylus, thus forming a rather formidable battery of claws. 1597 d/2 and d/8 seem to indicate that the coxa of the anterior thoracomeres is short and that there is a moderately well developed precoxa proximal to the body. The telson and tail fan are still not well known. The uropods are visible as broad lobes on 1597 d/12, and to a lesser extent on d/4. The telson is smooth and undecorated, and has an oval shape, somewhat more pointed at the distal end (1597, d/4, d/12, d/13, d/14). There is no indication that the telson is developed terminally as a spike, as in *Perimecturus* and *Bairdops*, though there is some indication of terminally located, small caudal furca (1597 d/13).

Meek (1875) described *A. vermiformis* from the Waverly Group, near Danville, Kentucky in association with the phyllocarid, *Ceratiocaris*. The Waverly fauna is generally considered to be marine because the fauna contains such genera as *Fenestrella*, *Lingula*, *Orbiculoidea*, *Productus*, *Spirifer*, *Aviculopecten*, *Palaeoneilo*, *Schizodus*, *Platyceras*, and *Conularia*, among others. The Princeton material comes from west of Junction City, Boyle County, Kentucky, a site which also yielded a specimen attributed to *Palaeopalaemon newberryi*.

Genus: *Bairdops* Schram, 1979

Diagnosis.—Circular or oval in body cross section; carapace rectangular in lateral outline, no dorsally exposed posterior thoracomeres: telson base rectangular with prominent posterior spike. Uropods blade-like.

Remarks.—Two species of *Bairdops* are recognized: the Viséan *Bairdops elegans* (Peach) 1908 from the Calciferous Sandstone Series of Scotland, and the Namurian *Bairdops beargulchensis* Schram and Horner, 1978, from the Bear Gulch Limestone in the uppermost Mississippian of Montana, USA. The principal differences between the 2 species are these. The telson spike in *B. elegans* is more than half the length of the telson base. The uropodal protopod in *B. elegans* has only a slight middorsal

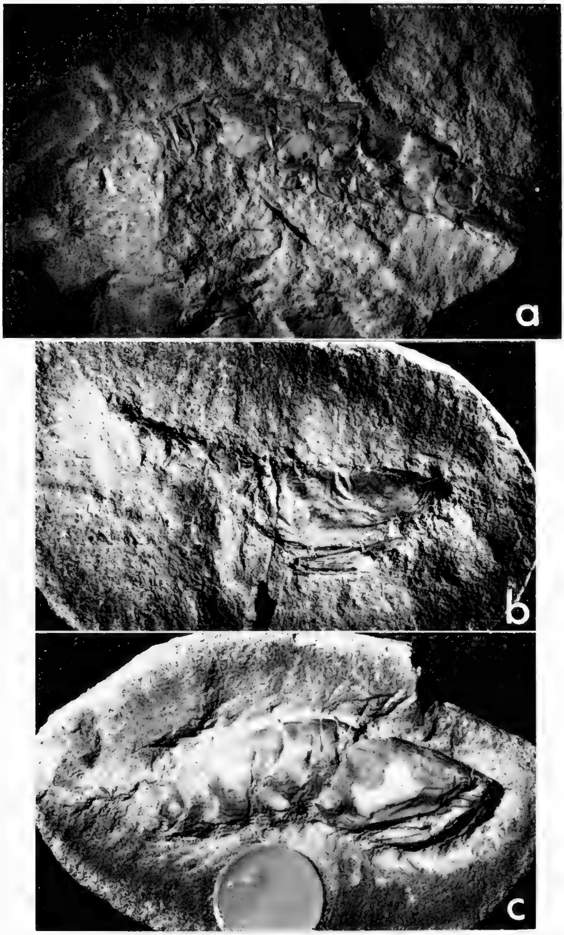

FIG. 5. (a) *Archaeocaris graffhami* Brooks, 1962; holotype MCZ 5849. (b) *Archaeocaris vermiformis* Meek, 1872; PU 1597 d/1 displaying the carapace and subchelate thoracopods. (c) *Archaeocaris vermiformis* Meek, 1872; PU 1597 d/3 displaying the abdominal pleurites.

posterior spike on the protopod. The uropodal exopod in *B. elegans* is a simple blade with no setae, while in *B. beargulchensis* it is laterally serrate and medially setose. The uropodal endopod of *B. elegans* is small and distally pointed with no setae, whereas in *B. beargulchensis* it is large, oval, and setose.

Although *Bairdops* is superficially similar to *Archaeocaris*, the former is generally larger. *Archaeocaris* has a carapace deeply excavated along the middorsal posterior margin, exposing several of the posterior thoracomeres dorsally, but *Bairdops* has no such excavation. In this regard, *Archaeocaris* is closer to the advanced tyrannophontid stomatopods, which reduce the length of the entire carapace and expose the 3 posterior thoracomeres completely. *Archaeocaris* does not have a telson spike and possesses thin, flap-like uropods, whereas *Bairdops* has a spiked telson and generally more blade-like uropods. *Archaeocaris* again resembles the more advanced tyrannophontids, in regard to the unarmored telson whereas *Bairdops* is similar to *Perimecturus*.

Genus: *Perimecturus* Peach, 1882

Diagnosis.—Dorsoventrally flattened body. Telson base broadly triangular. Uropodal exopods strongly blade-like. Uropodal endopods small and atrophied.

Remarks.—There are 2 species of *Perimecturus*: the Viséan *Perimecturus parki* (Peach) 1882 in the Calciferous Sandstone Series of Scotland, and the Namurian *Perimecturus rapax* Schram and Horner, 1978, from the Bear Gulch Limestone at the top of the Mississippian of Montana. In addition, Brooks (1969) considered *Anthracomysis* Van Straelen, 1923, synonymous with *Perimecturus* but gave no reasons.

The differences between the 2 recognized species of *Perimecturus* are largely restricted to the tail fan. Long, delicate setae decorate the entire tail of *P. parki*, but *P. rapax* has no setae. The telson spike is less than half the length of the telson base in *P. rapax*. The uropodal protopod of *P. parki* is smooth and unadorned laterally, whereas that of *P. rapax* is distally serrate. The abdominal tergites and carapace of *P. parki* are decorated with 4 longitudinal ridges, but *P. rapax* has 3 ridges and scattered wart-like decorations.

The generally large size and distinct dorsoventral flattening of *Perimecturus* make it one of the most distinct of the Late Paleozoic malacostracans.

Order: Palaeostomatopoda *incerta sedis*

Rodendorf (1961, 1970) described supposed insect wings from the Upper Devonian of the USSR, *Eopterum devonicum* and *Eopteridium striatum*. Later he suggested (1972) these might be the uropods of palaeostomatopods. I have examined the original material in Moscow and agree, but am unable to give a definitive identification. They are definitely tail fans of some hoplocaridan or even eumalacostracan, but the specimens do not permit more precise identification.

Schram (1979) suggested *Perimecturus pattoni* Peach 1908 was not a palaeostomatopod, but possibly a tyrannophontid stomatopod.

Van Straelen (1923) described *Perimecturus fraiponti* from the Chokier Beds, Namurian, near Liege. From the description and illustration, however, the short carapace and completely exposed posterior thoracomeres would indicate this is a tyrannophontid stomatopod. The stratigraphic position of the material would tend to confirm this because palaeostomatopods are not found this high in the section.

Discussion

Members of the subclass Hoplocarida were important constituents of Late Paleozoic crustacean faunas. Their morphological diversity and ecologic distribution exceeded that of modern hoplocaridans, now restricted to the highly specialized order, the Stomatopoda (mantis shrimp). The modern stomatopods are the only rapacious, active carnivores among the living crustaceans, other forms such as lobsters and crabs being scavenging, low-level carnivores. This rapacious trend in hoplocaridan evolution developed very early, by Early Mississippian or possibly Late Devonian time. The trend continued without interruption from the primitive palaeostomatopods through the Late Carboniferous archaeostomatopodan tryannophontids into the Mesozoic, where essentially modern stomatopods are first encountered.

The Hoplocarida as a whole have fared poorly in comparison with the Eumalacostraca. Two of the 3 Paleozoic hoplocaridan orders, Aeschronectida Schram, 1969*b*, and the Palaeostomatopoda Brooks, 1962, became extinct in Permo–Triassic time, whereas the Paleozoic eumalacostracan superorders generally persisted to Mesozoic time and increased their morphologic diversity and geographic dispersion.

The singular success of the modern stomatopods is undoubtedly due to the evolution of complex behavior patterns used for a variety of purposes. Resources in limited areas are partitioned with interspecific behavior patterns (Dingle et al., 1973), and complex patterns of behavior have evolved to communicate both within and between various stomatopod entities (Dingle 1969). In addition, the females of at least some species brood the young in cavities until stage IV molting occurs, effectively protecting the young until an advanced stage in development is reached (Dingle and Caldwell 1972), a habit found elsewhere only in the very successful peracarid eumalacostracans.

Caldwell and Dingle (1975) discuss the degree of armor and aggressive behavior in stomatopods. There are 2 types of raptorial appendages in living stomatopods, spearing and smashing forms. The smashers are the more vicious of the 2, possess heavy thoracic appendages with powerful muscles, display very intense and complex aggressive behavior patterns, have heavy telson armor, and tend to occupy rock or coral habitats. The spearers are not as heavily armored, less intense in their behavior, and burrow in soft substrates.

Such behavioral and morphologic parameters may have been at least incipiently at work in the palaeostomatopods. None of the palaeostomatopods can be considered heavily armored. The exoskeletons appear to have been only poorly to moderately sclerotized and no evidence of massive mineral deposits for armor is evident. In addition, the palaeostomatopods and tyrannophontid stomatopods had spearing type appendages. *Archaeocaris vermiformis* and *B. beargulchensis* clearly had serrate propodi on the thoracic raptorial subchelae. The habitats of all the palaeostomatopods seem to have been soft bottom and the dorsoventral flattened morphology of *Perimecturus* suggests a form adapted to lying partially buried and hidden in the sediment while waiting to ambush its next meal.

Modern stomatopod evolution seems to have moved from the less armored to the more armored, and there are indications the same might have occurred in paleostomatopod lines. For example, the tail fan of the Viséan *Perimecturus parki* is more delicately ornamented and seemingly not as well sclerotized than that of the simpler, blade-like, and serrated elements in the tail of the Namurian *P. rapax*. Viséan *Bairdops elegans* has a small undistinguished tail fan when compared to the spiked and serrate elements in the tail of *B. beargulchensis* of the Namurian.

As to what the events were that preceded the extinction of the palaeostomatopods and the rise of the stomatopods is difficult to assess. The success of stomatopods is undoubtedly related to the sophistication of their behavior. Palaeostomatopod behavior, aside from the generalities expressed above, is impossible to determine. Behavior in stomatopods is linked with limb specializations (Caldwell and Dingle 1975). Cisne (1974) used the Brillouin Expression ($h = [1/N]\log_2[N!/(N_a!N_b! \ldots N_s!)]$) to measure limb specialization and tagmatization, and employing this method the following values are obtained:

Palaeostomatopoda	2.12?
Perimecturus parki	
Archaeostomatopodia	2.25?
Tyrannophontes theridion	
Opisterostomatopodia	2.35
Squilla mantis.	

Some question exists for the exact values of the fossil groups. The morphology of the 1st thoracopod is unknown in any of these forms as to whether it is raptorial like the 2nd through 5th thoracopods (value of 2.12), or whether the 1st thoracopod is specialized in some way (value of 2.25) like that seen in the living stomatopods. It would seem from body morphology that the values given here express the lower level of palaeostomatopod limb specialization and body tagmatization, i.e., the stomatopod morphology (even that of the primitive tyrannophontids) was probably more effectively able to handle the ecologic and behavioral parameters to survive as active, rapacious carnivores.

This replacement of palaeostomatopods by archaeostomatopodeans was going on by Namurian time in the middle of the Carboniferous. *Tyrannophontes* existed with palaeostomatopods in the uppermost Mississippian Bear Gulch Fauna (Schram and Horner 1978), and may have come into being somewhat earlier (Schram 1979). Later faunas such as the Middle Pennsylvanian, Westphalian C, Mazon Creek, Essex Fauna completely lack any palaeostomatopods (Schram 1969*b*, 1976).

KEY TO PALAEOSTOMATOPODA

Because the hoplocaridans and especially the palaeostomatopods are such important crustacean elements in Late Paleozoic faunas, a key is provided here to act as a guide in identifying the known forms.

1a.	Seven segments in the abdomen	Phyllocarida
1b.	Six segments in the abdomen	2
2a.	Abdomen and cephalothorax about equal in size	Eumalacostraca
2b.	Abdomen larger than cephalothorax	3
3a.	Thoracic appendages unspecialized	Aeschronectida
3b.	Anterior thoracic appendages subchelate	4
4a.	Carapace completely exposing the last 3 thoracic segments dorsally and laterally	Tyrannophontidae
4b.	Carapace covering all thoracic segments, at least laterally	5
5a.	Carapace covering thoracic segments dorsally and laterally, telson with prominent, terminal spike	6
5b.	Carapace excavated along dorsal, posterior margin to expose dorsal portion of thoracomeres, telson suboval with no prominent spike	9
6a.	Body dorsoventrally flattened	(*Perimecturus*) 7
6b.	Body subcylindrical	(*Bairdops*) 8
7a.	Telson spike less than half the length of telson base, entire tail fan with long, hair-like setae, uropodal protopod with posterior spike between endo- and exopods	*Perimecturus parki*
7b.	Telson spike more than half the length of telson base, no setae, endopods distally serrate, and telson serrate near caudal furca, uropodal protopod with posterior spike flanking the telson	*Perimecturus rapax*
8a.	Tail fan without setae or serrations, telson spike less than half the length of telson base	*Bairdops elegans*
8b.	Uropod margins setose, uropodal exopod laterally serrate, telson spike more than half the length of the telson base	*Bairdops beargulchensis*
9a.	Exoskeleton moderately well sclerotized, abdominal pleura sculptured and marked with furrow, mandible well developed with a mandible width: body length ratio approximately .043	*Archaeocaris vermiformis*
9b.	Exoskeleton thin and poorly sclerotized, abdominal pleura simple, mandible-width:body ratio about .023 or less	*Archaeocaris graffhami*

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TRANSACTIONS
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Limulines of the Mississippian Bear Gulch Limestone of Central Montana, USA

Frederick R. Schram

Abstract. The limuline Merostomata of the Bear Gulch Limestone of the Mississippian of Montana are described. Two forms are recognized. *Paleolimulus longispinus* sp. nov. is the more frequent of the forms, and *Euproops* sp. occurs as only a few poorly preserved specimens.

INTRODUCTION

The invertebrates of the Mississippian Bear Gulch Limestone are known to contain malacostracan Crustacea (Schram and Horner, 1978), Annelida and other worm groups (Schram, *in press*), and conodont eaters (Melton and Scott, 1972; Scott, 1973), as well as pelecypods, gastropods, cephalopods, and articulate and inarticulate brachiopods. The fauna of the Bear Gulch Limestone is collected from several outcrops in Fergus County, near Beckett, Montana.

Two limuline merostomes have been found in the fauna. The more common of the two is a new species of *Paleolimulus* Dunbar, 1923. In addition, some material assignable to the genus *Euproops* Meek, 1867, is recognized, but the specimens are too poorly preserved to identify as to species.

Abbreviations: UM—University of Montana, Missoula; CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

DISCUSSION

The merostome material is not particularly common in the Bear Gulch fauna as a whole. Twelve specimens of *Paleolimulus longispinus* are presently known. Only 1 specimen can be identified definitely as *Euproops,* but 2 other fragmentary specimens may be assignable here.

All specimens are generally preserved as molds, and/or texture differences in the rock with little actual relief. Specimens UM 5558, CM 33986, and CM 33987 do have some organic residues preserved but these contribute nothing to the understanding of the fossils as such. CM 33985 preserves a prosomal appendage as a color difference in the rock, a form of preservation common in the Carboniferous Lagerstätten.

In terms of faunal affinities, these merostomes verify what was seen in the crustacean (Schram and Horner, 1978) and worm (Schram, *in press*) elements of the Bear Gulch fauna. There is a close similarity to the Mazon Creek Essex fauna. *Paleolimulus* is the dominant merostome. *Euproops danae* is the characteristic limuline of the Mazon Creek fresh to brackish water Braidwood Fauna and rarely occurs in the nearshore marine Essex Fauna.

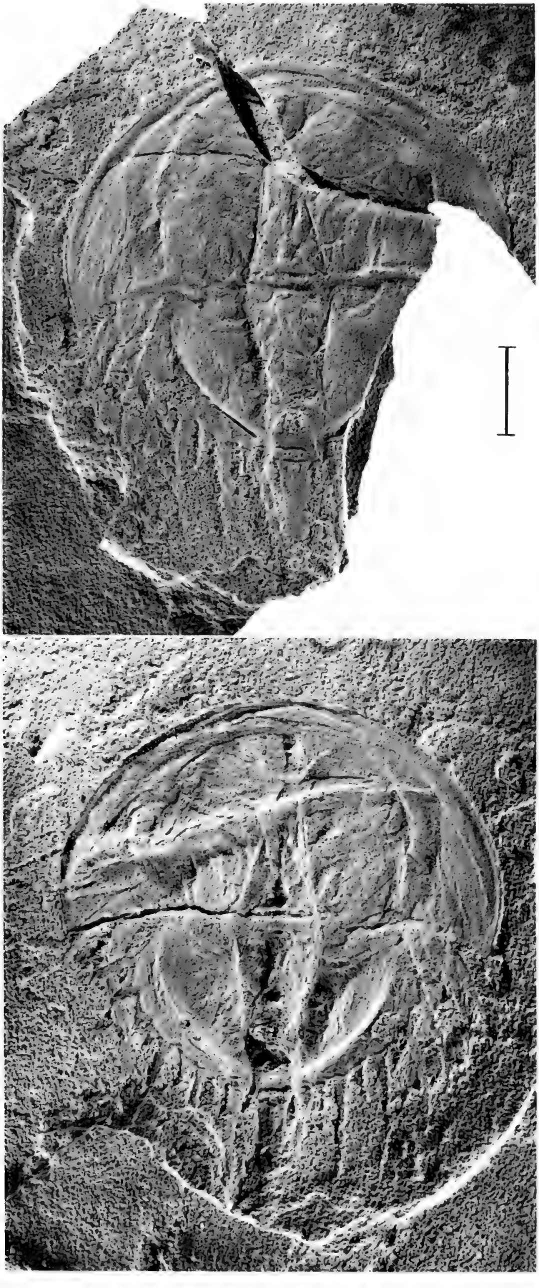

FIG. 1. *Paleolimulus longispinus* sp. nov., UM 5559, counterparts of holotype. Scale = 1 cm.

TABLE 1. Measurements (in centimetres) of *Paleolimulus longispinus*. *holotype.

	Prosoma		Opisthosoma		
Specimen	Length	Width	Length	Width	Telson length
UM 5559*	2.57	5.20	2.07	≈4.10	>1.66
CM 33946	2.54	...	1.84	...	...
CM 33947	2.87	5.55	1.87	...	...
CM 33983	2.75	5.23	1.88	3.55	>2.15
CM 33984	2.33	4.65	1.66	≈3.05	>1.60
CM 33985	2.78	4.24	1.65	3.25	...
CM 33994	...	5.48	2.17	3.60	5.45
CM 33995	2.90	...	2.35	...	3.98
CM 33996	2.30	4.72	1.82	3.28	...
CM 33997	2.92	...	≈2.0	...	...
CM 33998	2.67	...	2.20	≈2.90	...

SYSTEMATIC PALEONTOLOGY

Phylum Cheliceriformes Schram, 1978
Subphylum Chelicerata Haymons, 1901
Class Merostomata Dana, 1852
Subclass Xiphosura Latreille, 1802
Order Xiphosurida Latreille, 1802
Suborder Limulina Richter & Richter, 1929
Infraorder Limulicina Richter & Richter, 1929
Superfamily Limulacea Zittel, 1885
Family Paleolimulidae Raymond, 1944
Genus *Paleolimulus* Dunbar, 1923
Paleolimulus **longispinus** sp. nov.

Holotype.—UM 5559 (Fig. 1).

Other material.—CM 33946, CM 33947, CM 33983–CM 33985, CM 33994–CM 34000.

Horizon and locality.—as indicated in the Introduction.

Diagnosis.—Ophthalmic ridges slight. Interophthalmic region broad, extending to near anterior prosomal margin. Slight genal spines. Opisthosoma rounded. Pretelsonic free segment flanked by spines from posterior of axial lobe. Eight or 9 marginal opisthosomal spines alternating in size. Telson very long.

Description.—The ratio of prosomal width to length is 1.9:1. The interophthalmic area is broad and semicircular and extends to near the anterior margin of the prosoma. The eyes are not well preserved. The cardiac lobe is subtriangular, about ⅔ the length of the prosoma, and is connected to the ophthalmic ridge by a faint anterior extension of the cardiac apex. Four faint muscle scar lobations flank the main cardiac lobe. The genal spines are small.

The opisthosoma is somewhat semicircular. The margin is developed as a shelf from which 8 or 9 spines are articulated. The spines alternate posteriorly in size between long and short. The axial lobe is narrower posteriorly than anteriorly. The lobe is produced posteriorly as 2 curved spines that flank the pretelsonic segment and extend beyond the posterior margin of the opisthosoma. The telson is moderately wide and very long, though seldom preserved in its entire length.

The holotype, UM 5559, and CM 33985 preserve portions of a prosomal appendage. Nothing is distinctive about them. They are chelate. The segment proximal to the chela on CM 33985 is quite long and the segment proximal to that is of indeterminate length.

Measurements of *P. longispinus* are given in Table 1, and a reconstruction is offered in Fig. 2.

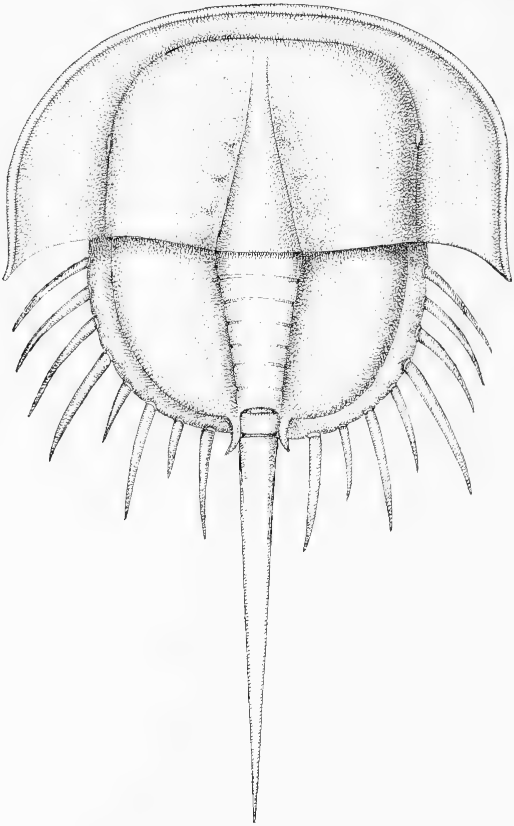

FIG. 2. *Paleolimulus longispinus* sp. nov. (reconstruction).

Remarks.—Dunbar (1923) described the genus and species *Paleolimulus avitus* from the Lower Permian Elmo Limestone Member of the Wellington Shale of Elmo, Kansas, USA. *Paleolimulus avitus* differs from *P. longispinus* in having somewhat longer and more outwardly directed genal spines. The ophthalmic ridges of *P. avitus* are very prominent and are bilobed, meeting with the apex of the cardiac lobe, and the interophthalmic area is relatively narrow. The opisthosoma is narrower and more elongate than that of *P. longispinus,* and there were apparently only 4 or 5 small marginal spines on the opisthosoma. The ratio of prosomal width to length of *P. avitus,* based on Dunbar's material and that of Raymond (1944), is 1.67:1.

A comparison of the known species of *Paleolimulus* is presented in Table 2. Dunbar (1923) included in the genus *Paleolimulus, P. signatus* (Beecher), 1904, and *P. randalli* (Beecher), 1902. *Paleolimulus signatus* is somewhat stratigraphically lower in the Fort Riley Limestone of Kansas than *P. avitus*. The single known specimen of *P. signatus* is an incomplete prosoma but it is >3× larger than that of *P. avitus*. The anatomy is very similar, however, and more and better material of these species may reveal that *P. avitus* is conspecific with *P. signatus*. *Paleolimulus randalli* is from the

TABLE 2. Comparison of the known species of *Paleolimulus*. *P. avitus* and *P. signatus* may be conspecific.

Species	Prosoma (width: length)	Genal spines	Opisthosoma shape	Opisthosomal spines	Age
P. longispinus	1.90	Small	Rounded	8–9 alternate long and short posteriorly	Upper Mississippian
P. signatus	?	?	?	?	Lower Permian
P. avitus	1.67	Moderate–large	Elongate	4–5 short	Lower Permian
P. randalli	?	None	?	?	Upper Devonian
P. juresanensis	1.86	Moderate	Elongate	8 uniform	Upper Carboniferous

FIG. 3. *Euproops* sp., UM 5558. Note: prosoma is much broader than long and opisthosoma is segmented. Scale = 1 cm.

Upper Devonian Chemung Sandstone. It too is an incomplete prosoma but differs from any other *Paleolimulus* material in having an anteriorly narrow cardiac lobe and, although the posterior prosomal margin is quite concave, apparently no genal spines.

Finally, Chernyshev (1933) described *Paleolimulus juresanensis* from the Upper Carboniferous of the Urals on the Yurezan River. He had a single ventrally preserved specimen. As a result, it is difficult to compare *P. juresanensis* to the other species. The prosomal width to length ratio is 1.86:1. Although there are 8 marginal opisthosomal spines, the spines appear to be all the same length, and the opisthosoma is more elongate than rounded. As far as can be deduced, *P. juresanensis* appears to be a distinct species, though probably taxonomically closer to *P. longispinus* than the other species of *Paleolimulus*. But it should be remembered that dorsal preservations of the Soviet material are necessary before definitive taxonomic judgments can be made.

Superfamily Euproopacea Eller, 1938
Family Euproopidae Eller, 1938
Genus *Euproops* Meek, 1867
Euproops sp.

Material.—UM 5558, ?CM 33986, ?CM 33987.

Horizon and locality.—as indicated in the Introduction.

Remarks.—One specimen, UM 5558 (Fig. 3), seems to be definitely a member of the genus *Euproops*. Though the specimen is poorly preserved, several features allow it to be identified as a euproopid. The prosoma is markedly wider than long, with a width to length ratio of 2.8:1, and appears to bear carinate ophthalmic spines. The opisthosoma is clearly segmented across its entire width. In addition, CM 33986 and CM 33987 may also be euproopids based on shape of what appears to be the prosoma. But these latter 2 specimens are very poorly preserved.

The measurements of UM 5558 are: prosomal length, 2.03 cm; prosomal width, 5.66 cm; opisthosomal length, 2.42 cm; opisthosomal width, 3.63 cm.

ACKNOWLEDGMENTS

Thanks must be extended to W. Melton, University of Montana, Richard Lund, Adelphi University, and John Carter, Carnegie Museum, for making these specimens

available for study. The reconstruction in Fig. 2 was executed by Tony D'Attilio of the San Diego Natural History Museum.

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TRANSACTIONS
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A new species of chiton (Mollusca: Polyplacophora) from the Hawaiian Islands and Tahiti

Antonio J. Ferreira and Hans Bertsch

Abstract. Chitons of the genus *Plaxiphora* are predominantly cold and temperate water southern hemisphere species. The new species described here occurs in tropical and northern subtropical central Pacific waters. To the impoverished Polynesian chiton fauna is now added the new species, ***Plaxiphora kamehamehae*** Ferreira and Bertsch, sp. nov.

INTRODUCTION

In over a century of malacological research, only 4 species of chitons have been described from the Hawaiian Islands: *Ischnochiton petaloides* (Gould, 1846), *Acanthochitona viridis* (Pease, 1872), *Acanthochitona armata* (Pease, 1872) (probably synonymous with *A. viridis*), and *Rhyssoplax linsleyi* (Burghardt, 1973). The marked scarcity of chitons in Hawaii (both in numbers of species and individuals) has been noted by Pease (1872), Kay (1967) and Burghardt (1973). Therefore it is rather surprising that intertidal collecting on the island of Oahu has yielded specimens of a hitherto undescribed species of chiton. Even more remarkable is the fact that the genus to which this species belongs is known mostly from the temperate and cold water faunal regions of the southern hemisphere.

This work is based upon material deposited in the California Academy of Sciences, Departments of Invertebrate Zoology (CASIZ) and Geology (CASG), San Francisco, California; San Diego Natural History Museum (SDNH), California; Australian Museum, Sydney (SAM); South African Museum, Cape Town; and in the A. J. Ferreira collection.

SYSTEMATICS

Class POLYPLACOPHORA Blainville, 1816
Order NEOLORICATA Bergenhayn, 1955
Suborder ISCHNOCHITONINA Bergenhayn, 1930
Family MOPALIIDAE Dall, 1889
Genus *PLAXIPHORA* Gray, 1847

Plaxiphora ***kamehamehae*** Ferreira & Bertsch, sp. nov.

Material examined.—1) 2 specimens; Ft. Kamehameha Beach, Oahu, Hawaii (approx. 21°19′N; 157°57′W), on the eastern shore of the entrance to Pearl Harbor; *leg.* H. Bertsch, 24 September 1977.

2) 1 specimen; Ft. Kamehameha Beach; *leg.* H. Bertsch, 15 October 1977.

3) 3 specimens; Ft. Kamehameha Beach; *leg.* H. Bertsch, 5 November 1977.

4) 8 specimens; Ft. Kamehameha Beach; *leg.* H. Bertsch, Shannon Norstrom and Erin Myhill, 12 November 1977. (Holotype specimen taken from this lot.)

5) 43 specimens; Ft. Kamehameha Beach; *leg.* Leonce Many and Neal Voelz (Earthwatch Expedition participants), Scott Johnson and H. Bertsch, 6 June 1978.

6) 5 specimens; Aue, Papeete, Tahiti (17°32′S; 149°34′W); *leg.* George Hanselman, July 1971.

Diagnosis.—Small chiton, oval shaped, round backed, light colored (Fig. 1A). Valves (Figs. 1B–D) strongly beaked, almost sculptureless. Tegmentum granulose,

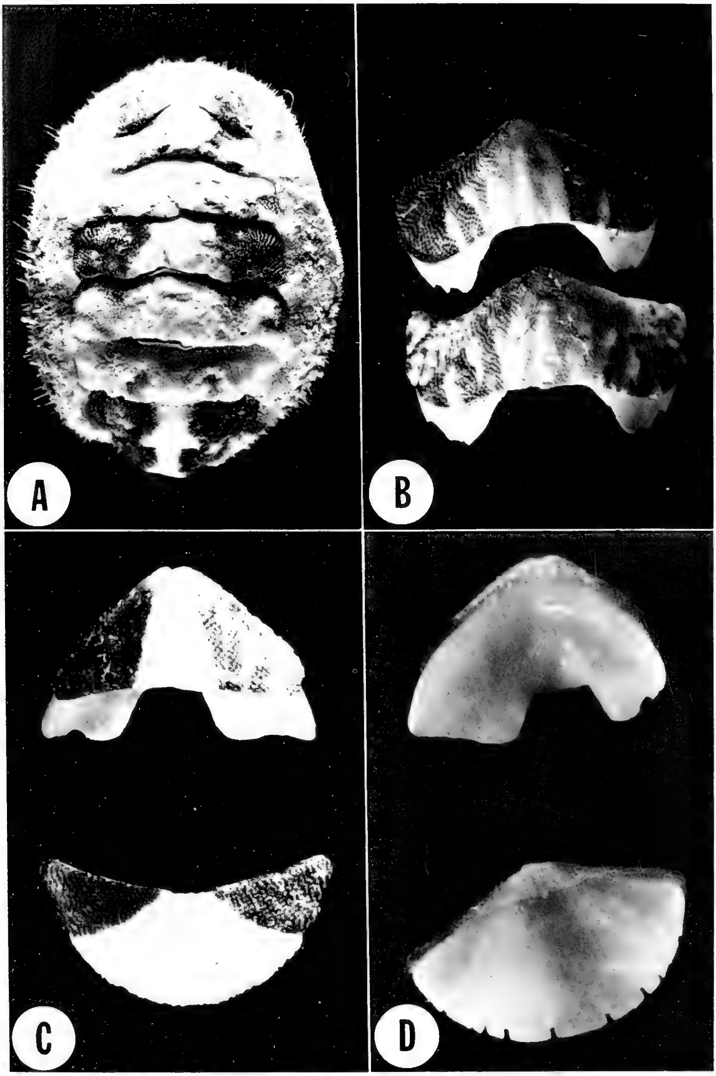

FIG. 1. (A). *Plaxiphora kamehamehae* Ferreira and Bertsch, sp. nov. Paratype, 10.5 mm long (including girdle); (B). *Plaxiphora kamehamehae;* holotype: close-up of valves v and vi; (C). *Plaxiphora kamehamehae*; holotype: close-up of valves i and viii, (D). *Plaxiphora kamehamehae*; holotype: articulamentar surface of valves i and viii.

granulations in quincunx except in pleural areas where arranged longitudinally. Lateral areas weakly defined by two shallow, rib-like radial undulations. Posterior valve triangular, mucro posterior. Articulamentum of 8–10 projecting teeth in valve i; intermediate valves one-slitted. No teeth in valve viii, insertion plate reduced to a callus

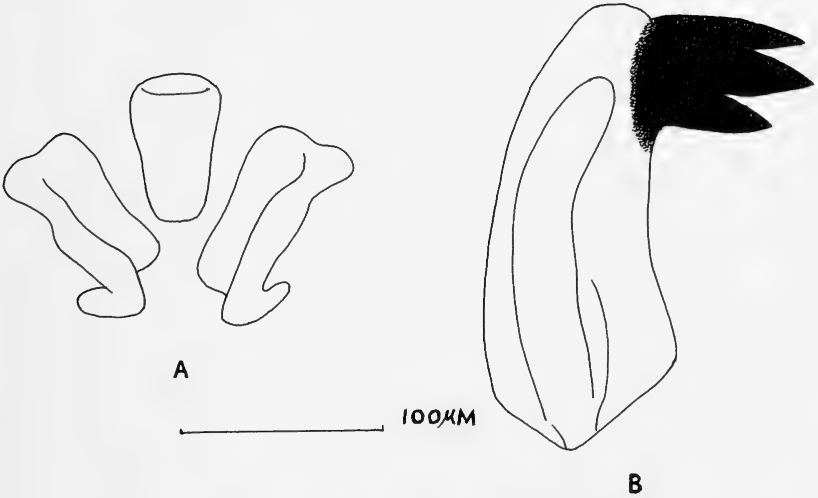

FIG. 2. *Plaxiphora kamehamehae*. Radula of holotype. (A). Median and first lateral teeth; (B). Major (second) lateral tooth.

vaguely hollowed out in the middle line by a shallow sinus. Sutural plates well developed, rectangular in valve viii, round to oval in other valves. Sinus round and deep. Radula (Fig. 2) with tricuspid major lateral teeth. Girdle (Fig. 3) covered with minute spiculoid scales and randomly placed hairy bristles.

Description of holotype.—The holotype is the largest in a series of 8 specimens collected at Fort Kamehameha Beach, 12 November 1977. It measures (including girdle) 13.0 mm long, and 8.7 mm wide at the iv valve level. The general shape of the specimen is oval, round backed, with strongly beaked valves. Once cleaned of encrustations, mostly algae, the specimen is seen to be light colored. It is white in the middle of valve i, and most of valves ii to vii, with a contrasting dark gray on the sides of valve i, and most of valves vi to viii, except for a white jugal area with linear smudges of red. Small spots of bright blue green and brown give a mottled appearance to the pleural areas of valves v and vi.

The tegmentum is sculptureless except for its coarsely granular surface that can be seen under magnification. The tegmental granulations are mostly round and arranged in quincunx; in the pleural areas, the granulations tend to be arranged in longitudinal rows, but not conspicuously. With the benefit of tangential light, the anterior valve shows approximately 8 very faint, almost imperceptible radial ribs. In the intermediate valves, the lateral areas are only slightly raised, and display 2 low-arched radial ribs or undulations with a shallow area in between; the lateral areas are much more in evidence in the anterior (ii and iii) than in the posterior (vi and vii) valves. The central areas are sculptureless, except for the quincunxially arranged granulations of the tegmental surface. The posterior valve is rather flat, slightly longer than wide, and triangular. The mucro is terminal on the somewhat thickened posterior edge of the valve, but not raised or upswept.

The articulamentum is white but translucent enough to allow some of the tegmental colors to show through. The sutural laminae are well developed, separated by a wide, round, deeply cut sinus; in shape, they are triangular on valve ii, semicircular on valves iii–vi, and mostly rectangular in valves vii and viii. Eaves are narrow but spongy.

The insertion plate of valve i is well developed, projecting downwards, cut into sharp, strong teeth, markedly striated on their outer surface; it displays 10 slits, 8 of

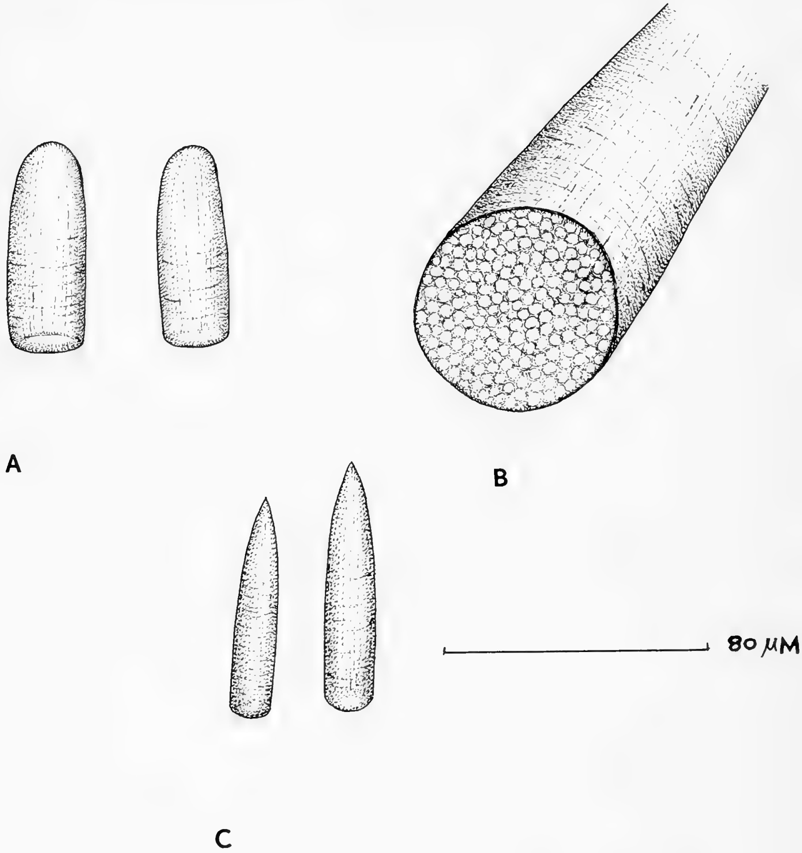

FIG. 3. *Plaxiphora kamehamehae*. Girdle elements. (A). Spiculoid scales of the upper surface; (B). Cross-section of corneous bristle; (C). Scales of the undersurface near outer margin.

which correspond in position to the very vaguely defined radial ribs of the tegmentum. The intermediate valves are one-slitted. The posterior valve has no slits or teeth; its insertion plate is limited to a thick callus, slightly ridged along its free edge, and hollowed out in the midline to form a shallow sinus.

The girdle, fleshy and light tan, is loosely covered with minute spiculoid scales (Fig. 3A) that do not imbricate. These scales measure about 60 μm in height, and 20 μm in width; they are translucent or golden, and mostly round with a blunt free end. Amid the spiculoid scales there are long, corneous, hairy bristles with a faintly longitudinal texture, bespeaking their fascicular makeup as seen in cross-section (Fig. 3B); these bristles attain as much as 0.8 mm in length, and 80 μm in width at the base. In the inner half of the girdle, these corneous processes show a tendency to aggregate in sutural tufts of 3–4 bristles; their distribution in the outer half of the girdle seems to be quite random. At the outer margin, the girdle displays a spicular fringe, the spicules having a clearly longitudinal texture and measuring as much as 300 μm in length and 45 μm in thickness.

The underside of the girdle is loosely covered with transparent scales, mostly round (10 × 10 μm) at the inner margin, but becoming pointed and elongated (75 × 10 μm) toward the outer margin (Fig. 3C).

The gills, abanal and merobranchial, extend for about ³⁄₅ of the length of the foot; they consist of about 24 plumes on each side.

The radula measures 4.0 mm in length (31% of the length of the specimen), and comprises some 40 rows of mature teeth. The median tooth (Fig. 2A) is about 60 μm long, 25 μm in width anteriorly, with a small blade. The tooth has a dumbbell shape. The first lateral teeth are about 60 μm in length, and show a twice undulated outer edge (Fig. 2A). The major lateral teeth measure about 210 μm in length; they bear a tricuspid blade, about 75 × 75 μm in size, with the middle cusp slightly longer than the other (Fig. 2B). The outer marginal teeth are elongated, measuring about 100 μm in length, 60 μm in width.

Type locality.—Fort Kamehameha Beach, Oahu, Hawaiian Islands (approximately 21°19′N; 157°57′W); intertidal zone on the eastern edge of the channel entrance to Pearl Harbor.

Type material.—Holotype, disarticulated, with radula and girdle mounted separately, is deposited at the San Diego Natural History Museum, Department of Marine Invertebrates (Type Series No. 503). Paratypes are deposited at the California Academy of Sciences (CASIZ Type Series No. 00713), the Natural History Museum of Los Angeles County, the Bernice P. Bishop Museum, and the San Diego Natural History Museum (Marine Invertebrates, Type Series No. 512).

DISCUSSION

There has been a tendency to recognize within the genus *Plaxiphora* Gray, 1847 (Type species: *Chiton carmichaelis* Gray, 1828 [=*Chiton auratus* Spalowsky, 1795] by original designation) many subgenera, mostly monotypic: *Frembleya* H. Adams, 1867, *Guildingia* Dall, 1882, *Diaphoroplax* Iredale, 1914, *Poneroplax* Iredale, 1914, *Maorichiton* Iredale, 1914, *Aerilamma* Hull, 1924, and *Mercatora* Leloup, 1942. This procedure seems taxonomically unsound in view of the relatively minor morphological differences that distinguish the taxa referable to *Plaxiphora*. Although a formal review of the genus *Plaxiphora* is not intended here, it is apparent that the use of such subgeneric group names is unwarranted.

The genus *Plaxiphora* is known mostly from the cold and temperate waters of the southern hemisphere (Fig. 4). In a review of the genus, Leloup (1942) reduced the 50-odd nominal species assigned to *Plaxiphora* to 11 valid species; to Leloup's list, 2 other species are here added, *P. primordia* (Hull, 1924), and *P. kamehamehae* (Table 1).

Plaxiphora kamehamehae is differentiated easily from all other species of *Plaxiphora*. Comparison was made between specimens of *P. mercatoris* (from Easter Island: CASIZ G-28236; CASG 34805; CASG 37061; AJF Coll. *ex* B. F. Alarcon), *P. simplex* (from Tristan da Cunha: CASG 54471; AJF Coll. *ex* P. Kaas), *P. albida* (from southern Australia: SAM c42055; SAM c42056; SAM c108791; SAM c108792; SAM c108793; CASG 34675; CASG 36339; CASG 36810; CASIZ 009290), *P. mathewsi* (from southern Australia: SAM c39877; SAM c108794; CASG 54385; AJF Coll. *ex* J. R. Penprase), *P. primordia* (from northeastern Australia: SAM c108795; SAM c108796), *P. obtecta* (from New Zealand: CASIZ 009292), *P. aurata* (from the Falkland Islands: CASIZ 00921; and from Chiloe Island, Chile, AJF Coll. *ex* E. Bay-Schmith), and *P. parva* (from Inhambane, Mozambique: South African Museum No 32624). *Plaxiphora kamehamehae* is distinct in size (Table 1), coloration, tegmental sculpture, and girdle elements. Furthermore, although the other species examined are holobranchial, *P. kamehamehae* is merobranchial.

In its small size, *Plaxiphora kamehamehae* ranks with *P. parva* and *P. primordia*, to which it is also similar in the color, the granular tegmental surface, and the form of the girdle elements. *Plaxiphora parva* is known only from Nierstrasz' original descrip-

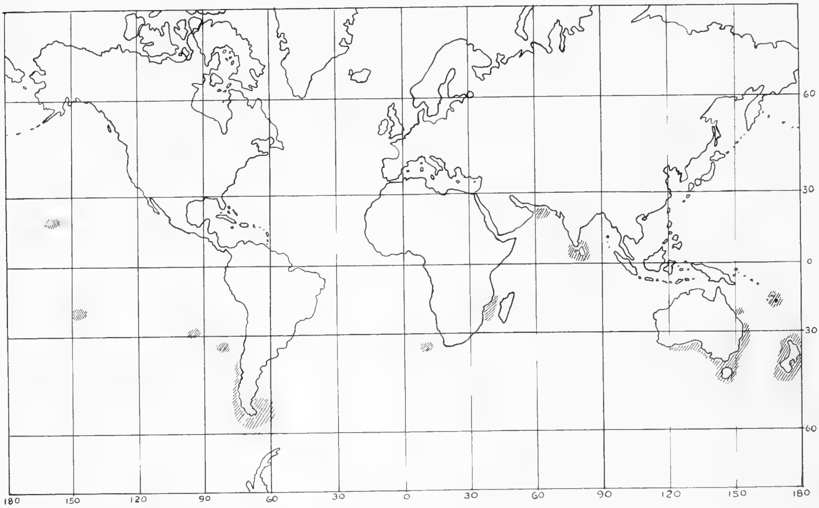

FIG. 4. Records of *Plaxiphora* species.

tion and a single specimen referred to by Barnard (1963:332–333, figs. 29c–e). This latter specimen was examined on a loan through the generosity of Elizabeth K. Giles, South Africa Museum. *Plaxiphora kamehamehae* differs from *P. parva* by (1) the finer, smaller, and more regular granulations to the tegmentum; (2) the much less defined lateral areas, and (3) the triangular (rather than semicircular) outline of the posterior valve.

Plaxiphora kamehamehae differs from *P. primordia* by (1) the much more uniform shape of the tegmental granulations, and their greater tendency to remain in quincunx, and (2) the structure of the median and first lateral radular teeth. For comparison, the

TABLE 1. Species of *Plaxiphora* Gray, 1847, presently regarded as valid, their general locality, and maximum reported size.

Species	Maximum reported length (mm)	Distribution
P. aurata (Spalowsky, 1795)	70	Sub-Antarctica to Valparaiso, and New Zealand
P. albida (Blainville, 1825)	70	South Australia, Gulf of Oman (?)
P. caelata (Reeve, 1847)	35	New Zealand
P. biramosa (Quoy and Gaimard, 1853)	50	New Zealand
P. egregia (Adams, 1867)	18	New Zealand
P. simplex (Haddon, 1886)	45	Tristan da Cunha Island
P. obtecta Carpenter in Pilsbry, 1893	45	New Zealand
P. parva Nierstrasz, 1906	7	Mozambique, Ceylon (?)
P. fernandezi Thiele, 1909	18	Juan Fernandez Island
P. mathewsi (Iredale, 1910)	15	S. Australia
P. primordia (Hull, 1924)	15	NE Australia
P. mercatoris Leloup, 1936	30	Easter Island
P. kamehamehae Ferreira and Bertsch, sp. nov.	13	Hawaii; Tahiti

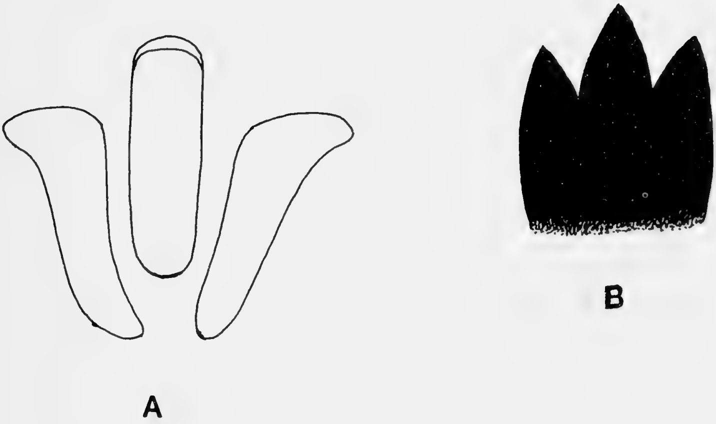

FIG. 5. Radula of *Plaxiphora primordia* (Hull, 1924). (A). Median and first lateral teeth; (B). Head of second (major) lateral tooth.

significant radular elements of *P. primordia* are illustrated here for the first time (Fig. 5). The specimen of *P. primordia* (SAM c108796: Lindeman Island, Queensland, Australia) measures 8.4 mm in length; the radula measures 2.4 mm in length (28% of the whole specimen) and comprises 30 rows of mature teeth. The outer marginal teeth are elongated, about 80 μm in length, 50 μm in width. Still, the similarities between *P. kamehamehae* and *P. primordia* are such as to suggest a common origin.

The specimens of *Plaxiphora kamehamehae* from Hawaii were found in <1 metre of water, attached to the sides of dead coral pieces, usually occupying a depression or pit suggestive of a homing scar. Most commonly both the substrate and the chiton were covered by encrusting coralline algae. The animals are extremely cryptic in their habitat and can be seen only by careful searching. Further details of this habitat (and associated organisms) are described by Bertsch and Johnson (1979).

During the writing of this paper, Col. George A. Hanselman recognized *Plaxiphora kamehamehae* as very similar to specimens that he had collected in Tahiti. The study of these Tahitian specimens showed that they were indeed conspecific with those from Hawaii. One specimen 8.7 mm long was disarticulated. It has a slit formula of 8-1-0, with a blue articulamentum (the only noted difference from the Hawaiian specimens examined, whose articulamentum is white). The radula of this disarticulated Tahitian specimen measures 3.0 mm long, and it comprises about 35 rows of mature teeth.

In Tahiti, *Plaxiphora kamehamehae* occurred "on the side of fairly smooth granite rocks, about head-size or larger . . . coated with a somewhat slimy mossy algae; they were uniformly nestled into small rough spots on the rocks. The site . . . has since been destroyed during highway construction" (*personal communication,* George A. Hanselman, 7 December 1978).

The presence of *Plaxiphora kamehamehae* in Tahiti as well as Hawaii strongly suggests that it might also be present on many other Indo-Pacific islands. Its cryptic nestling behavior, common to the Hawaiian and Tahitian animals, may prevent it from readily being found.

Six additional specimens of *Plaxiphora kamehamehae* were collected at Ft. Kamehameha Beach on 14 July 1979 by Dean Pitts and Tom Knapik, members of the Hawaiian Mollusks 1979 Earthwatch team.

Etymology.—This new species of *Plaxiphora* is named *kamehamehae* (genitive ending, first declension masculine noun) after the first king of all the Hawaiian Islands. King Kamehameha I ruled from 1795 (when he finally conquered the island of Oahu at the Battle of Nuuanu by his forces pushing the opposing troops over the steep Pali cliffs) to 1819. Prior to his rule, the islands had been governed by regional rulers. His was a signficant, pivotal role in Hawaiian history, and even today the monarchy he established affects aspects of life in the Hawaiian Islands.

Other invertebrates named in honor of King Kamehameha include a butterfly (*Vanessa tameamea* Eschscholtz, 1821), a Pleistocene oyster from the Waianae coast of Oahu (*Ostrea kamehameha* Pilsbry, 1936), a pulmonate from Molokai (*Endodonta kamehameha* Pilsbry & Vanatta, 1905), and the prosobranch *Mitra kamehameha* Pilsbry, 1921 (which is a synonym of *M. ustulata* Reeve, 1844).

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We thank The Center for Field Research for a grant that enabled H. B. to collect specimens in Hawaii during June 1978. Appreciation is expressed to Leonce Many and Neal Voelz, members of the Hawaiian Mollusks 1978 Earthwatch team who collected some of the specimens reported in this paper, and Scott Johnson and Judi Bertsch for assistance in the field.

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TRANSACTIONS
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Fossil carrion beetles of Pleistocene California asphalt deposits, with a synopsis of Holocene California Silphidae (Insecta: Coleoptera: Silphidae)

Scott E. Miller[1] and Stewart B. Peck

Abstract. Fossil Silphidae occur in three late Pleistocene asphalt deposits in California: Rancho La Brea in Los Angeles County, McKittrick in Kern County, and Carpinteria in Santa Barbara County. Pierce's 1949 *Nicrophorus* taxa from Rancho La Brea and McKittrick are all new junior synonyms: *Nicrophorus guttula labreae*, *Nicrophorus mckittricki*, *Nicrophorus obtusiscutellum*, and *Nicrophorus investigator latifrons* = *Nicrophorus marginatus* Fabricius; *Nicrophorus guttula punctostriatus* = *Nicrophorus guttula* (Motschoulsky); *Nicrophorus investigator alpha* = *Nicrophorus nigrita* (Mannerheim). Lectotypes are designated for *N. g. labreae* and *N. i. alpha*. The following resurrected generic combinations are used: *Thanatophilus lapponicus* (Herbst), *Heterosilpha ramosa* (Say), *Heterosilpha aenescens* (Casey). A neotype is designated for *Heterosilpha ramosa*. *Heterosilpha aenescens* is a valid species and a lectotype is designated for it. The fauna of each deposit includes: Rancho La Brea: *T. lapponicus*, *H. ramosa* (and perhaps *H. aenescens*), *N. marginatus*, *N. guttula*, and *N. nigrita*; McKittrick: *N. guttula* and *N. marginatus*; Carpinteria: *N. guttula* and *N. nigrita*. *Nicrophorus marginatus* is the best represented species of *Nicrophorus* in the asphalt, although it is the least common species of the genus in the modern southern California fauna. Possible reasons for this apparent faunal change include real faunal changes and biased preservation. Due to limited knowledge of silphid ecology, detailed paleoecological conclusions cannot be made at the present time. All silphid species presently known from California are reviewed, and a key is given. *Aclypea bituberosa* (LeConte) (new combination) occurs in the Sierra Nevada Mountains, *Thanatophilus sagax* (Mannerheim) (new combination) is raised from synonymy, *Pelatines latus* (Mannerheim) is recorded from northern California, a lectotype is designated for *Nicrophorus hecate* (Bland), and several other geographic ranges are extended.

INTRODUCTION

Pierce (1949) recognized 6 species and 5 subspecies of Silphidae from the Rancho La Brea and McKittrick asphalt deposits. Two of these species and 4 subspecies were described as new. This study reevaluates Pierce's (1949) taxa and records newly found specimens. In order to place the fossils properly, we review the taxonomy and distribution of the Holocene Silphidae of California.

Although most of Pierce's basic concepts (Pierce 1961) regarding fossil insects were valid, his publications and taxonomic procedures were replete with errors. Serious identification problems result from his erection of taxa based on fragmentary specimens. In addition to poor descriptions, some of his drawings were inaccurate (e.g., Carpenter 1968, Matthews and Halffter 1968). Our study was hampered by past improper labeling by Pierce and some errors in cataloging many type specimens by Sphon (1973).

All the Pleistocene specimens studied represent Holocene species and fall within reasonable ranges of morphological variation. The use of subspecific names is not

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justified, because the fossil forms are not geographic races and there is no morphological basis upon which to found chronosubspecies. Studies by other workers indicate that almost all Pleistocene insect fossils represent extant species (Coope 1970, Matthews 1977).

There is confusion regarding proper application of generic and specific names in the Silphidae. Members of the Silphini discussed here usually have been included in *Silpha* Linnaeus 1758. However, we are presenting several resurrected and new combinations, in agreement with R. B. Madge's (*personal communication*) as yet unpublished review of the world Silphini.

Our synonymies cite only original descriptions and important references; more complete synonymies are given by Hatch (1928) and Madge (1958). All fossil silphids we examined are listed in the text, along with appropriate specimen numbers (LACMIP type number, RLP entomology number, and/or Pierce's number [with "C" or "McK" prefix]). All are in LACM, except those from UCMP localities 2051 and 7139. Those not cited by Pierce (1949) are preceded by an asterisk (*).

Abbreviations for collections consulted and cited in the text are:

ANSP	Academy of Natural Sciences of Philadelphia;
CAS	California Academy of Sciences;
CDA	California Department of Food and Agriculture;
CIT	California Institute of Technology (VP collection now housed at LACM);
CMNH	Carnegie Museum of Natural History;
LACM	Natural History Museum of Los Angeles County;
LACMIP	LACM Invertebrate Paleontology collection;
MCZ	Museum of Comparative Zoology, Harvard University;
RLP	Rancho La Brea Project (current LACM excavation of Pit 91);
SBMNH	Santa Barbara Museum of Natural History;
UCMP	University of California Museum of Paleontology, Berkeley;
UCR	University of California at Riverside;
USNM	United States National Museum of Natural History.

We also examined Holocene silphids from the American Museum of Natural History, British Museum (Natural History), California Insect Survey (University of California at Berkeley), Field Museum of Natural History, Peabody Museum (Yale University), San Diego Natural History Museum, University of California at Davis, and our personal collections. Records from the California Channel Islands, compiled in ongoing SBMNH research, are included in the Holocene distribution summaries.

Other abbreviations used in the text are:

BD	below datum (for depths within Pit 91, Rancho La Brea);
B.P.	before present (in radiocarbon dating, present calculated as 1950);
loc.	locality number;
VP	vertebrate paleontology.

LOCALITIES

Pierce (1949) studied fossil silphids only from the Rancho La Brea and McKittrick asphalt deposits (Pierce 1946, 1947*a*, 1947*b*). We studied silphids from these localities and the Carpinteria asphalt deposit. Additional vertebrate fossil bearing asphalt deposits near Maricopa in Kern County (Macdonald 1967) have yielded no silphids.

RANCHO LA BREA

The Rancho La Brea asphalt deposits are located in Hancock Park, Los Angeles, Los Angeles County, California. More than 100 individual excavations or "pits" have been made since 1905. Most of these were unproductive test holes and fewer than 15 were major sources of fossil vertebrates (Howard 1962, Marcus 1960, Stock 1956). Before the reopening of Pit 91 in 1969, emphasis was placed on large vertebrates;

insects and other small fossils were neglected by the early excavators. In addition to Pierce's material, we have studied silphids salvaged from miscellaneous unsorted material from several original excavations and silphids recovered in the modern excavation of Pit 91.

Most of the silphids from older LACM excavations were studied by Pierce (1949). Silphids from Pits 9, 28, 37, and 81 (excavated between 1913 and 1915) bear no further data than pit number. Pits A and B were excavated in 1929, and Pierce's "Bliss 29" specimens were collected in 1929 by W. Bliss from Pits A, B and C after the official LACM excavation ended. The age of "Bliss 29" insects is questionable due to unknown locality and possible contamination. Pierce's "Pit X" consisted of "mixed material lacking data" (Pierce 1954), and may not be fossil. We have also seen silphids from UCMP loc. 2051, a large excavation made in 1912 (Stoner 1913).

Pit 91, partially excavated in 1915, was reopened in 1969 by the Rancho La Brea Project of LACM. The current excavation is laid out on the basis of 3 foot square (≈.8 square metre) grids, normally excavated in 6 inch (≈15 cm) layers (each assigned a grid number), within a coordinate system, lettered from south to magnetic north and numbered from east to west. Once separated from the surrounding matrix (G. Miller 1971), the insects are cleaned with 1,1,1-trichloroethane (other solvents such as xylene may also be used) in ultrasonic cleaners. Each insect fragment (or conspecific specimens with the same data) is assigned an RLP entomology catalog number and is stored dry in a gelatin capsule housed in a glass vial.

Due to the enormous quantity of fossil insects recovered and the limited support available for processing them, most of the Pit 91 insects are not available for study at present. Thus, our treatment of Pit 91 silphids is only preliminary, and we hope to continue our research. We have specimens from 13 grids in 7 columns in the northeast corner of the excavation, as follows: column G-3: grid GJM 360 (5′4″ to 7′ BD); J-6: GJM 346 (8′8″ to 9′6″ BD); L-4: GJM 408 (6′ to 6′6″ BD), GJM 612 (7′ to 7′6″ BD), GJM 856 (7′6″ to 8′ BD); L-5: GJM 364 (5′4″ to 5′10″ BD), GJM 568 (6′4″ to 7′ BD); M-3: GJM 275 (5′ to 5′3¾″ BD), GJM 295 (5′3¾″ to 6′3″ BD), GJM 550 (7′ to 7′6″ BD); M-4: GJM 777 (7′ to 7′6″ BD); and N-3: GJM 273 (5′ to 6′9½″ BD), GJM 838 (8′6″ to 9′ BD). These grids range in depth from 5 to 9½ feet BD, with most between 6 and 8 feet BD. Two radiocarbon dates from the northeast corner of the excavation can be approximately correlated with the silphids. The dates, both from bone collagen of *Smilodon californicus* Bovard, are (Berger and Libby, *in press*): 30 800 ± 600 radiocarbon years B.P. from 6′¾″ to 7′1″ BD in column L-5 (UCLA-1718) and 32 600 ± approximately 2800 radiocarbon years B.P. from 7′2½″ to 7′6″ BD in columns M-3 + 4 (UCLA-1738D). These dates and others (L. F. Marcus, *personal communication*) from elsewhere in Pit 91 indicate that most of our silphids are probably ≈30 000 radiocarbon years old. Higher grids (GJM 273, 275, 295) should be younger and the deeper grids (especially GJM 838) older. The silphid-bearing deposit in the northeast corner was generally a productive deposit for vertebrates (mostly small) that terminated at a depth of ≈8 feet 6 inches [2.59 m] (A. Tejada-Flores, *personal communication*). Silphids may be present in other sectors of Pit 91, in material which has not yet been sorted.

McKITTRICK

The McKittrick asphalt deposit is ≈0.8 km south of McKittrick, Kern County, in the southern San Joaquin Valley. The biota is considered late Pleistocene, although there is some "admixture of a later (Recent, but not present-day) assemblage" (DeMay 1941*a*:59). Berger and Libby (1966:492) dated the flora reported by Mason (1944) at 38 000 ± 2500 radiocarbon years B.P. (UCLA-728) based on UCMP plant material which lacked specific excavation data (D. I. Axelrod, *personal communication*). However, the age of Pierce's material is questionable and it may be subfossil.

The described fossil localities are all in the NE¼ of the NE¼ of Section 29, Township 30 South, Range 22 East (Mount Diablo base line and meridian). The original 1921 excavation (UCMP loc. 4096) was on the southeast side of the present northern fork of State Highway 58, but the 1925–1927 excavations (UCMP loc. 7139 and CIT VP loc. 138 = LACMIP loc. 5103) were across that road on the southeast side. The CIT VP loc. 138 "comprises essentially the same area as U.C. locality 7139" (Schultz 1938:130). Pierce's sites 3 and 4 (LACMIP loc. 260) were southeast of the original localities, on the east side of the present State Highway 33 about 1.2 km south of McKittrick. In 1945, Pierce excavated matrix from a depth of 2 feet (≈.6 metres) below the surface in a fracture in the recently exposed bank, designating this "site 3" (Pierce 1947*b* and unpublished notes). In 1947, Leonard Bessom of LACM collected from a depth of 4 feet (≈1.2 m) near site 3. Pierce designated Bessom's locality "site 4," and wrote that the 2 foot (≈.6 m) depth at site 3 would correspond to the 24 to 30 inch (.6–.76 m) layer at site 4. Pierce believed site 3 was younger than site 4, and that the insects from site 3 indicated drier conditions than those from site 4. Stratigraphic and age relationships of Pierce's localities to the CIT and UCMP localities have not been determined, but Pierce's localities appear to be much younger.

CARPINTERIA

The Carpinteria asphalt deposit is located on a seaside bluff overlooking the Pacific Ocean ≈1.5 km southeast of Carpinteria, Santa Barbara County, California. Fossils were discovered in the Carpinteria asphalt quarry in February 1927, and paleontological excavations were undertaken by the SBMNH, CIT and UCMP (CIT VP loc. 139 = LACMIP loc. 5102). The quarrying operation was later abandoned and the site was used as a refuse dump beginning in the 1940s. Natural topography at the site has been so drastically changed by human activities that the locations and depths of the fossil excavations can only be approximated.

The deposit is situated in a raised marine terrace of beach sands, considered middle to late Pleistocene in age (R. S. Gray, *personal communication*), that disconformably overlie shales of the Monterey Formation of Miocene age. However, the terrestrial fossil-bearing zone (not to be confused with the underlying marine zone of Grant and Strong 1934), which apparently graded into the beach sands, is considered late Pleistocene in age. Two cones of *Pinus radiata* Don, which were among the first fossils collected at the site in early 1927, yielded dates ≥44 500 (QC-468), >41 000 and >53 000 (QC-467B) radiocarbon years B.P. The differences in the maximum ages of the 2 portions of QC-467B are due to differences in the statistics of separate counting in different vials (R. R. Pardi, *personal communication*). Asphalt-impregnated wood collected in 1962 from a roadcut in the asphaltic sands near the original fossil sites yielded dates >38 000 radiocarbon years B.P. (UCLA-180 and UCLA-181 in Fergusson and Libby 1964), but their stratigraphic relationship to the original excavations is unknown.

Synopsis of California Silphidae

Family Silphidae[2]
Tribe Pterolomini
Genus *Apteroloma* Hatch 1927

These small beetles (length 5–7 mm) are found under stones and debris, especially at stream margins. We are giving *Apteroloma* generic status rather than subgeneric status under *Pteroloma* Gyllenhal 1827 in accordance with studies by R. B. Madge and A. F. Newton. Papers by Van Dyke (1928), Hatch (1957), and Bolivar y Pieltain and Hendrichs (1972) are useful for identification of species. The genus has no known fossil record in California.

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[2] According to a study in preparation by A. F. Newton, the tribes Pterolomini and Agyrtini should be removed from the Silphidae and combined into a distinct family. Awaiting this change, we will follow the traditional inclusion of these tribes in the Silphidae.

Apteroloma caraboides (Fall)

Pteroloma caraboides Fall 1907:235
Apteroloma caraboides of Hatch 1928:70
Pteroloma (Apteroloma) caraboides of Hatch 1957:6

Ranges from British Columbia and Idaho to northern California. Only one specimen (a syntype) is known from southern California: Mount San Antonio [="Old Baldy"], 9000 feet [≈2740 m], 19 June 1904 (C. A. Richmond:MCZ).

Apteroloma tenuicorne (LeConte)

Necrophilus tenuicornis LeConte 1859*a*:84
Pteroloma tenuicorne of Horn 1880:245
Apteroloma tenuicorne of Hatch 1927*b*:12
Pteroloma (Apteroloma) tenuicorne of Hatch 1957:6

Ranges from British Columbia, Montana and Colorado to northern California. Only one specimen is known from southern California: Mill Creek, San Bernardino Mountains, 4800 feet [≈1460 m], 15 April 1965 (CDA).

Apteroloma tahoecum (Fall)

Pteroloma tahoeca Fall 1927:136
Apteroloma tahoeca of Hatch 1928:70
Pteroloma (Apteroloma) tahoeca of Hatch 1957:6

Found primarily in the Sierra Nevada Mountains, but also in other areas of northern California and Oregon. Several old and questionable records exist for Nevada and Utah.

Tribe Agyrtini
Genus *Pelatines* Cockerell 1906

The following is the first record of the genus in California; it has no known fossil record in the state.

Pelatines latus (Mannerheim)

Necrophilus latus Mannerheim 1852:331
Pelates latus of Horn 1880:244
Pelatines latus of Cockerell 1906:240

This small (3–4 mm long) species ranges from southeastern Alaska to northern California. In California, it is known from Alameda, Del Norte and El Dorado counties (specimens in ANSP, CDA, CMNH, and MCZ).

Genus *Agyrtes* Froelich 1799

The small (length 3–5 mm) and little known North American species of *Agyrtes* were reviewed by Peck (1975). The genus has no known fossil record in California.

Agyrtes longulus (LeConte)

Necrophilus longulus LeConte 1859*b*:282
Agyrtes longulus of Horn 1880:246

Ranges from central California northwards through coastal mountains to southern Alaska and inland to Idaho, presumably associated with forest habitats.

Agyrtes similis Fall

Agyrtes similis Fall 1937:29

Known only from a few specimens from the coastal ranges of central and southern California.

Genus *Necrophilus* Latreille 1829
Necrophilus hydrophiloides Mannerheim

Necrophilus hydrophiloides Mannerheim 1843:253

Adults (length 9–11 mm) and larvae are found on carrion and decomposing vegetable matter from southeastern Alaska to southern California (extension of published range south into Los Angeles County). The species has no known fossil record in California.

Tribe Silphini
Genus *Aclypea* Reitter 1885

We are using *Aclypea* as it was used by Seidlitz (1888:311), whom we regard as the first reviser in accordance with article 24(a)(i) of the International Code of Zoological Nomenclature. These species have often been placed in *Blitophaga* Reitter 1885. The genus has no known fossil record in California.

Aclypea bituberosa (LeConte), **comb. nov.**
Figure 1A, B

Silpha bituberosa LeConte 1859*c*:6

The occurrence of *A. bituberosa* in the Sierra Nevada Mountain region has been confused and unconfirmed since Horn's misidentified record of *Silpha opaca* "near Mono Lake" (Horn 1880), based on a single specimen (now in MCZ). California occurrence of *A. bituberosa* is now well documented by these additional specimens: Alpine County: Ebbetts Pass, 8 July 1970 (F. G. Andrews: CDA), Sonora Pass, 24 June 1937 (N. W. Frazier: CAS), 27 June 1951 (E. L. Silver: LACM); El Dorado County: Echo Lake (7400 feet [≈2260 m]), 15 July 1933 (A. E. Michelbacher: CAS), [Mount] Tallac, July (A. Fenyes Colln.: CAS); Tuolumne County: no further data (A. Koebele Colln.: CAS); and Yosemite National Park: Mount Lyell, 7 August 1935 (E. C. Van Dyke Colln.: CAS). The species is also known from Colorado and Manitoba to Alberta and Oregon; its biology is discussed by Cooley (1917). The primarily Palearctic species *Aclypea opaca* (Linnaeus 1759), which is often confused with *A. bituberosa,* occurs in North America only in Alaska.

Genus *Thanatophilus* Leach 1815
Thanatophilus lapponicus (Herbst)
Figure 1C

Silpha lapponica Herbst 1793:209, plate 52: Fig. 4
Thanatophilus lapponicus of Portevin 1926:33
Silpha (Thanatophilus) lapponica of Pierce 1949:59, Figs. 1, 2 (specimens LACMIP 5722–5724)

Pleistocene.—12 specimens as follows: RANCHO LA BREA: Pit A: 2 complete and 2 partial left elytra (C3b [♂], C3c, C3d = LACMIP 5722 [♀?], C3e), *pronotal fragment; "Bliss 29": 2 complete and 2 partial right elytra (C3f = LACMIP 5723 [♂], C3g = LACMIP 5724 [♀], C3h, C3i); "Pit X": broken left elytron (C3a); *Pit 91: Grid GJM 346: complete left elytron (RLP 3366E); Grid GJM 273: elytral fragment (RLP 4040E); Grid GJM 550: broken left elytron (RLP 4041E).

Holocene.—This 11–14 mm long carrion feeder is widely distributed through Arc-

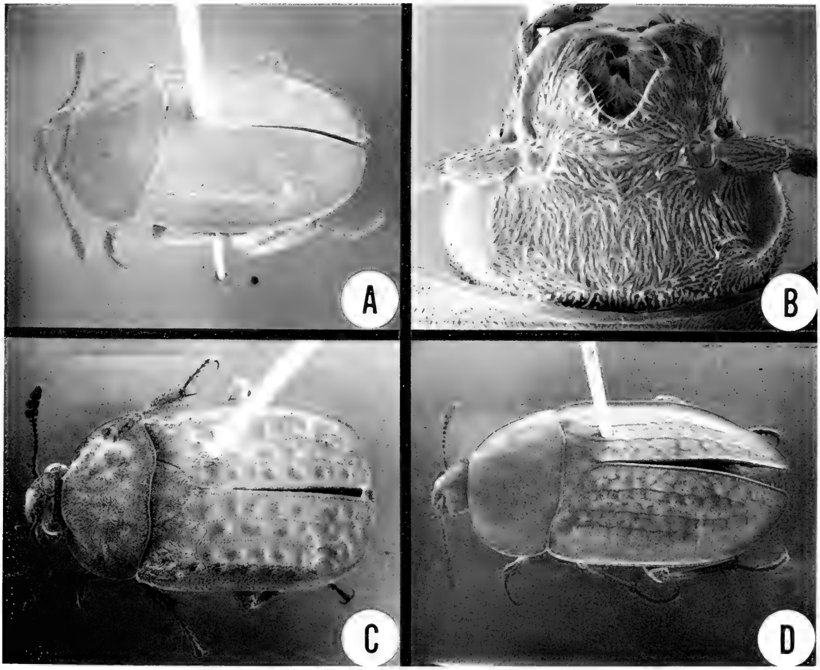

FIG. 1. A–B, *Aclypea bituberosa* (Manitoba, Canada), A, habitus; B, head; C, *Thanatophilus lapponicus*, habitus (Colorado); D, *Heterosilpha ramosa*, habitus (Colorado).

tic Europe and Asia, and in North America from Alaska and Greenland to the District of Columbia, Pennsylvania, Michigan, Iowa, Kansas, New Mexico, California and northern Mexico. *Thanatophilus lapponicus* was recorded from Santa Rosa Island, California by Fall (1897), but we have seen no specimens (which may have been destroyed in the 1906 CAS fire). It occurs more commonly in arctic and arctic alpine tundra, grassland, or open woodland habitats than in heavily forested habitats.

Thanatophilus sagax (Mannerheim), **comb. nov.**

Silpha sagax Mannerheim 1853:173

This 9–11 mm long species is poorly known, as *T. sagax* long has been considered a junior synonym of *Thanatophilus trituberculatus* (Kirby 1837). The distinguishing characteristics are as follows: In *T. sagax* the intervals between elytral striae lack tubercles, but the middle elytral stria has a single broad tubercle two thirds of the way to the apex. This tubercle slightly elevates the outer stria, which continues into the posterior quarter of the elytron. In *T. trituberculatus*, the outer stria terminates at the tubercle, with a small disjunct tubercle in the posterior quarter of the elytron.

Pleistocene.—Unknown from California.

Holocene.—*Thanatophilus sagax* ranges from northern California (Brockway, Placer County, 15 July 1941, G. S. Mansfield in CAS) through British Columbia to Alaska (Kenai Peninsula) and eastward to the Northwest Territories and Manitoba. We have seen *T. trituberculatus* from only the Northwest Territories and Manitoba.

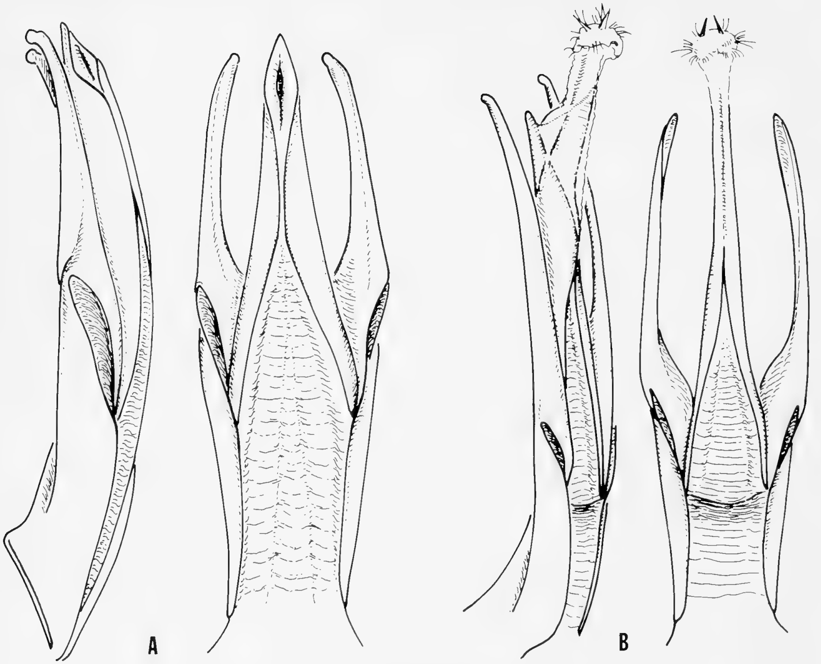

Fig. 2. Male genitalia of *Heterosilpha* species: A, *H. ramosa* (Platteville, Colorado); B, *H. aenescens* with internal sac everted (Alameda County, California). The chord of the arc from the edge of the basal sclerotization to the paramere tips is 2.8 to 3.0 mm in *H. aenescens* and 3.5 to 4.0 mm in *H. ramosa*.

Genus *Heterosilpha* Portevin 1926

Two superficially similar species, *Heterosilpha ramosa* (Say 1823) and *Heterosilpha aenescens* (Casey 1886), occur throughout most of California. *Heterosilpha aenescens* has been considered a synonym of *H. ramosa* (Arnett 1944, 1946). However, as stated by Hatch (1927*a*, 1946) and Portevin (1926), they are distinct species. Distinguishing characters (in decreasing order of reliability) are found in the male genitalia, secondary sexual characters and color. The male genitalia (Fig. 1 A, B) are distinct and offer the most reliable identification characteristics. *Heterosilpha ramosa* is sexually dimorphic in the elytral apex of females and in the tarsi of males, but it is nearly impossible to distinguish the sexes of *H. aenescens*, except by reference to the genitalia. In females of *H. ramosa* the apex of the elytra is prolonged, rather than gradually rounded as in *H. ramosa* males and both sexes of *H. aenescens*. The anterior and middle tarsi of *H. ramosa* males are strongly dilated, but there is no such tarsal dilation in male *H. aenescens*. Except for minor color and tarsal differences, *H. ramosa* males look very similar to both sexes of *H. aenescens*. The external distinguishing characteristics of *H. aenescens* are the aeneous lustre and coarser elytral sculpture. Adults of both species are 12–15 mm long.

Heterosilpha ramosa (Say)
Figures 1D, 2A

Silpha ramosa Say 1823:193
Heterosilpha ramosa of Portevin 1926:85 (as synonym, in error, of *Heterosilpha cervaria* [Mannerheim 1843]).

Silpha (*Heterosilpha*) *ramosa* of Pierce 1949:61, Figs. 3a, 3b (specimens LACMIP 5720 [rounded tip due to breakage] and 5721)

Heterosilpha ramosa was described from a specimen collected by Thomas Nuttall on "the upper Missouri" (Say 1823:193, reprinted by LeConte 1859*d*:123). Because of the complete loss of the Say collection (LeConte 1859*d*, Lindroth and Freitag 1969), we designate as **neotype** a male (MCZ 32444) in the LeConte collection bearing the following labels on its pin: a greenish disk; a handwritten label "S. ramosa/Say/cervaria/Mann."; and our neotype label.

It is generally accepted (Lindroth and Freitag 1969) that LeConte had the opportunity to compare his specimens with those in Say's collection, and that LeConte's collection is the most reliable indication of Say's concepts of his species. The greenish disk is LeConte's locality code for the area including the upper Missouri River and its tributaries, so the type locality is unchanged. In accordance with Article 75 of the International Code of Zoological Nomenclature, this neotype designation is in the interest of stability of nomenclature, is in connection with the revisionary work necessary to establish the identity of the asphalt deposit fossils, and characters differentiating the taxa are given. Our proposed designation has been discussed with other specialists on North American Silphidae and does not arouse objections.

Pleistocene.—Pierce (1949) apparently did not consider the possibility that some of his *Heterosilpha* specimens may have been *H. aenescens.* On the basis of elytra and pronota, it is impossible to separate *H. aenescens* from male *H. ramosa* with present knowledge. At least some of Pierce's Rancho La Brea elytra are *H. ramosa,* as they show female sexual dimorphism. However, *H. aenescens* elytra may be mixed with the male *H. ramosa.* Although 8 of the 11 *Heterosilpha* elytra from Pit 91 have broken tips, the 3 with the apex intact are rounded, so *H. ramosa* cannot be positively recorded from this excavation. Only future study of the morphology of Holocene *Heterosilpha* and additional *Heterosilpha* specimens from Pit 91 will resolve this question.

Heterosilpha is represented by 20 elytra and 2 pronota. The elytra fall into 3 categories: (A) female *H. ramosa,* (B) elytra with rounded apexes; which could be male *H. ramosa* or either sex of *H. aenescens,* and (C) elytra with broken or damaged tips which cannot be placed in the 2 former groups; the category and side (R = right, L = left) of each is noted below. RANCHO LA BREA: Pit A: CR (C1d); *Pit 9: AR (C1i); "Bliss 29": CL (C1a = LACMIP 5720), CR (C1b), AR (C1c = LACMIP 5721), two AL (C1e, C1f), CR (C1g), CL (C1h); *Pit 91: Grid GJM 273: BL (RLP 3247E), CL (RLP 4038E), CR (RLP 4039E); Grid GJM 295: CR (RLP 3303E); Grid GJM 360: CL (RLP 3431E); Grid GJM 364: pronotum (RLP 3486E); Grid GJM 408: BR, CL (RLP 3938E); Grid GJM 568: BL (RLP 27E), pronotum (RLP 28E); Grid GJM 612: CL (RLP 3549E, associated with *Felix atrox* skull): Grid GJM 777: CL (RLP 1180E, associated with *Smilodon californicus* skull); Grid GJM 838: BR (RLP 1824E); Grid GJM 856: CR (RLP 2164E).

Holocene.—Literature records of *H. ramosa* cannot be trusted, due to past confusion with *H. aenescens. Heterosilpha ramosa* occurs in much of western North America (including Santa Rosa, Santa Cruz, and San Miguel islands). Brewer and Bacon (1975) have treated the biology of *H. ramosa* in Colorado. Linsley (1942) gives additional ecological notes on *H. ramosa,* but these may refer to *H. aenescens* (we have been unable to locate voucher specimens).

Heterosilpha aenescens (Casey)
Figure 2B

Silpha aenescens Casey 1886:171
Heterosilpha aenescens of Portevin 1926:85

Heterosilpha aenescens was described from an unspecified number of specimens from San Francisco, California (Casey 1886). A **lectotype** is hereby designated as a male in the USNM bearing the labels "Cal." (with black dot in middle of the "C"),

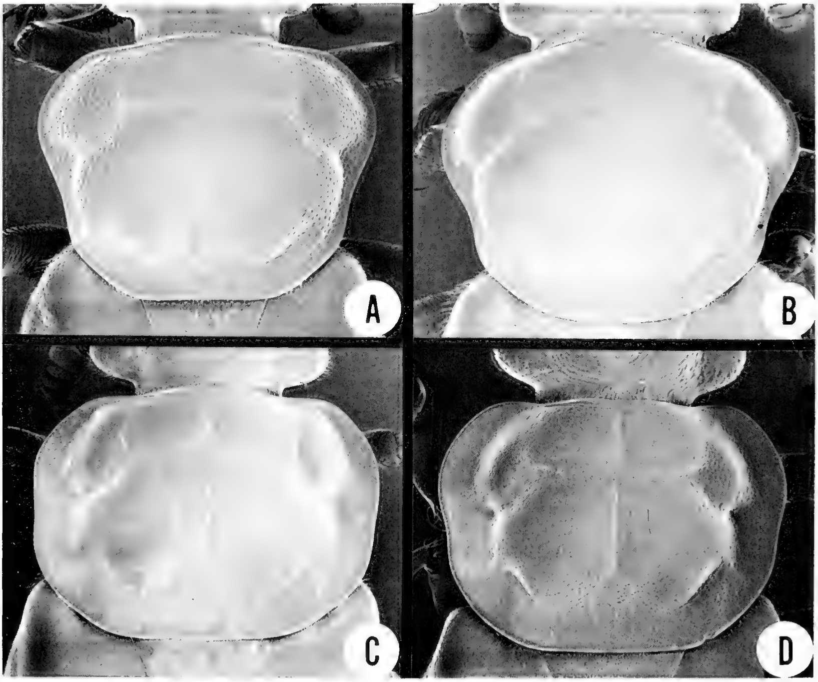

FIG. 3. Pronota of *Nicrophorus* species: A, *N. guttula* (Santa Barbara, California); B, *N. marginatus* (New Mexico); C, *N. nigrita* (Santa Barbara, California); D, *N. defodiens* (Northwest Territories, Canada).

"CASEY/bequest/1925," red type label "TYPE USNM/48743," and our lectotype label. The lectotype and 7 paralectotypes (4 males and 3 females, all with same labels as lectotype, but red type labels "aenescens/paratype USNM/48743") were all examined. The USNM type labels were placed on the assumed types during curation of the Casey collection at the USNM (Buchanan 1935). Casey's locality code indicates these specimens came from "San Francisco and immediate vicinity as far south as Redwood City and Purissima." Seven other specimens from "Alameda/Co. Cal." and "Cal" are assigned to *H. aenescens* in the Casey collection, but these were not considered part of the type series by Buchanan and do not bear paratype labels.

Pleistocene.—As discussed above, *H. aenescens* may be represented by Rancho La Brea fossils, but cannot be differentiated from *H. ramosa* at this time.

Holocene.—*Heterosilpha aenescens* ranges at least from Baja California, Mexico through California into southern Oregon.

Tribe Nicrophorini
Genus *Nicrophorus* Fabricius 1775

The proper spelling is *Nicrophorus*, not *Necrophorus* Illiger 1798 (Herman 1964). Arnett (1944) and Madge (1958) treat the North American species, and a revision is in preparation by R. B. Madge (*personal communication*).

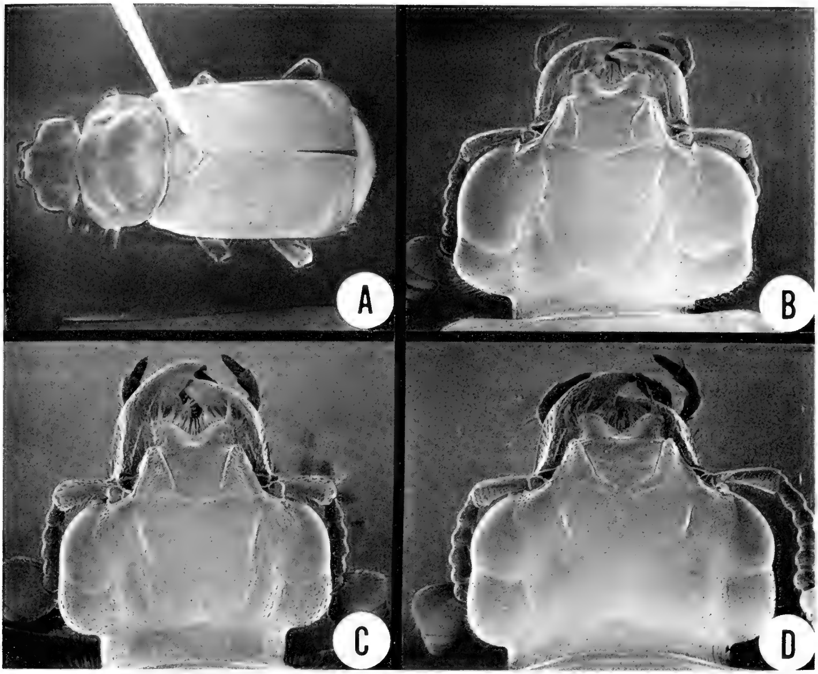

FIG. 4. *Nicrophorus* species: A–B, *N. nigrita* (Santa Barbara, California), A, habitus; B, head; C, *N. guttula*, head (Santa Barbara, California); D, *N. marginatus*, head (New Mexico).

Nicrophorus defodiens (Mannerheim)
Figure 3D

Necrophorus defodiens Mannerheim 1846:513
Nicrophorus defodiens of Hatch 1927*a*:355
Nicrophorus conversator of Leech 1934:36 (misidentification)

Nicrophorus defodiens long has been confused with *Nicrophorus vespilloides* (Herbst 1784). Despite the work of Leech (1937), unpublished studies by R. B. Madge indicate that *N. defodiens* is a distinct species.

Pleistocene.—Unknown from California.

Holocene.—This species occurs along the Pacific Coast of North America from Alaska into central California. Leech (1934) discussed its natural history, but misidentified the beetles as *N. conversator* (Walker 1866).

Nicrophorus nigrita (Mannerheim)
Figures 3C, 4A, B

Necrophorus nigrita Mannerheim 1843:251
Nicrophorus investigator nigritus of Hatch 1927*a*:357
Nicrophorus nigrita of Arnett 1944:15
Nicrophorus investigator alpha Pierce 1949:67, fig. 13 (specimen LACMIP 3048), NEW SYNONYMY

This species was once considered a subspecies of *N. investigator* (Zetterstedt 1824), but it is specifically distinct. True *N. investigator* has not been recorded in California. Pierce's *N. investigator alpha* is *N. nigrita*, which was not considered a valid species by Hatch (1927*a*), upon which Pierce based his work. *Nicrophorus investigator alpha* was described from 6 syntype pronota (LACMIP 3048–3052, 5263; C121a–f) all from Pit A, Rancho La Brea. Pierce labeled syntype LACMIP 3048 (C121d) as holotype, although it was published (Pierce 1949) as a syntype. We are hereby designating 3048 as **lectotype** because it was labeled as holotype by its author, it was illustrated (Pierce 1949: Fig. 13), and it is the syntype in best condition. Specimen LACMIP 3048 was mistaken by Sphon (1973) as the holotype of *N. investigator latifrons* Pierce and bears a notation to that effect.

Pleistocene.—Eleven specimens as follows: RANCHO LA BREA: Pit A: LACMIP 3048–3052, 5263 (*N. i. alpha* type series); *Pit 91: Grid GJM 295: head (RLP 3339E) and pronotum fragment (RLP 4034E); Grid GJM 408: head fragment (RLP 3944E); *CARPINTERIA: pronotum fragment and right elytron fragment.

Holocene.—This distinctive large black species is the most common *Nicrophorus* in southern California today. It ranges along the Pacific Coast from California (including Santa Rosa, Santa Cruz, West Anacapa, Santa Barbara and San Clemente Islands) to British Columbia and inland to Nevada.

Nicrophorus marginatus (Fabricius)
Figures 3B, 4D

Necrophorus marginatus Fabricius 1801:334
Nicrophorus marginatus of Hatch 1927*a*:360
Nicrophorus guttulus labreae Pierce 1949:63, Figs. 4–10, NEW SYNONYMY
Nicrophorus mckittricki Pierce 1949:66, Fig. 11, NEW SYNONYMY
Nicrophorus investigator latifrons Pierce 1949:67, Fig. 14, NEW SYNONYMY
Nicrophorus obtusiscutellum Pierce 1949:67, Fig. 12, NEW SYNONYMY

Nicrophorus guttulus labreae was described from 166 syntypes from Rancho La Brea as follows: Pit A: 31 heads (LACMIP 2950, 2951, 4339, 5633–5660), 31 pronota (2953–2979, 4334, 4353, 4354, 5270), 2 right elytra (2952, 4336), left elytron (4348), 6 scutella (4337, 4341, 4343, 4345, 4351, 4352), and 8 tibia (4335, 4338, 4340, 4342, 4344, 4346, 4349, 4350); Pit B: head (4355), 2 pronota (2980, 2981); "Bliss 29": 2 heads (4370, 4371), 9 pronota (4362–4369, 4374), left elytron (4372); Pit 28: pronotum (3045); Pit 37: pronotum (3046); Pit 81: 3 tibia (4357–4359), elytral fragment (4361); "Pit X": 34 heads (3011–3044), 28 pronota (2982–3010), left elytron (4356); unknown pit: head (4374). Syntype 4351, an elytral fragment from Pit 81, is apparently not a silphid. Syntype 2952 (C2al, a complete right elytron from Pit A) was labeled by Pierce as holotype, but this designation is invalid as the taxon was published on the basis of syntypes. We are hereby designating 2952 **lectotype** (Pierce 1949: Fig. 4). Unpublished notes and specimen labels indicate that Pierce first considered this a subspecies of *N. marginatus*, but published it under *N. guttula*. *Nicrophorus mckittricki* was described from the holotype pronotum (LACMIP 3054 = McK3a) and 2 paratype elytra (5733 and 5734; McK3b and McK3c) from site 3, depth 2 feet [≈0.6 m] at McKittrick, 6 paratype elytra (5735–5740; McK3d–McK3i) from site 4, depth 4 feet [≈1.2 m] at McKittrick, and 8 "tentatively associated" specimens (not paratypes) from Pits A, B, "X", 28, and "Bliss 29", Rancho La Brea (C120a–c and unnumbered). One "tentatively associated" specimen has not been located, and may not be *N. marginatus*. Although the holotype does have characteristics that tend toward *N. guttula*, it is a specimen of *N. marginatus*. *Nicrophorus investigator latifrons* was described from the holotype head (LACMIP 3053 = C120d) from "Pit X", Rancho La Brea. *Nicrophorus obtusiscutellum* was described from the holotype scutellum (LACMIP 3055 = C120e) from Pit A, Rancho La Brea. Although it is possible that this specimen represents a distinct taxon, there is not enough evidence to convince us at present. We consider it *N. marginatus* because it falls within the range of variation of this species.

Pleistocene.—Two hundred forty-four specimens and 1 literature record: RANCHO LA BREA: Pits A, B, 28, 37, 81, "Bliss 29", "Pit X", and an unknown pit; LACMIP 2950–3046, 4334–4359, 4361–4374, 5270, 5633–5660 (type series of *N. g. labreae*); Pit A: LACMIP 3055 (holotype of *N. obtusiscutellum*), head, pronotum (C120a), *2 complete and 2 fragmentary pronota, *5 complete and 3 fragmentary heads, *scutellum, *6 elytral fragments (elytral determinations questionable); Pit B: head; "Bliss 29": pronotum (C120c); Pit 28: pronotum (C120b); Pit 81: *head fragment; "Pit X": head, *head, 3 fragmentary pronota, LACMIP 3053 (holotype of *N. i. latifrons*), 3 heads (1 recorded by Pierce but now missing); * Pit 91: Grid GJM 295: right and partial left elytra (RLP 3314E), 2 pronotum fragments (RLP 4035E); Grid GJM 408: pronotum fragment (RLP 3941E); *UCMP loc. 2051: 10 complete and 1 fragmentary heads, 13 pronota; McKITTRICK: Pierce's Site 3, depth 2 feet: LACMIP 3054, 5733, 5734 (holotype and paratypes of *N. mckittricki*); Pierce's Site 4, depth 4 feet: LACMIP 5735–5740 (paratypes of *N. mckittricki*); *CIT VP loc. 138: 7 heads.

Holocene.—Ranges over much of the United States and southern Canada, but is less common in California than *N. nigrita*. This species seems to prefer open woodland or grassland situations to dense forests.

Nicrophorus guttula (Motschoulsky)

Figures 3A, 4C

Necrophorus guttula Motschoulsky 1845:53
Nicrophorus guttulus of Hatch 1927*a*:359
Nicrophorus guttulus punctostriatus Pierce 1949:66, NEW SYNONYMY
Nicrophorus guttulus guttulus lajollae Hatch of Pierce 1949:66

Nicrophorus guttula has been confused with *N. hecate* (Bland 1865), a questionably distinct species (**see below**). We see no justification to consider *N. g. punctostriatus*, described from holotype left elyton from Pit A, Rancho La Brea (LACMIP 3947 = C132b), a distinct subspecies.

Pleistocene.—Twenty-eight specimens as follows: RANCHO LA BREA: Pit A: LACMIP 3947 (holotype of *N. g. punctostriatus*), 3 elytra (C131a, C131b, C132a), *head fragment; *Pit 9: head (C2bu); *"Bliss 29": 1 complete and 1 fragmentary right elytron; *Pit 91: Grid GJM 275: head (RLP 3338E), pronotum (RLP 3101E), 3 pronotum fragments (RLP 3315E); *UCMP loc. 2051: 2 heads, pronotum; *McKITTRICK: UCMP loc. 7139: 2 complete and 4 fragmentary elytra, 3 heads; CIT VP loc. 138: 2 heads, 1 pronotum; *CARPINTERIA: 3 heads (bearing grid notation 6B3 ± 8′), left elytron.

Holocene.—The species is primarily limited to California (including San Clemente Island) and Oregon.

Nicrophorus hecate (Bland)

Necrophorus hecate Bland 1865:382
Nicrophorus guttulus hecate of Hatch 1927*a*:360
Nicrophorus hecate of Arnett 1944:15

Nicrophorus hecate was described from an unspecified number of specimens collected in the Colorado Territory by James Ridings (Bland 1865). Two specimens are placed as syntypes in the ANSP, with labels "Col.", "LectoTYPE/3283", "TYPE/N. hecate/Bland" and "Col.", "PARATYPE/3283". The lectotype and paratype labels were apparently placed on the specimens in routine curation and are not valid designations. We hereby designate the first, and larger, specimen **lectotype.**

Some populations from central California to southern Oregon show an intergradation of the characteristics of *N. guttula* into those of *N. hecate*. We do not presently have adequate material to document the nature of this intergradation. These are probably the same species (R. B. Madge, *personal communication*), but we lack adequate data to formally synonymize *N. hecate* under *N. guttula*.

Pleistocene.—Unknown from California.

Holocene.—Ranges from central California to British Columbia and east through the Rocky Mountains to the western Great Plains.

Dubious California Records

Several species have been recorded in literature or are represented in collections by specimens labeled California. Some of these represent introductions of Palearctic species which are not established in North America. Most, however, are old specimens from "California" which we think are mislabeled, as follows: *Necrodes surinamensis* (Fabricius 1775): "Cal." (LACM)—does not occur in California (Ratcliffe 1972); *Nicrophorus germanicus* (Linnaeus 1758): "California" (holotype of *Necrophorus grandior* Angell 1912; Hatch 1927*a*)—Palearctic; *Nicrophorus humator* (Gleditsch 1767): "California" (paratype of *N. grandior*; Hatch 1927*a*)—Palearctic; *N. investigator* (Zetterstedt 1824): "Cal." (F. C. Bowditch Collection: MCZ); *Nicrophorus orbicollis* (Say 1825): San Jacinto Mountains (Madge 1958), "Cal." (MCZ); *Nicrophorus pustulatus* (Herschel 1807): "Cal." (Hatch 1927*a*); *Nicrophorus tomentosus* (Weber 1801): Trabuco Canyon, Orange County, 10 July 1963 (D. Hubbard: LACM); *Oxelytrum discicolle* (Brulle 1840): "Southern California" (Hatch 1927*a*); *Silpha tristis* Illiger 1798: Santa Ana, in soil 9 March 1959 (J. L. Bath: UCR)—Palearctic.

Two species that live in adjacent regions may range into California. These are *Oxelytrum discicolle* (Brulle 1840) known from northern South America to northern Mexico and *Thanatophilus truncatus* (Say 1850), occurring from Arizona and western Mexico northward and eastward through the Rocky Mountain chain to the prairies of Colorado and Kansas.

KEY TO CALIFORNIA SILPHIDAE

1. a. Elytra with 3 longitudinal ridges or smooth; generally large beetles (usually >10 mm) 8
b. Elytra with 9 longitudinal depressed lines, rarely becoming indistinct; generally small beetles (usually <10 mm) 2
2. (1) a. Antennae filiform; 7th antennal segment twice as long as wide, or nearly so .... (*Apteroloma*) 3
b. Antennae clavate; 7th antennal segment nearly as wide as long .... (Agyrtini) 5
3. (2) a. Pronotum distinctly narrowed posteriorly, much narrower at base than base of elytra, somewhat cordate .... *Apteroloma caraboides*
b. Pronotum only slightly narrowed posteriorly, almost as broad at base as base of elytra, not cordate 4
4. (3) a. Hind angles of pronotum sharp cornered .... *Apteroloma tahoecum*
b. Hind angles of pronotum rounded .... *Apteroloma tenuicorne*
5. (2) a. Maxillary palpi with terminal segment about same width as penultimate segment; terminal antennal segment subequal or more than twice as long as penultimate segment 6
b. Maxillary palpi with terminal segment much wider than penultimate segment; terminal antennal segment less than twice as long as penultimate segment .... (*Agyrtes*) 7
6. (5) a. Length 8 mm and greater .... *Necrophilus hydrophiloides*
b. Length <5 mm .... *Pelatines latus*
7. (5) a. Antennal club of 4 segments; 3rd antennal segment appreciably longer than the 2nd; aedeagus in side view with a pronounced bend .... *Agyrtes longulus*
b. Antennal club of 5 segments; 3rd antennal segment only slightly longer than the 2nd; aedeagus in side view relatively straight *Agyrtes similis*
8. (1) a. Elytra truncate, exposing at least tip of abdomen; general shape elongate (as in Fig. 4A) .... (*Nicrophorus*) 9

b. Elytra covering most or all of abdomen; general shape oval (as in Figs. 1A, 1C, 1D) 13

9. (6) a. Pronotum (Figs. 3C, 3D) sides feebly sinuate; pronotum base nearly as wide as apex; pronotum not cordate 10

b. Pronotum (Figs. 3A, 3B) sides strongly sinuate; pronotum base much narrower than apex; pronotum cordate 11

10. (9) a. Elytra black; 3 terminal segments of antennae orange; metasternal pubescence brown .... *Nicrophorus nigrita*

b. Elytra with red fascia (sometimes faint); 3 terminal segments of antennae black; metasternal pubescence golden ... *Nicrophorus defodiens*

11. (9) a. Basal segment of antennal club black or orange; anterior face of procoxae with very long hairs on basal half 12

b. Basal segment of antennal club orange; anterior face of procoxae with only short hairs on basal half .... *Nicrophorus marginatus*

12. (11) a. Basal segment of antennal club black; no elytral fascia; elytral epipleuron red at humerus .... *Nicrophorus guttula*

b. Basal segment of antennal club red; red elytral fascia present; elytral epipleuron usually predominantly red .... *Nicrophorus hecate*

13. (8) a. Clypeus broadly and shallowly emarginate; eyes normal, comparatively large 14

b. Clypeus sharply and deeply emarginate (Fig. 1B); eyes comparatively small (Fig. 1B) .... *Aclypea bituberosa*

14. (13) a. Elytral intervals with reticulate sculpturing (Fig. 1D); labrum narrowly emarginate; pronotum not tomentose .... (*Heterosilpha*) 15

b. Elytral intervals with isolated tubercles (Fig. 1C) or smooth; labrum broadly emarginate; pronotum usually tomentose .... (*Thanatophilus*) 16

15. (14) a. Not sexually dimorphic, ♂♂ and ♀♀ superficially alike; male genitalia as in Fig. 2B .... *Heterosilpha aenescens*

b. Sexually dimorphic, elytral apex of ♀♀ elongated, front and middle tarsi of ♂♂ dilated; male genitalia as in Fig. 2A .... *Heterosilpha ramosa*

16. (14) a. Intervals between elytral striae with 8–10 tubercles; common species (Fig. 1C) .... *Thanatophilus lapponicus*

b. Intervals between elytral striae without tubercles; rare species .... *Thanatophilus sagax*

PALEOECOLOGY

Silphid ecology

Silphids are found mostly on carrion and occasionally on decaying vegetation. Some feed on the carrion or plant matter, whereas others are predaceous on maggots and other animals present on the carrion. Adults of *Nicrophorus* species bury carrion such as mice and reptiles (Milne and Milne 1976).

Pierce (1949) considered silphids to be characteristic inhabitants of carrion in "ammoniacal fermentation" (his fifth period of decomposition), occurring in the 4th to 8th months following death. His conclusion, based on forensic studies of insects associated with human corpses, is excessive, as silphids inhabit carrion much sooner after death. In some cases, silphids find carrion within an hour after death (Milne and Milne 1944). Shubeck (1969) found that "Carrion seemed to be most attractive to carrion beetles from the fifth to the tenth days when it was in the fresh-bloated, bloated, and decay stages. Since this is the period of time during which the maggots were present . . . , it is possible that they are in some way involved in making the carrion habitat attractive to carrion beetles." Illingworth (1927), at Upland, California, found adult *Nicrophorus nigrita* "feeding on maggots" under a cat dead 3 days. He found *Thanatophilus lapponicus* under the cat after 7 days. After 27 days, "Many fat silphid larvae were present. They had destroyed a large percentage of the dipterous larvae." The ecology of the California silphids is poorly known, although most are large, conspicuous, and easy to attract (Newton and Peck 1975) and capture. Until such information is obtained, silphids can contribute only a fraction of their potential to an understanding of California Pleistocene paleoecology.

Accumulation and Preservation of the Fossils

The popular generalization regarding accumulation of fossils at Rancho La Brea presents a picture of great pools of continuously active liquid asphalt which trapped unwary animals, which in turn attracted scavengers which also became trapped (Stock 1956 and others). However, recent studies (Woodard and Marcus 1973) indicate that such great "death traps" had little role in the accumulation of fossils. Reinterpretation of stratigraphy and radiocarbon dating indicates that the fossil deposits were formed at the sites of discontinuously active asphaltic seeps during the accumulation of alluvium from the late Pleistocene to the present. Most deposits are stratified and can be correlated with facies of surrounding sediments which are not oil impregnated. The "pits" at Rancho La Brea were artifacts of excavation, and did not represent naturally occurring deep pools of liquid asphalt. Woodard and Marcus (1973) further state that "While the larger and more continuous pockets may represent areas of asphaltic quicksand in which animals became mired, it is apparent from the abundance of coarse, stream-worn debris that many of the smaller pockets more likely represent localized fluviatile concentrations of bones in stream channels or ponds. Once buried, the abraded and fragmented fossils were enveloped in asphalt permeating upwards and laterally into the sediments from active vents and fissures." Penetration by asphalt was prompt in some cases, preserving fragile specimens such as leaves. Some trapping of small animals may have taken place in shallow pools of asphalt concealed by leaves, dirt or water and/or covered with a thin and weak layer of hardened asphalt.

Deposition at McKittrick was discussed by Shultz (1938): "During late Pleistocene time sedimentation was active in the area, and as the oil reached the surface [from numerous small discontinuously active petroleum seeps] and spread out in sheets of a fraction of an inch or so in thickness it became intercalated with clay, sand, gravel, and windblown material. The resulting product is a rudely stratified material consisting of fine and coarse sediments more or less uniformly saturated with petroleum. The upper layers which contain a Recent vertebrate fauna seem to be somewhat better stratified than the lower levels which contain the Pleistocene vertebrates. Vander Hoof (1934) . . . contends that it was mainly during the summer months that the oil became fluid enough to spread over large areas; while the winter rains carried in most of the clastic material." The result is a brea belt representing a complicated sequence of events.

The geology of the Carpinteria asphalt deposit also indicates fluviatile deposition of the fossils (Putnam 1942). Many plant fossils (especially wood) are water worn and partially decayed, indicating stream alluvium subsequently impregnated with asphalt (Chaney and Mason 1933, Mason 1940, Webber 1933). Ralph Hoffman wrote (unpublished letter to R. W. Chaney, 4 June 1932) that "the steam shovel at the asphalt beds has struck a tangle of stumps and logs so dense that they had to stop work at that point . . . ." This "tangle" was probably flood debris similar to one found in Pit 91 at Rancho La Brea.

Interpretation of accumulation and preservation by asphaltic matrix is difficult, especially in light of our present poor knowledge of and problems inherent in insect paleoecology (Kenward 1976, Coope 1977). Research in progress at Rancho La Brea eventually may provide more definitive answers, but 2 distinct processes appear to be involved: direct preservation (trapping in viscous asphalt) and indirect preservation (impregnation with asphalt subsequent to death and burial). Entrapment of insects occurs in 4 ways. (1) Insects can be attracted to carrion or other material already trapped or otherwise in contact with asphalt. (2) Insects, especially aquatic species, can be attracted to pools of oil and water which appear as water, but this probably has little affect on silphids. (3) Insects can be attracted to the asphalt itself. Some insects are attracted to fresh tar coating roads (Saylor 1933, Hubbs and Walker 1947), but we are not aware of any silphids being attracted to asphalt. (4) Insects can be accidentally trapped, without being attracted, by crawling, flying, or falling into asphalt and not being able to free themselves. In practice, preservation/entrapment is a product of all these processes, all of which have been observed to occur at modern asphalt seeps, but the relative importance of each process is not known. Also, some species may have been more attracted than others to the particular microhabitats present.

A special case of preservation has been observed at the Maricopa deposit. At this site, asphaltic outcroppings occur in large mounds which are often penetrated by large cracks and rodent burrows. Tenebrionid beetles (Coleoptera: Tenebrionidae) often live in and about these orifices, and their remains, apparently only several seasons old, are found along with seeds and other debris in low points in these holes. Although not presently impregnated with asphalt, future changes in the activity of the asphalt could easily mix this Holocene material into surrounding Pleistocene matrix. This should especially be considered when evaluating Pierce's McKittrick fossils. These cracks may also be responsible for movement of fossils within the deposit (similar to a Vertisol, *see* Johnson and Hester 1972).

Late Pleistocene Environments

At Rancho La Brea, several apparently contemporaneous late Pleistocene plant communities existed in the vicinity of the site of deposition now known as Pit 91 (Warter 1976). A cool, moist coastal closed-cone pine forest was probably dominant near the site, whereas chapparal and foothill woodland occurred inland on warmer, drier sites at higher elevations. Stream-drifted wood of *Sequoia sempervirens* (D. Don) Endlicher suggests the occurrence of coast redwood forest in sheltered canyons in nearby mountain foothills. Riparian woodland and aquatic plants are also represented from Pit 91, as are herbs from drier situations. Plants recovered from the silphid-bearing grids indicate the presence of nearby standing water at the time of preservation (J. K. Warter, *personal communication*). Thus, the silphids were apparently deposited in a placid pool in a slow stream or a pond margin.

As shown by differences in faunal composition (Howard 1962, Marcus 1960, Stock 1956) and radiocarbon dates (L. F. Marcus, *personal communication*), the many Rancho La Brea "pits" are not equivalent accumulations representing the same time periods and ecological conditions. Unfortunately, most of the pits from which insects are available are not among the important vertebrate-bearing pits, and have not been included in papers analyzing paleoecology, age, or vertebrate faunal composition. Also, many of the faunal differences may be attributable to selective entrapment and/or selective preservation due to differences in the physical characteristics of the individual asphalt seeps and their methods of accumulating organic material. Because of differences between periods of activity of the Rancho La Brea asphalt seeps, several environments and associated biotas are represented. Thus, older conclusions about the Pleistocene environment and climate at Rancho La Brea (i.e., Stock 1956), most of which assumed that the pit faunas were contemporaneous, must be used with caution. Even more recent conclusions must be used with care due to new data from the current excavation of Pit 91. However, the general conclusions of Brattstrom (1953*a*) seem safe. He suggested "that from Late Pleistocene to Recent there was a local transition from a moist climate of *Pinus* and *Cupressus* through a stage of decreasing rainfall and a vegetation of *Quercus agrifolia* and *Juniperus californica*, to the present-day climate and vegetation of Oakwoodland Savanna and Coastal Sage-scrub with subsequent changes in the fauna." Available radiocarbon dates indicate that asphalt seeps at Rancho La Brea have been active over most of the last 40 000 yr (Woodard and Marcus 1976). Further information on late Pleistocene climate and fauna can be found in Johnson (1977*b*) and W. Miller (1971).

At McKittrick, the late Pleistocene climate and environment were similar to those of the region today, except that there was probably more rainfall and perhaps a nearby

TABLE 1. Occurrence of silphids in California Pleistocene deposits

Taxa	Rancho La Brea	McKittrick	Carpinteria
Heterosilpha ramosa	X		
Thanatophilus lapponicus	X		
Nicrophorus nigrita	X		X
Nicrophorus guttula	X	X	X
Nicrophorus marginatus	X	X	

lake or marsh (Brattstrom 1953*b*, DeMay 1941*a*, Mason 1944, and Schultz 1938). DeMay (1941*a*) reconstructed the environment as ". . . sparsely timbered mountain slopes giv[ing] way to brush-covered hills and arid or semi-arid plains lying adjacent to a desert lake." The flora was a pinyon–juniper woodland similar to that presently occurring in the foothills of the Sierra Madre Mountains bordering the Cuyama Valley in northeastern Santa Barbara County, about 50 km south of McKittrick (Mason 1944).

At the Carpinteria deposit, the fossil assemblage indicates that the environment in the immediate vicinity of the site was more moist than at present (Chaney and Mason 1933, DeMay 1941*b*, Wilson 1933). Most components of the assemblage indicate an environment similar to that now present on the Monterey Peninsula (320 km northwest), although with less oceanic influence. However, xeric components indicate the presence of a drier environment nearby, or perhaps at a different time. DeMay (1941*b*) suggested, due to the scarcity of aquatic bird fossils, that the site was more remote from the seacliff than it presently is, and that no large body of freshwater, such as apparently was present at McKittrick, existed in the vicinity. The few studies on insects of this deposit agree with these conclusions (Lance 1946, Miller 1978, Moore and Miller 1978).

Silphid Faunal Composition

The fossil record indicates that the composition of the southern California silphid fauna during the Pleistocene differed from that of the region today, although the fossil record may not be a representative sampling of Pleistocene populations. Of the 16 Holocene California silphids, only 6 are important to the fossil study: *Thanatophilus lapponicus*, *Heterosilpha aenescens*, *H. ramosa*, *Nicrophorus nigrita*, *N. guttula*, and *N. marginatus*. *Nicrophorus nigrita* is the most abundant species of *Nicrophorus*, followed by *N. guttula*, with *N. marginatus* being found only occasionally. The habitat preferences of these species are poorly known.

The fossil record (Table 1) shows that *Thanatophilus lapponicus* and *Heterosilpha ramosa* were present in Pleistocene southern California. *Heterosilpha aenescens* may have been present, but cannot be distinguished from *H. ramosa* on the basis of elytra. Fossils of *Nicrophorus marginatus* are most abundant, but *N. guttula* and *N. nigrita* are also present. Pierce's Rancho La Brea material is dominated by *N. marginatus* (90%), with a small percentage of *N. guttula* and even less *N. nigrita*. The UCMP loc. 2051 at Rancho La Brea yielded mostly *N. marginatus* (87%) with some *N. guttula* (13%). Overall, the current excavation of Pit 91 has produced similar numbers of *N. marginatus* and *N. guttula* with slightly fewer *N. nigrita*. *Nicrophorus marginatus* and *N. guttula* have not been found in the same grids in Pit 91. Grid GJM 275 yielded only *N. guttula*, but grids GJM 295 and GJM 408 yielded only *N. marginatus* and *N. nigrita* in almost equal numbers. At Carpinteria, only *N. guttula* and *N. nigrita* are found, with the former more abundant. At McKittrick, UCMP loc. 7139 yielded only *N. guttula* whereas Pierce's sites 3 and 4 yielded only *N. marginatus*. The CIT VP loc. 138 yielded both *N. guttula* and *N. marginatus*, but considerably more *N. marginatus*. This apparent change in faunal composition could be due to (1) the inadequacy of the fossil record and/or to (2) true differences in faunal composition due to climatic shifts.

True changes in faunal composition could be due to (1) alterations in the relative abundances of populations *in situ* over time and/or (2) movement of new populations into the region, replacing the previous populations. Such changes, initiated by the climatic shifts associated with glaciation, could have occurred multiple times during the late Pleistocene. With these climatic shifts came variations in vegetation and the kinds of carrion available, including extinction of the large mammals that were present in the region during the Pleistocene. This extinction was probably largely due to sudden climatic changes, with perhaps some influence from human hunting (Axelrod 1967, Johnson 1977*a*). At least some *Nicrophorus* species show no interest in carrion too large for them to bury (Milne and Milne 1944), so the Pleistocene *Nicrophorus* may not have utilized large mammal carrion. Climatic variations would have also affected the rate of decomposition of carrion, changing its insect fauna. These factors could have favored certain species over others, thus modifying the relationships of populations present in the region, or they could have favored species not previously present in the region, thereby allowing new populations to displace the previous resident species. Research at Rancho La Brea, Searles Lake (Smith 1968, 1976), and other places may eventually correlate late Pleistocene climatic shifts with floral and faunal changes.

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Worms of the Mississippian Bear Gulch Limestone of central Montana, USA

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Abstract. A fauna of worm body fossils representing the phyla Nemertina, Nematoda, and Annelida (some with scolecodonts in place) is described from the Bear Gulch Limestone, uppermost Mississippian (Namurian), of central Montana. Many of the Bear Gulch worms have taxonomic affinities with worm fossils from the Mazon Creek Essex fauna, Upper Pennsylvanian, of Illinois. Some comments on possible paleoecology of Late Paleozoic worms is offered.

Introduction

Intact body fossils of worms are rare. The Burgess Shale in the Middle Cambrian of British Columbia has an extensive worm assemblage, originally described by Walcott (1911) and most recently restudied in part by Whittington (1975) and Conway Morris (1977*a*, 1977*b*). Størmer (1963) described some Lower Carboniferous nematodes. Schram (1973) described a nemertine and pseudocoelomates from the Upper Pennsylvanian Mazon Creek Essex fauna of Illinois, and Thompson and Johnson (1977), Jones and Thompson (1977), and Thompson (1979) described various coelomate worms from Mazon Creek. The only other fossil nematodes are Tertiary in age and found in amber in association with insects and pieces of arthropod cuticle (Taylor, 1935; Dollfus, 1950). Ehlers (1868) named a eunicid polychaete from the Middle Jurassic Solenhofen Limestone. Polychaetous annelids have been known from the fossil record as scolecodonts, but associated jaw apparatuses are rare (Kielan-Jawarowska, 1966).

Melton (1971) called attention to the unusually preserved fauna of the Mississippian Bear Gulch Limestone as collected from several outcrops in Fergus County, near Beckett, Montana. The fauna contains bony fish (Melton, 1969) and Chondrichthyes (Lund, 1974, 1977*a*, 1977*b*; Lund and Zangerl, 1974), a number of invertebrates including conodont animals (Melton and Scott, 1972; Scott, 1973), and various "articulate groups" of which the Crustacea are the most prominent (Schram and Horner, 1978). The fauna is of unusual preservation such that soft bodied animals as well as shell fossils are found in abundance, many of the former representing the worm phyla Nemertina, Nematoda, and Annelida. The worm fossils are preserved as external molds of the body, casts, actual organic remains, and color differences in the rock. This paper described the worm fauna of the Bear Gulch Limestone.

Prefixes to numbers denote specimens from the following collections: UM—University of Montana, Missoula; CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Discussion

The Bear Gulch worms are the second complete fauna of such forms to be described from the Carboniferous. The worms as a whole bear a striking resemblance to the worms of the Middle Pennsylvanian Essex fauna. Schram (1973) described the nemertine and pseudocoelomates of the Essex fauna, and Bear Gulch has specimens

TABLE 1. Relative abundance of worms in the Bear Gulch fauna.

Taxa	Specimens (*N*)	Worm species (%)
Nemertina		
Archisymplectes rhothon	4	5.4
Nematoda		
Nemavermes mackeei	15	27.0
Annelida		
Phyllodocida		
Goniadidae		
Carbosesostris megaliphagon	7	12.7
Nephtyidae		
Astreptoscolex anasillosus	3	5.4
Eunicida		
Lumbrinereidae		
Phiops aciculorum	4	7.2
Order and family uncertain		
Soris labiosus	2	3.6
Ramesses magnus	6	10.9
Phylum uncertain		
Deuteronectanebos papillorum	5	9.1
Unassignable worms	10	18.2

assignable to some of those Essex genera and species, viz., *Archisymplectes rhothon* and *Nemavermes mackeei.* Thompson and Johnson (1977) described the eunicid polychaete *Esconites zelus,* which corresponds to *Phiops aciculorum* at Bear Gulch. Among the 17 species of annelids mentioned by Thompson (1979), one, *Astreptoscolex anasillosus,* is apparently found in both faunas, and another, *Pieckonia helenae,* is closely paralleled by *Carbosesostris megaliphagon* at Bear Gulch. Two Bear Gulch species, *Soris labiosus* and *Rameses magnus,* do not appear to have any ready counterparts in the Mazon Creek Essex annelids described by Thompson. Although much of the Bear Gulch worm fauna (Table 1) is matched by virtually identical or similar forms in the Mazon Creek Essex fauna, the Essex worm fauna is much more diverse, especially in regard to polychaetes.

The mode of preservation between the two assemblages is different as well. The Mazon Creek material is preserved in iron carbonate concretions with superb detail of preservation. For example, Schram (1973) reported cuticular and subcuticular structures in *Priapulites konecniorum,* Thompson and Johnson (1977) recorded gills in *Esconites zelus,* and Thompson (1979) was able to observe detailed setal and acicular structure. The Bear Gulch material is preserved in a fine-grained grey to brown limestone. Preservation in the Bear Gulch Limestone of structures such as jaw apparatuses is equivalent to that of Mazon Creek, but details of purely soft anatomy are not quite as good as that latter fauna. For example, gills, setae, and paropodial details were not observed on the Bear Gulch material.

The correspondence of Bear Gulch worms to Mazon Creek Essex worms remains a striking one, however, and reinforces the similarity between the crustaceans of the two faunas already noted by Schram and Horner (1978). Schram (1979) suggested a nearshore marine chronofauna of invertebrates persisting through most of the Carboniferous of Laurentia. The Bear Gulch fauna roughly marks a midpoint in the range of the chronofauna.

The Bear Gulch worms confirm only some of the paleoecological observations of Thompson (1979) on the Mazon Creek polychaetes (Table 2). First, she commented on the generally "large" size of Mazon Creek polychaetes and this appears to be true for the Bear Gulch forms as well. Second, she documented the predominance of epifaunal predaceous types in the worm assemblage. In the Mazon Creek Essex fauna 59% of the species and 54% of the individuals were epifaunal, and 76% of the species

TABLE 2. Habitat and feeding type of Bear Gulch worms.

Taxa	Habitat	Feeding type
Archisymplectes rhothon	epifaunal	predator
Nemavermes mackeei	epifaunal	predator
Astreptoscolex anasillosus	epifaunal	predator
Carbosesostris megaliphagon	infaunal	predator
Phiops aciculorum	?	predator
Soris labiosus	?	?
Ramesses magnus	?	?
Deuteronectanebos papillorum	?	?

and 96% of the individuals were predator-scavenger types. The Bear Gulch worm fauna is not as diverse as the Essex fauna and some species are difficult to assign to habitat and feeding type, but the importance of epifaunal habit (Table 3) and predominance of predaceous life style (Table 4) is generally upheld.

Thompson compared her fossil biotas with similar data derived from Parker (1956) on Mississippi delta polychaetes, where 61% of the species were predaceous, and from Day et al. (1971) on the North Carolina coast, where 29% of individuals were predaceous. Thompson's comparisons are of limited value, however, because they deal with contemporary temperate faunas (not all deltaic), whereas contemporary tropical deltaic faunas would have perhaps been more appropriate. Parker (1956) actually deals with species from 7 distinct environments of varying sediment types collected from 280 biological stations and 130 geological cores.

Thompson concluded that the epifaunal predominance in the Essex fauna was due to the large influx of migrating adult forms (epifauna) into a small area. This area had limited access to the open sea with freshwater inflow causing salinity fluctuations. She postulates such conditions did not favor survival of migrating larval types. The issue of predator dominance is left fallow by Thompson. But current understanding of regional Mazon Creek paleogeography (Shabica, 1979; Baird, 1979) would not seem to bear out her migrating-adult explanation. Nor is such an explanation perhaps applicable to Bear Gulch. Furthermore, the migratory abilities of adult errantians is limited, dispersal in all polychaetes being generally achieved by larvae. Nor do salinity fluctuations act as real long-term barriers to many polychaete forms, because Oglesby (1969) points out that all polychaetes and sipunculids investigated are osmotic conformers or develop physiologic adaptations to handle changing salt balance. Smith (1955) pointed out that at least for *Nereis diversicolor*, ability to spread into fresher water was more related to the length of the larval stages of a particular population rather than salinity intolerance. Thus Thompson's explanation for peculiarities in the nature of Mazon Creek polychaete assemblage is perhaps needlessly complicated and not in accord with what we know about living polychaete biology.

There still remains the problem of explaining the dominance of epifaunal predator-scavenger worms in these faunas. The fact that this is so for both Mazon Creek and Bear Gulch suggests that perhaps this was a distinctive yet normal feature of the Carboniferous nearshore marine chronofauna of Laurentia. Any attempt to use preservational anomalies to explain this dominance must remain weak because both sites are Konservat-Lagerstätten (Seilacher, 1970). The circumstances of burial and fossilization mitigated to preserve the entire autochthonous fauna of those times and places

TABLE 3. Breakdown of habitat preferences of Bear Gulch worms.

Habitat	Species (%)	Specimens (%)
Epifaunal	37.5	38.2
Infaunal	12.5	12.7
Unknown	50.0	49.1

TABLE 4. Breakdown of feeding type preferences of Bear Gulch worms. Feeding types taken from Thompson (1979) and included for comparison.

Feeding type	Species (%)	Specimens (%)
Predator	62.5	58.2
Selective deposit feeder	...	...
Nonselective deposit feeder	...	...
Suspension feeder	...	...
Unknown	37.5	41.8

essentially intact. Thus the species of worms and their relative proportions in the biotas of these localities are probably fairly close to those of the original state.

The answer as to why this peculiar epifaunal predator-scavenger dominance existed in the Carboniferous nearshore marine chronofauna lies with further study and more complete understanding of the early history and origin of the nearshore marine chronofauna in the Late Devonian–Early Carboniferous. Certainly the chronofauna as such does not lack for epi- and infaunal suspension and deposit feeders. The Bear Gulch fauna has, besides some crustaceans of these types (Schram and Horner, 1978), brachiopods, pelecypods, and sponges (these last at least in the lowermost beds of the Bear Gulch Limestone). The more diverse Mazon Creek fauna has pelecypods, inarticulate brachiopods, a problematic hemichordate *Etacystis communis* (Nitecki and Schram, 1976), as well as some filter feeding crustaceans (Schram, 1979). These would have effectively augmented those few epi- and infaunal suspension and deposit feeding annelids Thompson (1979) did note.

The evidence of the overall faunal constitution and preservational nature seems to indicate that the predominance of epifaunal predaceous-scavengers in the worm contingent of the Laurentian Carboniferous nearshore marine chronofauna is a real one, distinctive to that period of time and related to the circumstances existing then.

SYSTEMATIC PALEONTOLOGY

Phylum Nemertina

Genus *Archisymplectes* Schram, 1973
Type species *Archisymplectes rhothon* Schram, 1973
Archisymplectes rhothon Schram, 1973
Fig. 1b

Material.—UM 5546, 6485; CM 33941, 33942.

Remarks.—These specimens preserve the familiar twisted and knotted form so characteristic of "ribbon worms" (Fig. 1b). As in the Mazon Creek Essex fauna species, *A. rhothon,* very little external anatomy is preserved on so relatively simple an animal as a nemertine. Conway Morris (1977*a*) agrees, however, that *A. rhothon* is probably a nemertine. Consequently, there is really very little to distinguish these Bear Gulch forms from those of Illinois, and the Montana specimens are placed in the same species of the latter. (Modern nemertine taxonomy is based on histology of the body wall and brain location, information not available in fossils.)

Phylum Nematoda

Genus *Nemavermes* Schram, 1973
Type species *Nemavermes mackeei* Schram, 1973
Nemavermes mackeei Schram, 1973
Fig. 1a

Material.—UM 5554, 5562, 5564, 5569, 5570, 5875; CM 33990, 33993 (≈9 individuals).

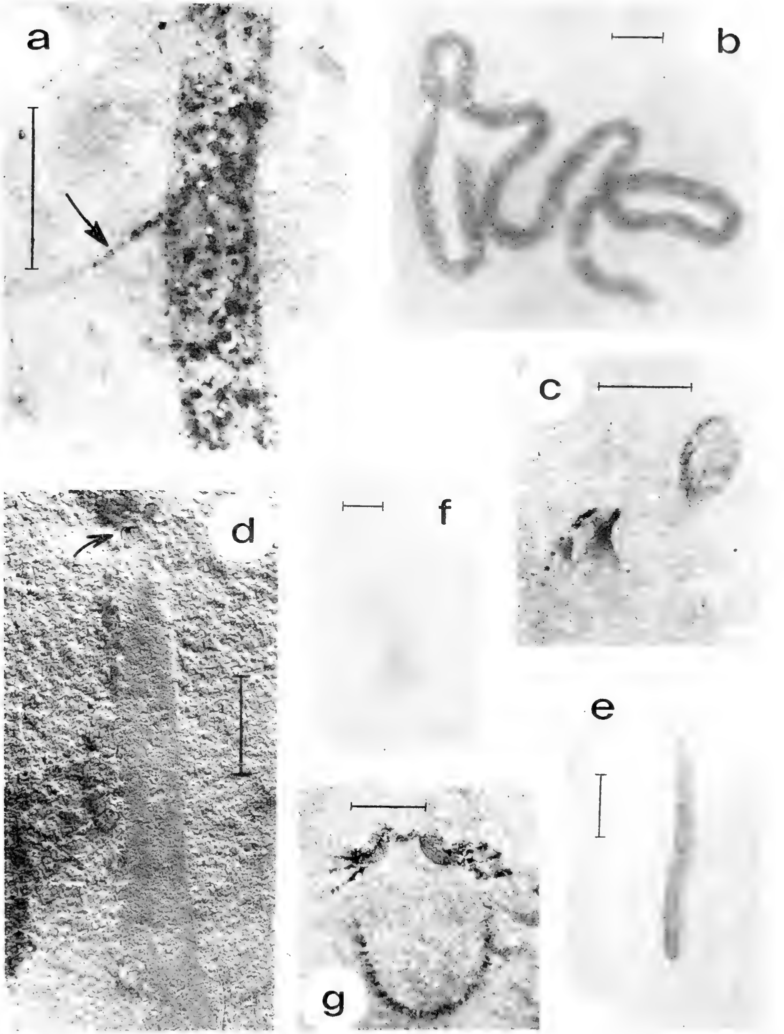

FIG. 1. a. *Nemavermes mackeei* Schram, 1973, UM 5554 with hair or seta (arrow), scale 5 mm; b. *Archisymplectes rhothon* Schram, 1973, CM 33941, scale 5 mm; c, d. *Soris labiosus* gen. et sp. nov., UM 5548, with paired jaws and lips, scale 1 mm in c, 1 cm in d (arrow indicates jaws); e. Unnamed shape resembling a nematode, scale 5 mm; f. UM 5557, unnamed shape resembling a sipunculid, scale 5 mm; g. *Carbosesostris megaliphagon* gen. et sp. nov., UM 5542, closeup of jaw apparatus, scale 1 mm.

Remarks.—Several specimens have been identified which possess a nematode-like body, and preserve fine hairs or setae-like structures (UM 5554) on the cuticle (Fig. 1a). These are virtually identical to the Essex fauna species *N. mackeei.* With so little anatomy to analyze it seems best to assign these Bear Gulch fossils to the Illinois species.

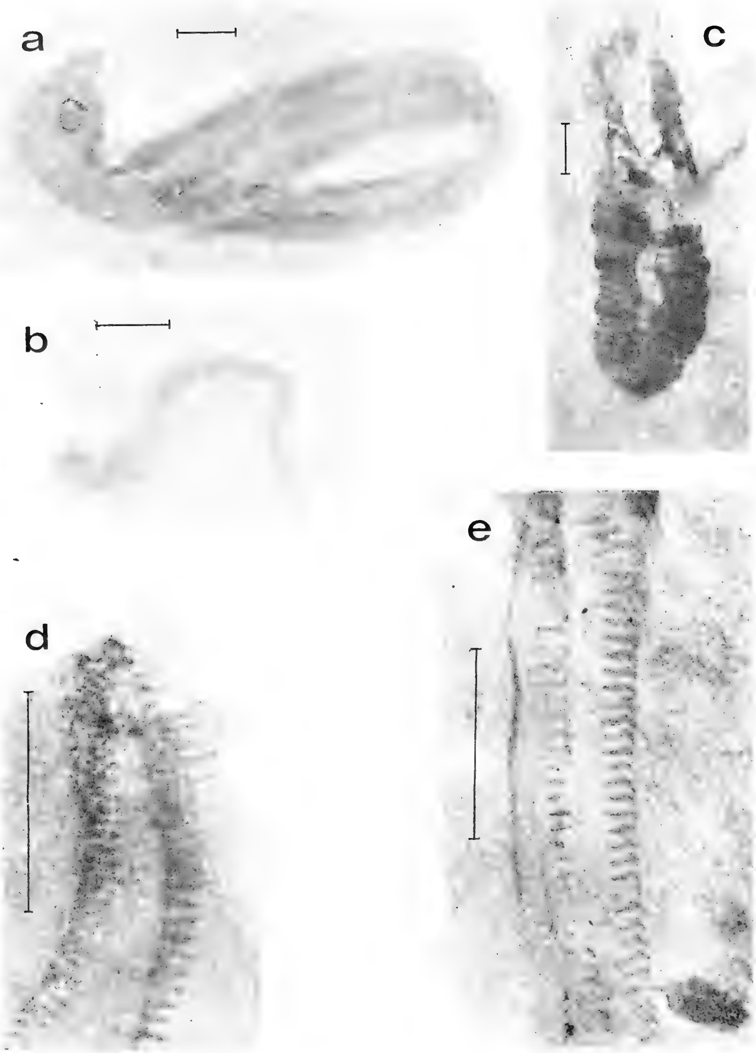

FIG. 2. a. *Carbosesostris megaliphagon*, gen. et sp. nov., UM 5542, scale 5 mm; b, c. Unnamed worms: b, CM 33939, probably polychaete, scale 5 mm, c, CM 33943, part of a segmented worm, scale 5 mm; d, e. *Ramesses magnus* gen. et sp. nov.: d, UM 5552, terminal end showing longer setae, scale 5 mm, e, UM 5553, midbody showing acicula along ventral surface, scale 5 mm.

Phylum Annelida
Class Polychaeta
Order Pyllodocida
Family Goniadidae
Genus *Carbosesostris* gen. nov.

Diagnosis.—The diagnosis of the genus is the same as that of the species.

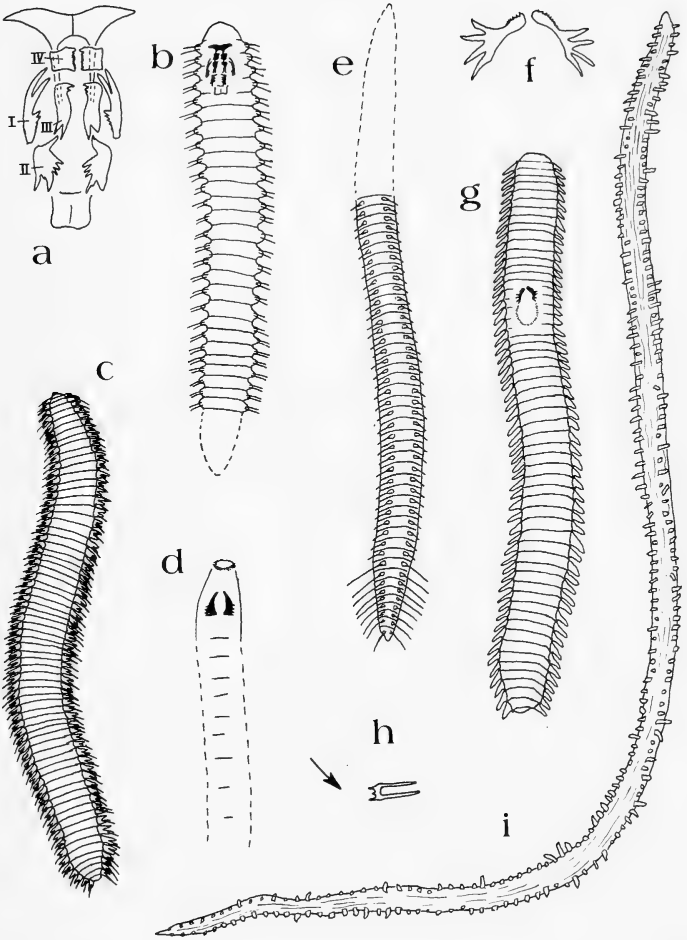

FIG. 3. Reconstruction of Bear Gulch worms. a. Jaw apparatus of *Phiops aciculorum*, with maxillae numbered; b. *Phiops aciculorum*; c. *Astreptoscolex anasillosus*; d. *Soris labiosus*; e. *Ramesses magnus*; f. Paired macrognaths of *Carbosesostris megaliphagon*; g. *Carbosesostris megaliphagon*; h. A micrognath element of *Carbosesostris megaliphagon*, arrow indicating inner edge of ring; i. *Deuteronectanebos papillorum*.

Etymology.—Name derived from the age of the fossils and after a series of XIIth dynasty pharoahs from the Greek kings list of the Ptolemaic historian, Manetho.

Carbosesostris megaliphagon sp. nov.
Fig. 1g; Fig. 2a; Fig. 3f, g, h

Diagnosis.—One pair of complex macrognaths; 30–40 "H"-shaped micrognaths in a ring; body long with apparently uniramous parapodia without acicula.

Holotype.—UM 5542 (Fig. 2a).

Type locality.—As described in the INTRODUCTION.

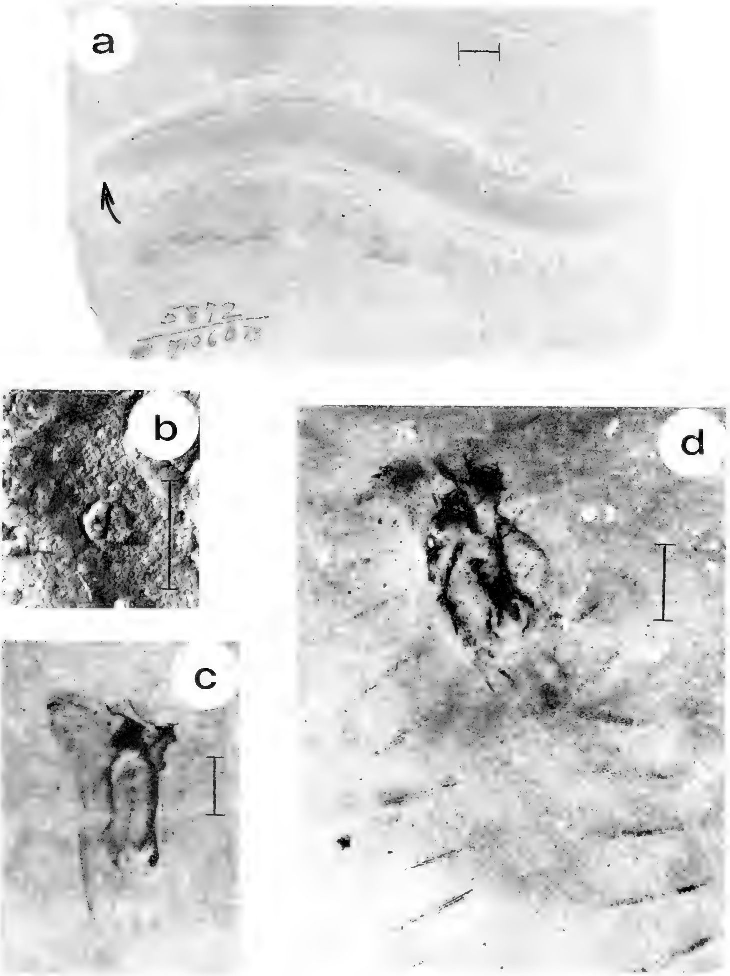

FIG. 4. a, b. *Astreptoscolex anasillosus* UM 5872, scale 5 mm in a, scale 1 mm in b; c, d. *Phiops aciculorum* gen. et sp. nov., UM 5543: c, CM 33945, closeup of jaw apparatus, scale 1 mm, d, head end with jaw apparatus and anterior acicula, scale 1 mm.

Etymology.—A reference to the magnificent jaw apparatus.

Material.—UM 5542, 5871, 6355 (3 individuals); CM 33988, 33989.

Description.—The macrognaths are 1–2 mm long and composed of 2 portions (Fig. 3f); a posterior region with 4 large denticles widely spaced in a fan-like arrangement, and an anterior region composed of a serrate blade (best preserved on UM 5542 [Fig. 1g] and UM 5871). The micrognaths number 30 to 40 and are arranged in an open ring posterior to the macrognaths. The micrognaths (Fig. 3h) are "H"-shaped, with the uprights facing the outside of the ring very long making the individual elements almost "U"-shaped; the crossbar of the "H" has an inwardly directed spine. The body of the animal is between 6 to 9 cm long, clearly segmented, and adorned with apparently simple uniramous, short parapodia (UM 6355) with no setae or acicula visible. The segments occur at a rate of 8 every 10 cm.

Remarks.—*Carbosesostris megaliphagon* is the most abundant of the Bear Gulch polychaetes and is related to a known living group. A large macrognath and the micrognath ring place it in the family Goniadidae. Thompson (1979) described a goniadid, *Pieckonia helenae,* which possessed a distinctive set of "chair-shaped" micrognaths, with 2 pronged roots and 4 pronged teeth, and no macrognaths. The distinctive differences in micrognaths between *P. helenae* and *C. megaliphagon,* and the presence of macrognaths in the latter, justify the erection of a separate genus and species for the Bear Gulch material. A reconstruction of *Carbosesostris megaliphagon* is offered in Fig. 3g.

Family Nephtyidae
Genus *Astreptoscolex* Thompson, 1979
Type species *Astreptoscolex anasillosus* Thompson, 1979
Astreptoscolex anasillosus Thompson, 1979
Fig. 4a, b; Fig. 3c

Material.—UM 5872, 5874, 5876.

Remarks.—The species is rare in the fauna and only 2 specimens have been definitively assigned to the species (UM 5872 and 5876) along with a questionable third (UM 5874). The body is large and fleshy (UM 5872 is just over 9 cm long and ≈1 cm at its widest, with about 74 segments). The segments are all well demarcated and possess large biramous parapodia. Several of the parapodia bear acicula which appear to have been somewhat flexible because some of them are bowed or curved. The anterior end of the animal is blunt and the posterior end somewhat tapered. Both good specimens have some organic remains which mark the gut and UM 5872 has pellets in the gut. UM 5872 also has what appear to be molds of a small set of jaws (Fig. 4b).

Although *Astreptoscolex* is the best preserved of the Bear Gulch polychaetes, the assignment to the family Nephtyidae must retain some query. The general form of the body and the apparent presence of a simple jaw apparatus suggests this family, but lack of better preservation of the prostomium, palp, and tentacle structures makes the family assignment less secure than I would like. The only other family this body form might suggest would be the Nereidae, but the nereids have paragnaths and large jaws in the proboscis. A reconstruction of the Bear Gulch *Astreptoscolex* is offered in Fig. 3c and closely resembles that of Thompson (1979).

Order Eunicida
Family Lumbrinereidae
Genus **Phiops** gen. nov.

Diagnosis.—The diagnosis of the genus is the same as that of the species.

Etymology.—Named after the VIth dynasty pharaoh, Pepi II, from the Greek kings list of the Ptolemaic historian, Manetho.

Phiops aciculorum sp. nov.
Fig. 3a, b; Fig. 4c, d; Fig. 5a

Diagnosis.—Complex jaw apparatus with mandible and at least 4 pairs of maxillae on each side; mandible with pointed lateral wing; maxilla I (forceps) anteriorly developed as 2 large denticles, maxillae II–IV multidentate through most of their lengths; large acicula on parapodia.

Holotype.—UM 5543 (Fig. 4d).

Type locality.—As described in the INTRODUCTION.

Etymology.—A reference to the prominent acicula.

Material.—UM 5543, 5873; CM 33944, 33945.

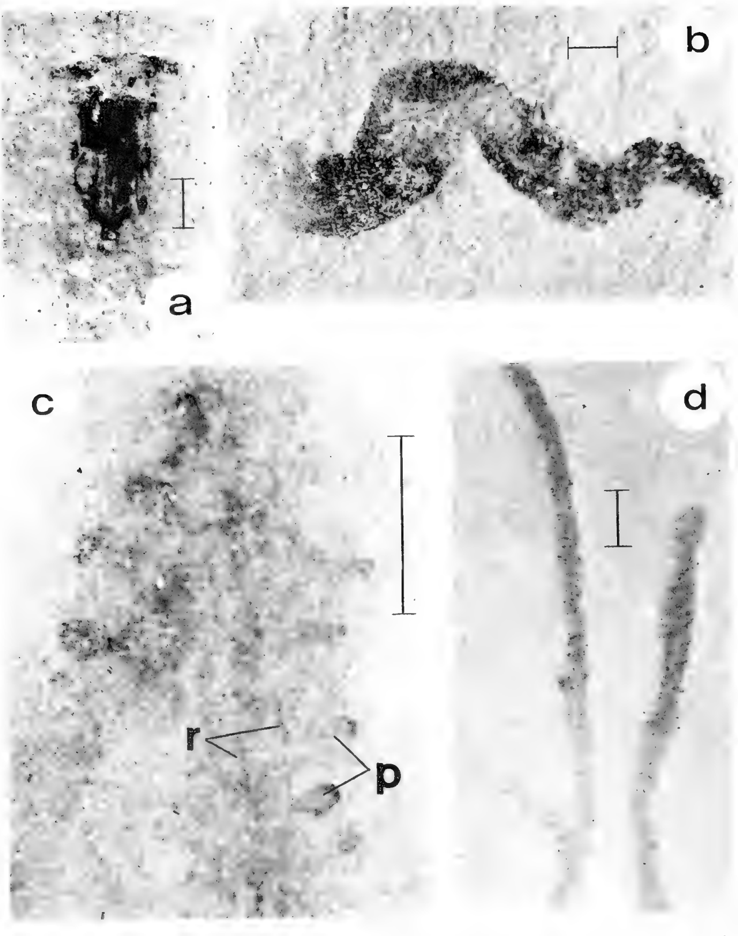

FIG. 5. a. *Phiops aciculorum*, CM 33945, closeup of jaw apparatus, scale 1 mm; b. Unnamed shape resembling a nematode, UM 5556, scale 1 mm; c, d. *Deuteronectanebos papillorum*, gen. et sp. nov., UM 5545: c, (r) longitudinal striations, (p) papillations, scale 5 mm, d, worm doubled back on itself off the edge of the slab, scale 5 mm.

Description.—The best specimen, UM 5543, has the jaw apparatus moderately well preserved on the left side, but somewhat less so on the right (Fig. 4d). CM 33944 and CM 33945 also preserve almost complete sets of jaws. The mandibles are fan-shaped, markedly pointed laterally (Fig. 5a), and appear to have been fused at the midline. There are at least 4 pairs of maxillae. Maxilla I (forceps) has 2 long denticles directed anteriorly from a serrated posterior region. Maxilla II has several large denticles in a fan-like arrangement with the denticles at either end of the series distinct from the center 5 (Fig. 4d). Maxilla III is developed as a long sigmoid blade with serrations on the anterior end (Fig. 4c). Maxilla IV is square-shaped with a serrated cutting margin (Fig. 4c, d). The carriers, though not well preserved, are short and broad (Fig. 3a).

The acicula are large and thick with longitudinal striations. There appear to have been 2 per parapodium. The parapodia themselves were lobate (UM 5873). The holotype (UM 5543) has at least 27 segments preserved, but the animal is missing the posterior end.

Remarks.—The complex jaw apparatus clearly marks *Phiops* as a eunicidan. The short carriers and paired elements along the whole series indicate a lumbrinereid. Eunicids have asymmetrical maxillae; arabellids and lysaretids would have long slender carriers; and dorvilleids would have the maxillary elements developed as numerous pieces in a long series. The serration pattern on the jaw elements of *Phiops* is clearly unlike anything Kielan-Jawarowska (1966) describes in her monographic treatment of intact jaw apparatuses.

A partial reconstruction of *Phiops aciculorum* is given in Fig. 3b.

Order *incerta sedis*

Genus ***Soris*** gen. nov.

Diagnosis.—The diagnosis of the genus is the same as that of the species.

Etymology.—Named after the founder of the IVth dynasty, Pharaoh Snofru, as taken from the Greek kings list of the Ptolemaic historian, Manetho.

Soris labiosus sp. nov.

Fig. 1c, d; Fig. 3d

Diagnosis.—Jaw a narrow falx; no denticles on the inner margin; some indication of faint serrations on the outer margin; prominent lips.

Holotype.—UM 5548 (Fig. 1c, d).

Type locality.—As described in the INTRODUCTION.

Material.—UM 5548, 5549.

Description.—The jaws on the holotype are ≈1 mm long and what has been preserved of the body is ≈5 cm (posterior end missing). The jaws are simple scimitars, having a single narrow falx arising from a nondenticulated base. There is some slight indication that the outer margin of the jaws may have been serrate. Anterior to the jaws on UM 5548 is a dark ring (possibly the remnants of the lips of the proboscis). The ring does not display any structure under high power, thus suggesting it represents preservation of dense organic tissue rather than any ring of jaw elements.

The body itself is only incompletely preserved on the holotype and hardly at all on UM 5549. The posterior terminus is missing. No parapodia can be seen. Only faintly delineated somite boundaries can be discerned.

Remarks.—Sufficient soft anatomy has not been preserved in *Soris* to be able to refer it to an order. The jaws alone are not sufficient to do so. There is some slight resemblance of the jaws of *S. labiosus* to the scolecodont genera *Glycerites* Hinde, 1879, and *Paraglycerites* and *Paranereites* Eisenack, 1939. But the relatively straight posterior margin and the apparent lack of a prominent myocoel opening at the base serves to separate *Soris* from these other genera.

Conway Morris (personal communication) has noted a *Soris*-like jaw in the gut of one of the "conodont-eating" animals.

A partial reconstruction of *Soris labiosus* is offered in Fig. 3d.

Genus ***Ramesses*** gen. nov.

Diagnosis.—The diagnosis of the genus is the same as that of the species.

Etymology.—Named after the series of XIXth and XXth dynasty pharaohs.

Ramesses magnus sp. nov.

Fig. 2d, e; Fig. 3f

Diagnosis.—Short body segments; short, stout parapodia with thick short acicula; terminus of body with parapodia armed with thick long setae.

Holotype.—UM 5552 (Fig. 2d).

Type locality.—As described in the INTRODUCTION.

Etymology.—After the great XIXth dynasty pharaoh, Ramesses II.

Material.—UM 5550–5553, 5560, 5877.

Description.—The body is very long and narrow. But the length is indeterminate since only one specimen (UM 5877) is anything approaching a complete animal, the two termini poorly preserved on one counterpart and only one preserved at all on the other. The body is composed of short somites (UM 5552) with the aciculate parapodia located along one surface (UM 5553; Fig. 2e). The aciculae are single, stout, and short. At one terminus (possibly the posterior), the last 8 to 10 segments have parapodia with long setae.

Remarks.—All the specimens at hand are best studied under water to bring out the details of preservation.

In some respects, the body form of *Ramesses*, with its short segments and short, stout parapods along one surface is similar in some respects to the modern polychaete family Orbiniidae. But without better information about the terminal ends, a definitive placement of *Ramesses* within a family cannot be undertaken.

A partial reconstruction of *Ramesses magnus* is offered in Fig. 3e.

Phylum uncertain
Genus *Deuteronectanebos* gen. nov.

Diagnosis.—The diagnosis of the genus is the same as that of the species.

Etymology.—Named after the XXXth dynasty and last native pharaoh, Nectanebo II, from the Greek kings list of the Ptolemaic historian, Manetho.

Deuteronectanebos papillorum sp. nov.
Fig. 5c, d; Fig. 3i

Diagnosis.—Body long and narrow; cuticle marked with faint longitudinal striations and prominent papillations.

Holotype.—UM 5545 (Fig. 5d).

Type locality.—As described in the INTRODUCTION.

Etymology.—A reference to the prominent papillae.

Material.—UM 5544–5546, 5561, 5819.

Description.—The specimens at hand range from 4 to 25 cm in length. The body is marked along its length by prominent papillations (Fig. 5c). In addition, longitudinal striations are noted and are best preserved on UM 5545. The body is narrow and tapered at what appears to be its posterior end. No jaws, cirri, or palps are noted on any of the specimens.

Remarks.—Though the diagnostic papillated and striated surface of *Deuteronectanebos* is very striking, the assignment to phylum must be uncertain. The order Capitellida in the annelids is suggested by the resemblance of *Deuteronectanebos* to certain living forms as illustrated by Hartman (1947). But the similarity is inconclusive.

The possibility of this rather nondescript species not being animal has been considered. A possible algal affinity is suggested, but Dr. Matthew Nitecki, Field Museum, examined the specimens and concluded (personal communication) they were not algal.

Genera and species uncertain

Several specimens were found in the Bear Gulch material which should not be named because of their poor preservation and paucity of material. Some of the more intriguing specimens are illustrated here. One can only speculate as to what they might be: e.g., UM 5557 (Fig. 1f) suggests the form of a sipunculid; CM 33939 (Fig. 2b) is obviously some type of polychaete; and CM 33943 (Fig. 1e) may be some type of segmented worm. UM 5555 (Plate 1, Fig. 5) and UM 5556 (Fig. 5b) resemble nematodes and may be synonymous with *Nemavermes*. In addition, there are numerous specimens which can only be characterized as "vermoid." The material itself is such poor quality, however, that one cannot really be sure whether some of these are real organic remains or just some preservational or sedimentary artifacts.

ACKNOWLEDGMENTS

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A revision of the subfamily Syneurycopinae (Isopoda: Asellota: Eurycopidae) with a new genus and species (*Bellibos buzwilsoni*)

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Abstract. To date, the subfamily Syneurycopinae has accommodated a single genus, *Syneurycope,* and 8 morphologically diverse species. The present taxonomic revision of the subfamily synonymizes 3 of these species, creates a new genus with 2 subgenera, *Bellibos* (*Bellibos*) and *B.* (*Bemerria*), and describes one new species, *Bellibos* (*Bellibos*) *buzwilsoni.* A key to the subfamily is provided. Size-frequency and meristic variability data are provided for a particularly well-sampled species, *B. buzwilsoni.* Biogeographic information is presented, based on material collected from all regions of the Atlantic Ocean. Those species that are known from more than one locality have widespread distributions.

INTRODUCTION

The Eurycopidae is one of the largest and most abundant families of deep-sea isopods. As with the other large families, its systematics badly needs revision. The diagnostic features of most of its higher taxa are unclear, likely synonymies go unattended, and a few genera tend to be made the repository for most new species, even though these species represent a range of morphologies well in excess of what a meaningful genus should contain. The present paper is the first of a series whose purpose is to revise the family in a useful way. We begin here with the Syneurycopinae, one of the smaller and more circumscribed of the 4 eurycopid subfamilies.

The genus *Syneurycope* was established by Hansen (1916) as one of a cluster of genera in his Group Eurycopini; *Syneurycope* contained a single species, *Syneurycope parallela.* Barnard (1920) erected a new genus and species, *Ilycthonos capensis,* and included it in an entirely different taxon, the Desmosomatidae (Wolff, 1962), although at the time Barnard recognized that the genus was ". . . perhaps congeneric with *Syneurycope* Hansen, 1916." Menzies (1956) synonymized *Ilychthonos* with *Syneurycope,* retaining the species as *Syneurycope capensis.* He established the family Eurycopidae, including *Syneurycope* as one of 4 genera, and described a new species, *Syneurycope hanseni.* Later, Menzies (1962) described 2 more species, *Syneurycope heezeni* and *Syneurycope multispina.* In his general revision of the Paraselloidea, Wolff (1962) divided the Eurycopidae into 4 subfamilies, including the monogeneric Syneurycopinae. In 1970, Birstein described *Syneurycope affinis.* Most recently, Chardy (1975) added 2 species: *Syneurycope dageti* and *Syneurycope monicae.*

Taken together, this collection of species encompasses a broad range of morphologies. The trunk may be dorsoventrally flattened or strongly vaulted. The cephalon may or may not bear large horns or other distinctive sculpturing. The first pereonite may be fused to the cephalon, or it may be free; it can be equal in size to the other anterior pereonites or much larger. The natasome (Hessler and Thistle, 1975) varies markedly in size relative to the ambulosome. The pleotelson is complexly contoured in some species, simple in others. Accepting the criterion that members of a genus should look much alike, this suite of species, although related, clearly should be considered representatives of more than one genus. In this paper we have defined two genera: a restricted *Syneurycope* Hansen, 1916, and a new genus, *Bellibos*. The extent of morphological similarity of congeners in each of the two resulting genera is somewhat different. The existence of more than one species in *Syneurycope* is well founded, with differences of the same order seen in genera of other deep-sea isopod families. However, *Bellibos* species encompass a wider range of morphologies than usual; we have therefore split them into 2 natural groupings which we diagnose as the new subgenera, *Bellibos* and *Bemerria*.

We have examined the available types of every published species except for the single Pacific species, *Syneurycope affinis* Birstein, 1970. It became obvious that the independence of *S. capensis* and *S. hanseni* from *S. parallela* could not be supported, and they are synonymized herein. The types of *B. dageti* and *B. monicae* have apparently been lost in the mail between Brest and Paris, France, en route to the National Museum of Natural History (M. M. Forest and P. Chardy, *personal communication*). We describe specimens from our collection that we have tentatively assigned to these 2 species; although our specimens differ from Chardy's descriptions of *B. monicae* and *B. dageti* in a few potentially diagnostic characters, there remains insufficient evidence to describe them as new species. The type-material of *B. multispina* stands as the only collected specimens of this unique species. A new species (*Bellibos buzwilsoni*) is described here which is quite unlike anything seen before. As redefined in this paper then, the Syneurycopinae contains 2 genera, 2 subgenera, and 7 species.

In spite of the morphological breadth of the Syneurycopinae, the subfamily is a strong natural unit. Its diagnosis contains a number of unusual and seemingly unrelated features: the fusion of pereonites 5–7, the absence of maxillipedal coupling hooks, the presence of medial denticles on the third article of the maxillipedal palp, the short branchial chamber, and the apical cleft of the female operculum.

The syneurycopine species most similar to other eurycopids is *B. buzwilsoni*. Compared to other members of the subfamily, it has the broadest, deepest body; the first pereonite is unspecialized and articulates freely with the cephalon; its natasome is the largest, relative to body size; its swimming pereopods (pereopods V–VII) have broad carpi and propodi; the pleotelson shape is simple; and the uropodal rami are both well developed. In general body shape, *B. buzwilsoni* is reminiscent of *Betamorpha* Hessler and Thistle (1975).

Syneurycope parallela is certainly the most specialized species, as seen in its slender body, the complete fusion of pereonite 1 and the cephalon, its short natasome, slender pereopods V–VII, complexly contoured pleotelson, and reduced uropodal exopod. *Bellibos buzwilsoni* and *Syneurycope parallela* bracket most of the morphological variation in the Syneurycopinae. The unique inflated cephalon of *B. multispina* and expanded pereonite 1 of *B. monicae* are the major exceptions to this.

Basically, the syneurycopine species are pan-Atlantic. The distributional map (Fig. 1) shows some gaps in this pattern which may be a result of unequal sampling effort. Only *Bellibos multispina* is restricted to a single station. *Syneurycope heezeni* and *Bellibos dageti* are restricted to the South and North Atlantic, respectively. The other species exhibit impressive horizontal distributional ranges. Although this is not atypical for a family or even a genus, it is unusual for most species of a subfamily to be known to range so widely. The existence of *Syneurycope affinis* extends the distribution of the Syneurycopinae to the Pacific Ocean as well.

The depth distribution is basically abyssal with most species occurring over a range of ≈2000 metres. The major exceptions to this scheme are *B. multispina* and *S. affinis*, known from but a single station, and *S. parallela*, which is very wide-ranging (from 1280 to 5122 metres, a range of nearly 4000 metres).

Materials.—The Woods Hole Oceanographic Institution deep-sea sampling program is the source for most of the material used in this study. This program has sampled, with an epibenthic sled, a series of transects originating on the continental shelf and running out to the abyssal plain. These transects are located off the north-

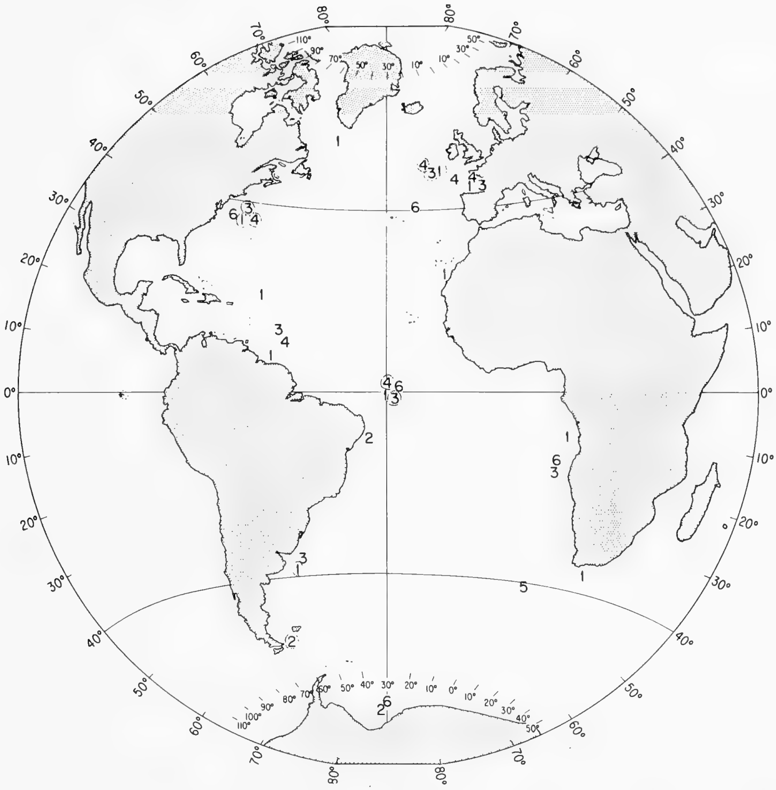

FIGURE 1. Geographical distribution of syneurycopine species in the Atlantic Ocean. Species are symbolized by numbers: 1, *Syneurycope parallela*; 2, *Syneurycope heezeni*; 3, *Bellibos buzwilsoni*; 4, *Bellibos dageti*; 5, *Bellibos multispina*; 6, *Bellibos monicae*. Each number locates a single station except where circled; circled numbers indicate approximate location of a cluster of 2 or more closely spaced stations (*see* **Table 1** for complete listing of station data).

eastern United States (Gay Head–Bermuda transect), Surinam, northern Brazil, Argentina, Namibia, Angola, Senegal, and Ireland. Additional isopod material comes from the Bay of Biscay (J. Allen, University of Newcastle-upon-Tyne), the Canary Islands (J. Allen), and the Weddell Sea (J. Rankin, University of Connecticut). Station data are given in Table 1.

Newly assigned type-specimens are deposited in the United States National Museum (USNM), Washington, D.C. Paratypes and/or additional material are also deposited in the Zoological Museum, University of Copenhagen (ZMUC), Copenhagen, Denmark. The remaining material resides in the second author's working collection at Scripps Institution of Oceanography (SIO), La Jolla, California, but will ultimately be deposited in the USNM.

Methods.—The methods used to collect and treat the samples, and to preserve the animals have been previously described (Sanders et al., 1965; Hessler and Sanders, 1967; Hessler, 1970).

TABLE 1. Station data for the Syneurycopinae of the present study. Species found at each station are listed by number: *1, Syneurycope parallela; 2, Syneurycope heezeni; 3, Bellibos buzwilsoni; 4, Bellibos dageti; 5, Bellibos multispina; 6, Bellibos monicae.* Source abbreviations: Woods Hole Oceanographic Institution (WHOI); Lamont Geological Observatory (LGO); John A. Allen (JA); J. S. Rankin/United States Coast Guard Cutter Glacier (R); Pieter Faure (PF); Danish Ingolf Expedition (IE); Biogas IV/RV Jean Charcot (BIV); Biacores/RV Jean Charcot (B).

Source	Station	Latitude	Longitude	Depth (m)	Species
WHOI	62	39°26.0′N	70°33.0′W	2496	*1*
	63	38°46.8′N	70°05.7′W	2891	*1*
	64	38°46.0′N	70°06.0′W	2886	*1, 3*
	66	38°46.7′N	70°08.8′W	2802	*1, 3*
	71	38°08.0′N	71°47.5′W	2946	*4*
	72	38°16.0′N	71°47.0′W	2864	*1, 6*
	76	39°38.3′N	67°57.8′W	2862	*1*
	100	33°56.8′N	65°47.0′W	4743–4892	*4*
	103	39°43.6′N	70°37.4′W	2022	*1*
	126	39°37.0′N	66°47.0′W	3806	*1, 4*
	131	36°28.9′N	67°58.2′W	2178	*1*
	155	00°03.0′S	27°48.0′W	3730–3783	*3, 4*
	156	00°46.0′S	29°28.0′W	3459	*1, 3, 4, 6*
	195	14°40.0′S	09°54.0′E	3797	*3, 6*
	200	09°41.0′S to 09°43.5′S	10°55.0′E to 10°57.0′E	2644–2754	*1*
	242	38°16.9′S	51°56.1′W	4382–4402	*1*
	245A	36°55.7′S	53°01.4′W	2707	*1, 3*
	256	37°40.9′S	52°19.3′W	3906–3917	*1*
	287	13°16.0′N	54°52.2′W	4934–4980	*3*
	288	11°02.2′N	55°05.5′W	4417–4429	*4*
	303	08°28.8′N	56°04.5′W	2842–2853	*1*
	313	51°32.2′N	12°35.9′W	1491–1500	*1*
	321	50°12.3′N	13°35.8′W	2868–2890	*1, 3*
	323	50°08.3′N	13°50.9′W to 13°53.7°W	3338–3356	*1*
	326	50°04.9′N to 50°05.3′N	14°23.8′W to 14°24.8′W	3859	*1*
	328	50°04.7′N	15°44.8′W	4426–4435	*1, 3, 4*
	330	50°43.4′N	17°52.0′W	4632	*3, 4*
LGO	I	20°32.2′N	60°28.1′W	4941–4959	*1*
	52	41°03.0′S	07°49.0′E	4960	*5*
	200	55°42.9′S	64°21.6′W	3813	*2*
	201	55°31.2′S	64°07.5′W	3839	*2*
	220	09°45.0′S	34°24.0′W	3222–3336	*2*
JA	50	43°46.7′N	03°38.0′W	2379	*1, 3, 4*
	6711	27°14.9′N	15°36.3′W	2988	*1*
R	1969/21 ES	73°52.0′S	31°18.0′W	2288	*2*
	1969/23 ES	72°47.6′S	30°29.7′W	3697	*6*
PF	"Cape Point North 89° East, distant 36 miles [≈58 km]"			1281	*1*
IE	22	58°10.0′N	48°25.0′W	3376	*1*
BIV	2	47°31.0′N	09°09.7′W	2835	*4*
B	245	40°57.0′N	22°16.0′W	4270	*6*

The illustrations were made using a compound microscope equipped with a camera lucida. Measurements were obtained from the drawings. Total body length was measured dorsally from the anterior edge of the cephalon to the posterior tip of the pleotelson, along the midsagittal line. Cephalon and pereonite length were also measured midsagittally; pereonite width was measured transversely at the greatest tergal span. The length of various antennal articles and podomeres was measured along the longest axis; the width was measured perpendicular to the length at the widest span. Uropodal ramal length included that part of the ramus which is embedded in the protopod.

Length:width ratios (hereafter abbreviated l/w) were obtained from these measurements. The reader should be cautioned that the morphological measurements and meristic counts cited in this paper were obtained from a single specimen unless a range of variation is given.

The various types of setae are defined and illustrated in Hessler (1970). "Natasome" refers to pereonites 5–7, pleonite 1 and the pleotelson along with the corresponding appendages (Hessler and Thistle, 1975). The female second pleopod is termed the operculum and frequently possesses a ventral, midsagittal ridge referred to as the "keel." The pleotelson is described as "complexly contoured" when it no longer has a simple undifferentiated shape with gently tapering sides, but exhibits well-defined surface topography with abrupt discontinuities in pleotelson width.

Descriptions and illustrations are based on previously undescribed material from the second author's working collection unless otherwise noted. The identity of these specimens was confirmed by direct comparison with the corresponding holotype. Specific mention is made wherever our material is known to differ from the type-material. The following type-material was examined for this study: (1) American Museum of Natural History, New York: *Syneurycope hanseni* Menzies, 1956, holotype; *Syneurycope heezeni* Menzies, 1962, holotype, paratype and additional material; *Syneurycope multispina* Menzies, 1962, holotype, allotype and paratype. (2) South African Museum, Cape Town: *Syneurycope capensis* (Barnard, 1920), syntypes. (3) Zoological Museum, University of Copenhagen, Denmark: *Syneurycope parallela* Hansen, 1916, holotype.

SYSTEMATICS

Syneurycopinae Wolff, 1962

Diagnosis.—Eurycopidae with elongate body, l/w >3.0. Pereonites 5–7 fused. Antenna I positioned terminally on cephalon, first article subcylindrical. Maxillipeds lack coupling hooks, may be fused in part; third article of palp with medial denticles; epipod large. Branchial chamber and operculum short with respect to length of pleotelson; ♀ pleopod II (operculum) apically cleft. Uropods biramous, flattened.

Syneurycope Hansen, 1916

Figures 2–6

Synonymy.—*Syneurycope* Hansen, 1916, pp. 130–131; Menzies, 1956, pp. 5–6; Menzies, 1962, pp. 150–151; Wolff, 1962, pp. 108–109, 116–117. *Ilychthonos* Barnard, 1920, pp. 414–415.

Type-species.—*Syneurycope parallela* Hansen, 1916, pp. 131–132, Pl. XII, Figs. 4a–4o.

Distribution.—Eastern and western Atlantic Ocean, 58°10′N to 73°52′S, 1280–5122 m. Northwestern Pacific Ocean, 44°48′N, 5005–5045 m.

Diagnosis.—Syneurycopinae with body l/w always >4.0. Combined length pereonites 1–4 always > pereonites 5–7. Cephalic spines absent; medial dorsal surface cephalon raised; cephalon fused to first pereonite. Pleotelson complexly contoured. Antenna I, ♀ flagellum a single article. Pereopod V carpus slender where known; l/w >2.5. Female operculum widest in proximal half, tapering distally; median keel poorly developed. Pleopod I, adult ♂ with outer ramus of distal end unusually elongate, equal in length to that of inner ramus, where known. Pleopod II, adult ♂ with distal tip of protopod elongate, extending distally far beyond exopod, where known. Uropod with strongly reduced exopod bearing 1 or 2 large, apical setae; length exopod ⅓ or less length endopod.

Additional description.—The characteristically elongate pereopods III and IV of *Syneurycope parallela* are now known for *S. heezeni* also. The merus, carpus, propodus, and dactylus are all greatly elongated, with carpus l/w > 10 and propodus l/w

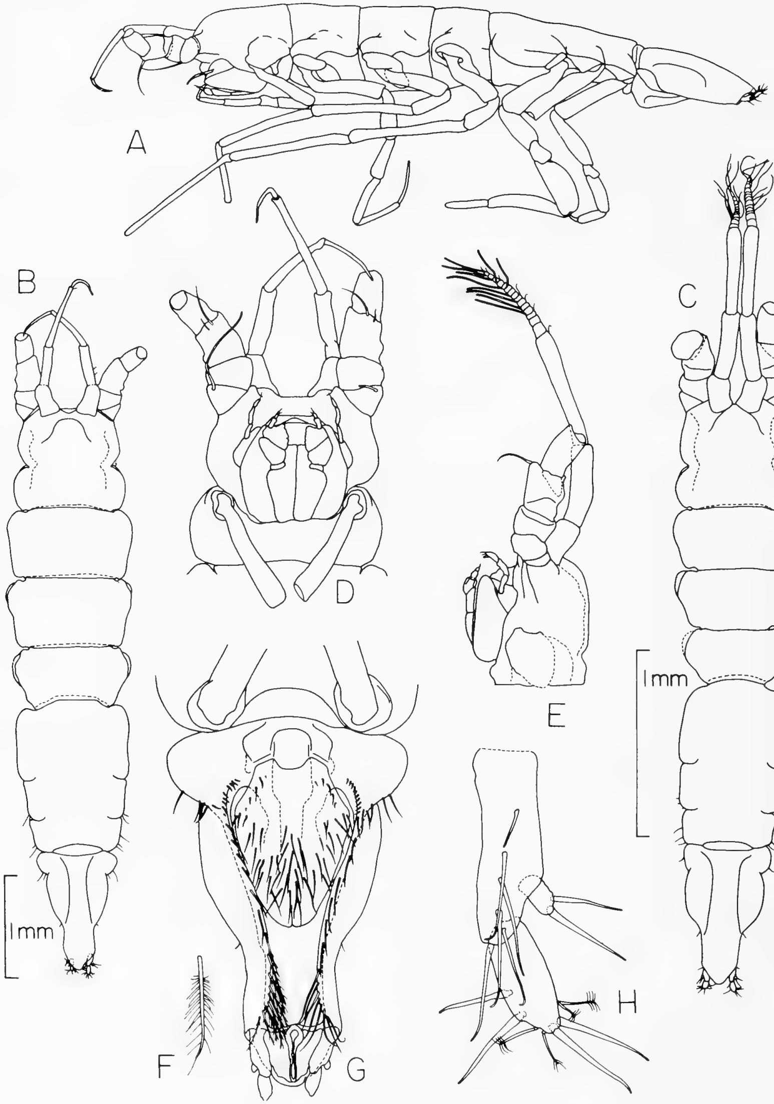

FIGURE 2. *Syneurycope parallela* preparatory ♀, WHOI 131: A. body, lateral view, setae omitted; B. body, dorsal view; D. cephalon-pereonite 1, ventral view; F. plumose seta, enlarged view, typical of setae on operculum and posterior medial margins of pleotelson; G. pleotelson, ventral view, setae omitted from uropod and edge of operculum; H. left uropod, ventral view, *in situ*. Male, WHOI 131: C. body, dorsal view; E. cephalon-pereonite 1, lateral view, pereopod I missing.

>20. This character is not diagnostic of *Syneurycope* because it remains unknown for most other syneurycopine species; it is likely to be diagnostic of the subfamily.

Remarks.—*Syneurycope* species are readily identifiable by the elongate body, the fusion of cephalon and first pereonite, the absence of cephalic horns, and the short uropodal exopod. One other syneurycopine species, *Bellibos monicae*, shares the general body proportions of *Syneurycope*; however, other features clearly differentiate it from this genus.

Hansen's original generic description is accurate only for the single species on which it was based, *Syneurycope parallela*. None of the later treatments of the genus are concise; they include specific and familial characters.

The genus has previously been made recipient of 8 species: *Syneurycope parallela* Hansen, *S. capensis* (Barnard), *S. hanseni* Menzies, *S. heezeni* Menzies, *S. affinis* Birstein, *S. multipsina* Menzies, *S. dageti* Chardy, and *S. monicae* Chardy. The present revision synonymizes the first 3 species with *S. parallela* and removes the last 3 species to a new genus. This leaves *Syneurycope* with 3 species: *S. parallela*, *S. heezeni* and *S. affinis*.

Syneurycope parallela Hansen, 1916

Figures 2–3

Synonymy.—*Syneurycope parallela* Hansen, 1916, pp. 131–132, Pl. XII, Figs. 4a–4o; Menzies, 1962, pp. 150–151, Fig. 41F; Wolff, 1962, pp. 116–117. *Ilychthonos capensis* Barnard, 1920, pp. 415–416, Pl. XVII, Figs. 14–16. *Syneurycope capensis* Menzies, 1956, pp. 5–6. *Syneurycope hanseni* Menzies, 1956, p. 6, Fig. 2.

Holotype.—Ingolf Station 22 (58°10′N, 48°25′W); ZMUC, ♂, 3.7 mm. Specimen in excellent condition; left maxilliped and left mandible dissected off, former lost and latter mounted on slide.

Other material.—*Syneurycope capensis* syntypes: "Cape Point North 89°E, distant 36 miles" (Barnard, 1920), SAM A4030. Subadult ♀ without uropods. Preparatory ♀ with single uropod, no pleopods. Badly damaged ♂, pleopods I present, no uropods. Fragment: cephalon and anterior 7 pereonites, pereopod I present. Fragment: pleotelson with uropod. Fragment: middle 6 pereonites, pereopod II present but detached. *Syneurycope hanseni* holotype: tropical Atlantic (20°32.2′N, 60°28.1′W), AMNH 11758, ♂, 3.8 mm. Specimen in very poor condition, flattened and badly decalcified. Absent limbs include: antennae II, maxilliped, and pereopods II, III, and IV. No additional material. Present collection: WHOI stations 62 (1 individual); 63 (2); 64 (17); 72 (1); 76 (5); 103 (5); 126 (1); 131 (60); 156 (5); 200 (1); 242 (6); 245A 20% fraction (26); 256 (7); 313 (8); 321 (83); 232 (7); 326 (4); 328 (2). John Allen stations 48 (1); 50 (199); 6711 (1). Illustrated preparatory ♀ and copulatory ♂ (WHOI 131) deposited at ZMUC. Copulatory ♂ (WHOI 103), copulatory ♂ (WHOI 62), preparatory ♀ (WHOI 66) and brooding ♀ (WHOI 131) USNM catalog nos. 173001, 173003, 173002, 173000, respectively.

Distribution.—Eastern and western Atlantic Ocean, 58°10′N to 38°17′S, 1280 to 5122 m.

Diagnosis.—*Syneurycope* with narrow body; body length preparatory female 4.4–4.6× tergal width of pereonite 2; not fringed laterally with numerous simple setae. Pleotelson with pair of strongly flaring, proximal ventral flanges, paired dorsolateral bulbous midsections, and narrow drawn-out distal end. Antenna I, ♀, first article approximately same width as second article, l/w >1.7; first 2 articles not fused although articulation is reduced; second article inserts centrally into first as their widths are approximately equal at this junction. Mandibular incisor process with 3–4 more or less distinct teeth; molar process truncate with marginal row of setae. Maxillipedal epipod pointed distally. Pereopod V carpus l/w 2.8; dactylus slender. Female operculum, apical cleft $<1/5$ length of operculum. Uropodal endopod with 2 large apical setae and 2 stout lateral setae; exopod bears 2 apical setae.

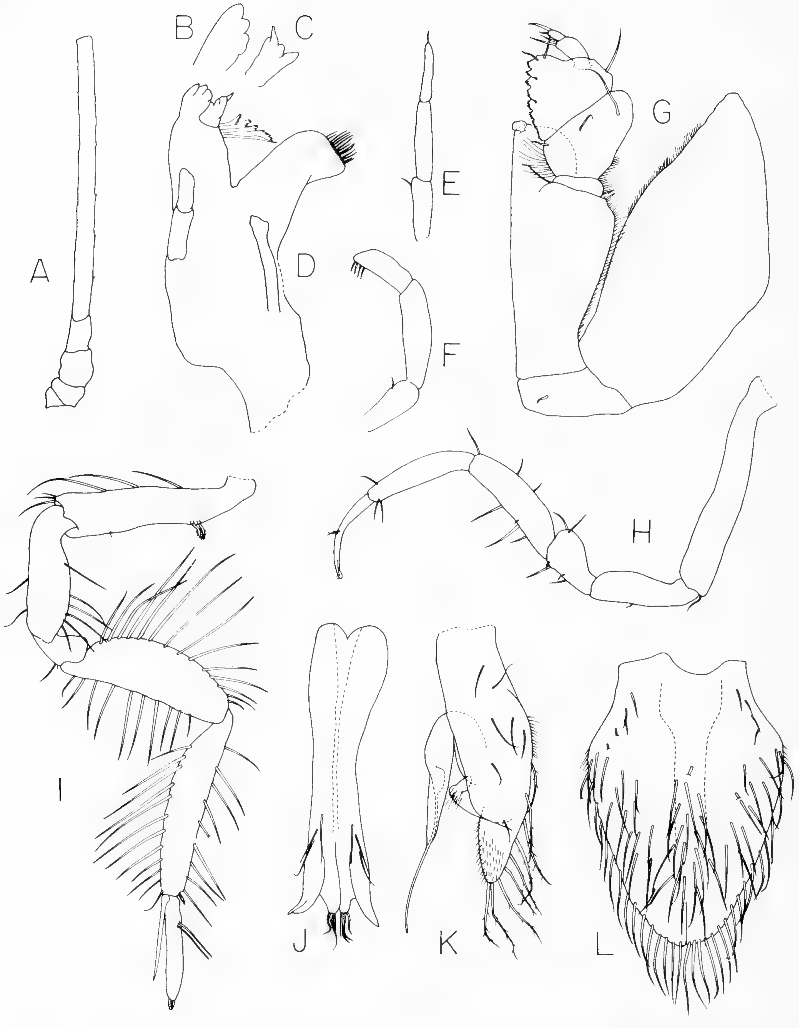

FIGURE 3. *Syneurycope parallela* ♂, WHOI 103: A. left antenna II, *in situ,* flagellum absent. Preparatory ♀, WHOI 131: B. incisor process, mandible, plan view; C. lacinia mobilis, mandible, plan view; D. left mandible, third article of palp absent; E. left mandibular palp; G. left maxilliped; L. operculum, setae are all plumose. Copulatory ♂, WHOI 62: F. left mandibular palp; H. left pereopod I, *in situ*; I. left pereopod V, *in situ,* setae are plumose; J. pleopods I; K. left pleopod II.

Additional description.—Preparatory ♀ larger than copulatory ♂: body length ♀5.5 mm, width 1.2 mm; body length ♂ 3.1 mm, width 0.6 mm; body length copulatory ♂ 4.9× tergal width of pereonite 2. Body widest at pereonite 2: l/w 0.6 preparatory ♀, 0.5 copulatory ♂. Antenna I, ♂ flagellum multiarticulated; bases of antennae I nearly touching in ♂, separated by a shallow depression in ♀. Mandibular palp, ♀, apical article reduced with single apical seta; apical article, ♂, palp robust with approximately 4 setae.

Remarks.—Syneurycope parallela is easily distinguished from *S. heezeni* by the narrower body, the antenna I peduncle, and the exaggerated topography of the pleotelson. It can be differentiated from *S. affinis* by the condition of the molar process of the mandible. The setation of the uropodal endopod is also distinct.

The single discrepancy between our material and Hansen's holotype is the number of setae on the natatory pereopods. Individual or geographic variation, ontogenetic development, and/or damage can easily account for this.

There are some problems with Hansen's description and illustrations. The cephalon is illustrated by Hansen as articulating with the first pereonite. Careful examination of the holotype and Scripps Institution of Oceanography specimens definitely indicates fusion of these 2 structures; no suture line is visible (Fig. 2B). This is a diagnostic feature of the genus in the present revision. Hansen illustrates coupling hooks on the maxilliped; coupling hooks are absent from all specimens examined throughout the entire subfamily (Fig. 3G). The holotype retains only the right maxilliped, the left having been dissected off and subsequently lost. Examination of the single remaining maxilliped on the holotype reveals no coupling hooks. Hansen correctly describes the male as "more than five times as long as the breadth of the fourth thoracic segment." Our male body l/w of 4.9 is obtained by measuring the width of the second pereonite, as this is usually the broadest pereonite throughout the subfamily; measuring width at the fourth pereonite gives a l/w of 5.8. Hansen noted that the operculum "is very far from reaching the end of the abdomen" (Fig. 2G); this becomes a diagnostic feature of the subfamily in the present revision. The antenna I female peduncle consists of 3 articles of the same rough proportions as described by Hansen for the male (Figs. 2D, 2E). The 16 articles of the antenna I flagellum he describes are typical of the male only; the female flagellum is a single segment (Fig. 2D).

Sexually dimorphic characters are not presently included in the species diagnosis because no male *S. heezeni* or *S. affinis* has been collected.

The antenna II fifth article is extremely elongate (Fig. 3A). This article is rarely present on collected specimens.

In this revision, *Syneurycope parallela* Hansen, *S. capensis* (Barnard), and *S. hanseni* Menzies are synonymized. The type-specimens of all 3 species were carefully examined; all proved indistinguishable from *S. parallela*. They were simply poorly illustrated and wrongly described. When circumstances dictated, we reillustrated the type-material. All problems and errors in the literature are treated below.

Syneurycope capensis
Figure 4: Barnard's syntypes reillustrated

Barnard's description contains many inaccuracies. Confusion results from his neglect to specify which of the 6 syntypes he has described. Barnard illustrated the first pereonite as discrete, yet careful inspection of the types shows it is fused with the cephalon (Fig. 4A). Pereonites 5, 6, and 7 are also illustrated as separate segments, but they are actually fused (Fig. 4A), as is typical of all species of Syneurycopinae. Barnard described a "pleon of a single segment"; the types actually have a reduced first pleonal segment, apart from the pleotelson (Figs. 4A, 4F). The antenna I flagellum is described as bearing "ca. twelve indistinctly separated joints" (Fig. 4B); this is true in the male alone, the female bears a flagellum of a single article (Fig. 4A). Furthermore, it indicates the immature condition of the male syntype, because adults typically bear closer to 16 articles. Additional evidence for an immature male syntype includes the truncate condition of the indistinctly bilobed distal end of the first pleopod (Fig. 4G), a second pleopod with a very stout stylet, and the feminine condition of the mandibular palp (Fig. 4D). The uropod is biramous, although described by Barnard as uniramous. The small exopod, ≈$1/5$ the length of the endopod, is easily overlooked (Fig. 4E). The remaining discrepancies between *S. parallela* and *S. capensis* involve the man-

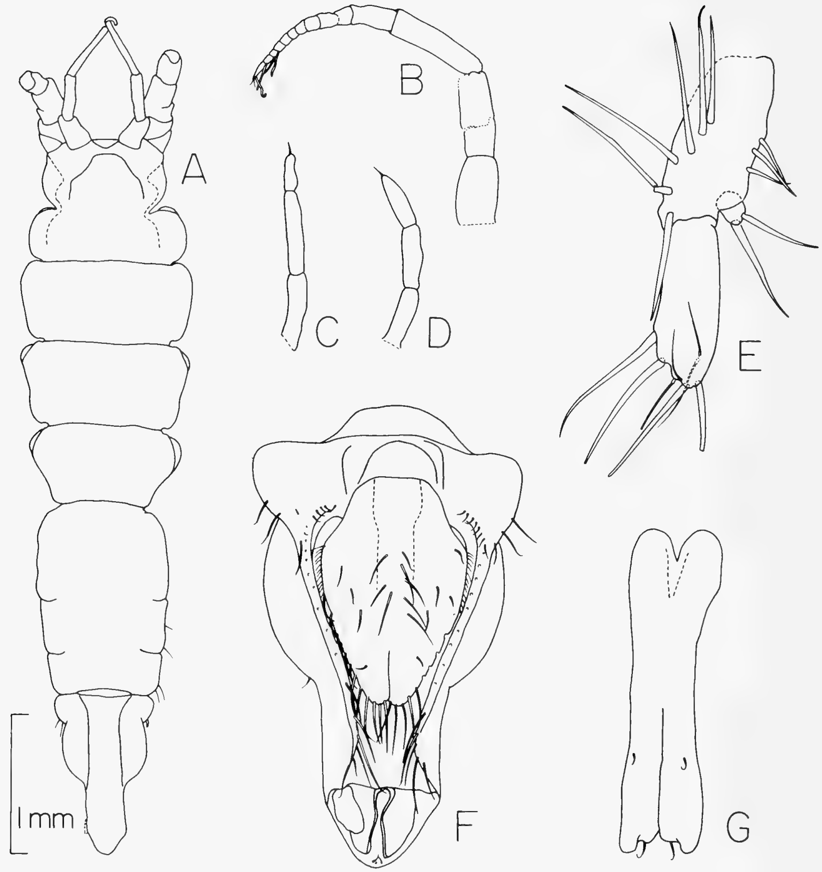

FIGURE 4. *Syneurycope parallela* (reillustration of Barnard's *Syneurycope capensis* syntypes, S.A.M. A4030) preparatory ♀: A. body, dorsal view, left distal edge of pleotelson damaged; C. left mandibular palp, *in situ*; E. left uropod, ventral view, *in situ*, setae are plumose. Nonpreparatory ♀: F. pleotelson, ventral view, setae are plumose, setae omitted from medial margins of pleotelson and left edge operculum, uropods missing. Immature ♂: B. left antenna I, *in situ*, second article damaged; D. left mandibular palp, *in situ*; G. pleopods I, *in situ*.

dible and maxilliped, which are unavailable. Barnard describes the mandible with a "secondary cutting edge [as] bifid." Presumably he is referring to the lacinia mobilis, which does appear bifid in lateral view, but is clearly quadradentate in plan view in *S. parallela* (Fig. 3C). Barnard describes the maxilliped as bearing an "inner distal margin of fifth [=third article of palp] with three denticles." In *S. parallela,* this margin is armed with numerous irregular spiniform teeth (Fig. 3G); these small teeth are grouped into units, which Barnard refers to as denticles. The number of denticles present varies both ontogenetically and between individuals. They are prominent and discrete distally, progressively diminishing in size and becoming less distinct proximally. The number of denticles varies too much to be useful as a diagnostic or descriptive character. The presence of numerous denticles along this margin is typical of all syneurycopine species. Data on the variability of this character are included in the treatment of *Bellibos buzwilsoni,* sp. nov.

Syneurycope hanseni

In 1956, Menzies described *S. hanseni.* Reexamination of the holotype demonstrated that it is a poorly preserved specimen of *S. parallela.* We have not reillustrated the holotype; Menzies' drawings (Menzies, 1956b, Fig. 2) can be directly compared with our *S. parallela* illustrations, with the corrections indicated below.

The holotype is originally illustrated as having a discrete cephalon and pereonite 1; our examination reveals that they are fused. The basal pleonite is distinct; the partial sutures in Menzies' drawings are incorrect. The original diagnosis contains other minor discrepancies. It includes the presence of "a well-developed mandibular palp" as a diagnostic character, but in the female it is reduced. The presence of "sixteen denticles along inner margin of second article" of the maxillipedal palp is also cited as diagnostic. Presumably, Menzies is referring to the third and not the second article, the variability of which has already been discussed. Menzies' terminology differs from Barnard's: a denticle now refers to a single projection or tooth. Reexamination of the holotype yields a different count from that of Menzies. Menzies' illustration depicts each male pleopod I inner ramus with 3 apical setae; close inspection of the type indicates a fourth seta broken off each ramus. Furthermore, Menzies' illustration lacks the simple setae present on the ventral surface of this appendage. The *S. hanseni* holotype is definitely a copulatory male as indicated by the form of the second pleopodal stylet, yet the antennular flagellum is described as having 10 articles, as opposed to approximately 16 on adult *S. parallela* males. This discrepancy may be real or is perhaps attributable to the difficulty of discerning whether or not flagellar articles are fused on a poorly preserved, decalcified specimen. The uropod illustrated by Menzies has fewer stout setae than that of *S. parallela.* Inspection of the uropod indicates that it has been compressed out of shape, such that setae could easily have been dislodged.

There have been no recent finds of *S. capensis* or *S. hanseni,* although much collecting has been done. We believe all of the above evidence strongly indicates the synonymy of these species with *S. parallela.*

Syneurycope heezeni Menzies, 1962
Figures 5 and 6

Synonymy.—*Syneurycope heezeni* Menzies, 1962, p. 151, Figs. 41A–E; Wolff, 1962, pp. 116–117.

Holotype.—L.G.O. Biotrawl No. 200 (55°42.9′S, 64°21.6′W); AMNH 12132, preparatory ♀, 4.5 mm.

Paratype.—L.G.O. Biotrawl No. 200 (55°42.9′S, 64°21.6′W); AMNH 12133, ♀.

Other material.—L.G.O. Biotrawl No. 201 (55°31.6′S, 64°07.5′W); AMNH 12280, 2 ♀♀: 1 ♀ anterior body fragment, 1 ♀ midbody fragment. L.G.O. Biotrawl No. 220 (9°45.0′S, 34°24.0′W); AMNH 12281, ♀. Present collection: 1969 Rankin Station No. 21, epibenthic sled (9 individuals); 2 preparatory ♀♀ (no. 1 and no. 2) deposited at ZMUC.

Distribution.—Southwest Atlantic Ocean and Weddell Sea, 9°45.0′S to 73°52.0′S, 2288–3839 m.

Diagnosis.—*Syneurycope* with broad body; body length 4.1 (♀) × tergal width of pereonite 2; body fringed laterally with numerous simple setae. Pleotelson contouring less complex than that of *S. parallela*: proximal ventral flanges less flaring, distal end less produced. Antenna I, ♀, first article wider than second, l/w 1.3; first 2 articles fused; first article much wider than second at their junction; second article inserts toward medial edge of first. Mandibular incisor process with 5 distinct teeth; molar process truncate with marginal row of setae. Maxillipedal epipod rounded distally. Pereopod V carpus l/w 2.7; dactylus paddle-shaped. Female operculum apical cleft

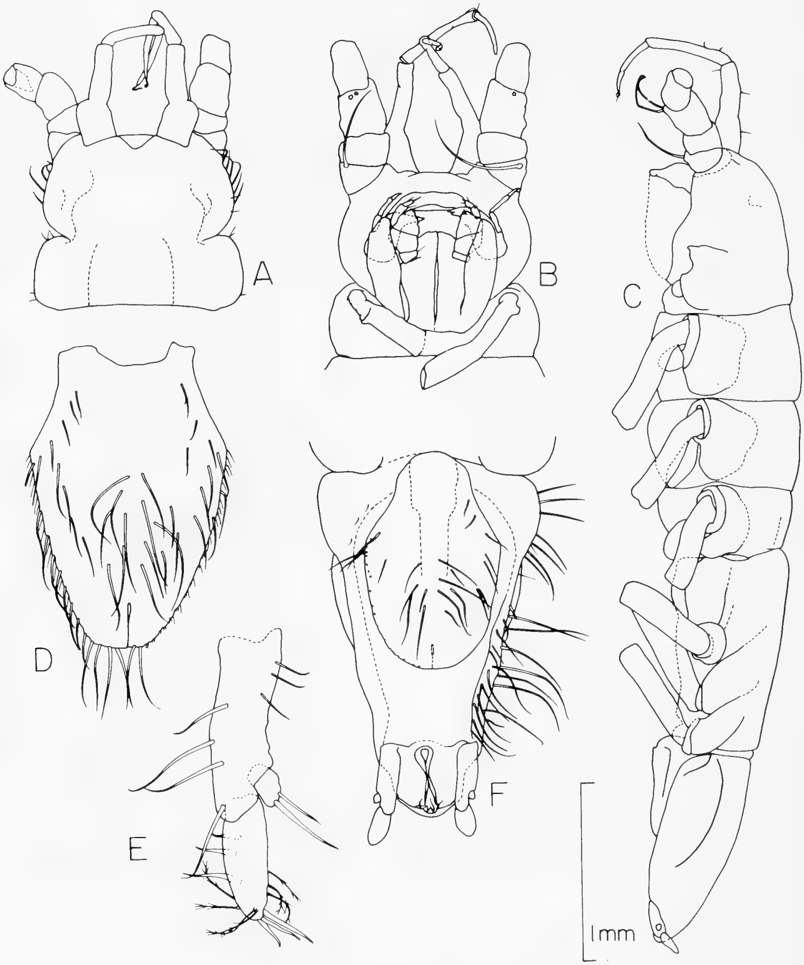

FIGURE 5. *Syneurycope heezeni* holotype ♀, L.G.O. Biotrawl 200 (AMNH 12132): A. cephalon-pereonite 1, dorsal view; C. body, lateral view, setae omitted from appendages, mouthfield simplified; F. pleotelson, ventral view, setae omitted from edge of operculum, right medial edge of pleotelson, and uropods, all setae are plumose. Preparatory ♀ no. 2, 1969 Rankin station 21, epibenthic sled (ES): B. cephalon-pereonite 1, ventral view, right pereopod damaged. Preparatory ♀ no. 1, 1969 Rankin station 21, ES: D. operculum, only bases of setae illustrated along left edge, all setae are plumose; E. left uropod, ventral view, *in situ*.

$<1/5$ length of operculum. Uropodal endopod with 3 large apical setae and 3 stout lateral setae; exopod bears 2 apical setae.

Additional description.—Body length ♀ 4.4 mm, width 1.1 mm. Body widest at pereonite 2, preparatory ♀ l/w 0.5.

Remarks.—*Syneurycope heezeni* is readily distinguished from its congeners by the distinctly broader body; the unique antenna I peduncle (Fig. 5A–C); and the setation of the uropodal endopod (Fig. 5E). It differs further from *S. affinis* by bearing a row of setae on the molar process of the mandible.

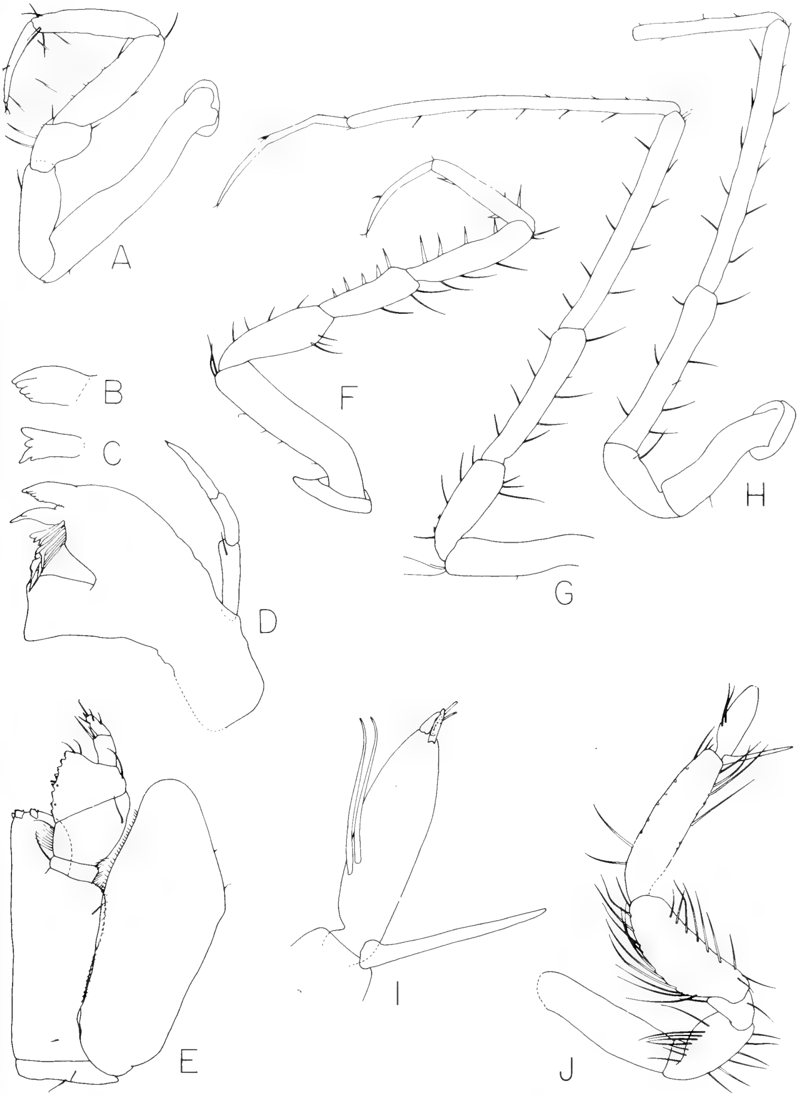

FIGURE 6. *Syneurycope heezeni* preparatory ♀ no. 2, 1969 Rankin station 21, ES: A. left pereopod I, *in situ*. Preparatory ♀ no. 1, 1969 Rankin station 21, ES: B. incisor process, mandible, plan view; C. lacinia mobilis, mandible, plan view; D. left mandible, setal row on distal edge of molar process not visible in this view; E. left maxilliped. Preparatory ♀, holotype, L.G.O. Biotrawl 200 (AMNH 12132): F. left pereopod II, *in situ*; G. left pereopod III, *in situ*; H. left pereopod IV, *in situ*; I. dactylus, pereopod V, enlarged; J. left pereopod V, *in situ*, tip of dactylus omitted.

Menzies' description and illustrations of *S. heezeni* are inadequate for modern requirements. We have therefore reillustrated it, drawing from both type-material and our working specimens, as circumstances dictated. For the most part, the original description refers to higher level characters. The fusion of the cephalon and first pereonite (Figs. 5A and 5C) is not unique to *S. heezeni,* but is diagnostic for the genus. The presence of a discrete first pleonal somite (Fig. 5C) and the absence of maxillipedal coupling hooks (Figs. 5B, 6E) are features of the Syneurycopinae. Menzies (1962) cites the absence of an apical seta on the distal article of the mandibular palp, but it is so small that he probably overlooked it (Fig. 6D). The relative proportions of the uropodal rami are characteristic of the genus; a precise ratio is difficult to establish because of both insufficient standardization of measuring technique and true variability. The approximate length ratio of exopod:endopod is 0.3 for the genus; Menzies cites 0.25 for *S. heezeni,* 0.20 for *S. parallela,* and 0.33 for *S. hanseni*; Birstein cites 0.33 for *S. affinis.* The available data indicate that the true ratio varies between 0.2 and 0.3 regardless of species.

The present revision is based on female specimens alone as males have not yet been collected.

Syneurycope affinis Birstein, 1970

Holotype.—Vityaz Station 5620 (44°48′N, 156°33′E): preparatory ♀, 4.8 mm.

Distribution.—Northwestern Pacific Ocean, 44°48′N, 5005–5045 m (known only from type-locality).

Diagnosis.—*Syneurycope* with narrow body; body length preparatory ♀ ≈4.6–4.7× tergal width of pereonite 2. Pleotelson complexly contoured, similar to that of *S. parallela.* Antenna I ♀ first article subequal in width to second article. Mandibular incisor process 4-toothed; molar process large with "rounded anterior margin and a characteristically curved grinding surface"; mandibular palp, ♀, lacking apical seta. Maxillipedal epipod rounded distally. Female operculum, apical cleft ¼ the length of operculum. Uropodal endopod bears 5 marginal setae; exopod with a single apical seta.

Additional description.—Body length, preparatory ♀, 4.8 mm, width 1 mm. Body widest at pereonite 2, preparatory ♀ l/w 0.5.

Remarks.—*Syneurycope affinis* appears to differ from its congeners by the characteristic form of the mandibular molar process, the number of incisor teeth, the absence of an apical seta on the mandibular palp, the extent of the apical opercular cleft, and the setation of the uropod.

Birstein (1970) compares *S. affinis* to *S. heezeni* as the most similar *Syneurycope* species. Although we were unable to examine the holotype and sole specimen of *S. affinis,* from Birstein's description and illustrations, we feel *S. affinis* more closely resembles the type-species for the genus, *S. parallela* Hansen. Both possess the narrow, elongate body and the unmodified antenna I peduncle. Birstein cites "a constriction between the anterior and posterior halves of the body" as a unique feature of *S. affinis.* We have seen a similar condition on some *S. parallela* specimens and believe this to be an artifact of preservation. The most outstanding difference, as we see it, is the grinding surface on the molar process of the mandible. This condition of the molar process, as described by Birstein (1970), is previously unknown in the asellote isopods and deserves more study when additional material of *S. affinis* is collected. The other differences, listed above, are subtle ones and the examination of additional specimens may even obscure them when the ranges of morphological variability for these particular characters are known.

Bellibos, gen. nov.

Figures 7–13

Synonymy.—*Syneurycope* (pars.) Chardy, Menzies.

Type-species.—***Bellibos* (*Bellibos*) *buzwilsoni,*** gen. et sp. nov., Figs. 7–8.

FIGURE 7. *Bellibos* (*Bellibos*) *buzwilsoni*, sp. nov., preparatory ♀, WHOI 66: A. body, dorsal view; B. body, lateral view; C. cephalon-pereonite 2, ventral view; D. left uropod, ventral view, *in situ*; E. pleotelson, ventral view, uropods missing, long setae on operculum are plumose, semicircles indicate setae not illustrated; F. operculum, setae on right distal edge omitted for clarity.

Distribution.—Eastern and western Atlantic Ocean, 50°43.4′N to 72°47.6′S, 2379–4980 m.

Etymology.—*bellus,* Latin, charming, pretty; *bos,* Latin, can be construed to mean "buffalo."

Diagnosis.—Syneurycopinae with body l/w usually <4.0. Combined length pereonites 1–4 usually < pereonites 5–7. Paired cephalic spines (=horns) present dorsally; cephalon demarked from first pereonite by a complete suture, articulation may be restricted. Topography of pleotelson simple; width tapers gradually from proximal to distal end. Antenna I ♀ flagellum multiarticulate where known; l/w first article < 2.0. Female operculum widest midway or in distal half; rounded distally; median keel may be well developed. Pleopod I adult ♂ with outer ramus of distal end shorter than that of inner ramus. Adult ♂ pleopod II exopod located at distal tip of protopod. Uropod with well-developed exopod where known, setation variable; length exopod at least ⅔ length endopod.

Remarks.—*Bellibos* species are identifiable by the presence of one or more pairs of cephalic spines, a complete suture line between the cephalon and pereonite 1, and a well-developed uropodal exopod. These characters will allow identification of the genus, although there is great morphological variability between congeners. Body shape varies from deep and robust to flat and fusiform; in one species the cephalon is greatly expanded and in another the first pereonite is expanded. These morphologies could have been as easily assigned to 4 monotypic genera; however the taxonomy would have become unnecessarily complicated without good purpose.

Within the genus, one species, *Bellibos monicae,* stands apart from all the rest. It is the sole exception to several otherwise firm diagnostic traits: its body l/w is almost always >4.0; the combined length of its pereonites 1–4 is > pereonites 5–7; articulation at the cephalon–first pereonite border is reduced; its uropodal exopod is shorter than the endopod, whereas in all other species the rami are equal. In order to group the most similar species together, we have therefore created 2 subgenera: *Bellibos,* which includes *B. buzwilsoni, B. dageti* and *B. multispina,* and *Bemerria* for the single species, *B. monicae.*

Bellibos, subgen. nov.
Figures 7–11

Type-species.—***Bellibos (Bellibos) buzwilsoni,*** sp. nov., Figs. 7–8.

Distribution.—Eastern and western Atlantic Ocean, 50°43.4′N to 41°03.0′S, 2379–4980 m.

Diagnosis.—*Bellibos* with combined length pereonites 1–4 < pereonites 5–7. Cephalon articulates freely with first pereonite. Uropodal rami equal in length where known.

Remarks.—Bellibos (*Bellibos*) includes 3 species: *B. buzwilsoni, B. dageti* and *B. multispina.*

Bellibos (Bellibos) buzwilsoni, sp. nov.
Figures 7 and 8

Holotype.—WHOI Station 321 (50°12.3′N, 13°35.8′W): USNM, 173004, ♂, 4.5 mm.

Paratypes.—WHOI 321, preparatory ♀ fragment, USNM 173005; WHOI 321, immature ♀, USNM 173006; WHOI 321, copulatory ♂, ZMUC; WHOI 321, preparatory ♀, ZMUC.

Other material.—Present collection. WHOI stations 64 (10 individuals), 66 (4); 155 (4); 156 (1); 195 (1); 245A (12); 287 (1); 321 (810); 328 (11); 330 (1). John Allen station 50 (28). Illustrated preparatory ♀ (WHOI 66) and ♀ fragment (WHOI 66) USNM 173008 and 173007, respectively.

Distribution.—Eastern and western Atlantic Ocean, 50°43.4′N to 36°55.7′S, 2379–4980 m.

Etymology.—In honor of our colleague, Mr. George (‘‘Buz’’) Wilson.

Diagnosis.—*Bellibos* with deep, robust body; body length 3.1 (preparatory ♀), 3.9 (copulatory ♂) × tergal width of pereonite 2. Single pair of pointed cephalic horns present, without apical setae; cephalon not expanded in length dorsally relative to first

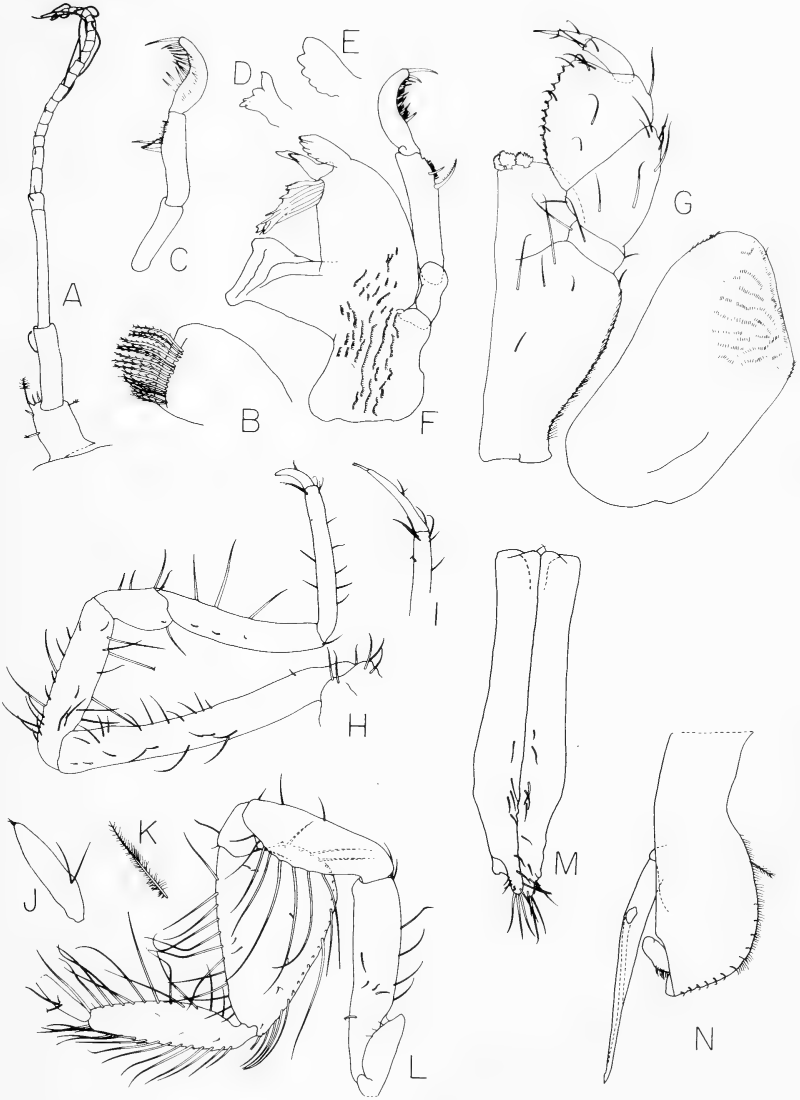

FIGURE 8. *Bellibos* (*Bellibos*) *buzwilsoni*, sp. nov., copulatory ♂, holotype, WHOI 321: A. left antenna I, *in situ*; C. left mandibular palp, *in situ*; M. pleopods I, damaged, distal end twisted; N. left pleopod II. Preparatory ♀, WHOI 66: B. molar process, mandible, enlarged view; D. lacinia mobilis, mandible, plan view; E. incisor process, mandible, plan view; F. left mandible, setae on molar process obscured in this view; G. left maxilliped, epipod detached. Preparatory ♀, paratype, WHOI 321: H. left pereopod I, *in situ*, dactylus foreshortened; I. dactylus, pereopod I, true length. Nonpreparatory ♀, paratype, WHOI 321: J. dactylus, right pereopod VI; K. long, slender plumose seta, typical of setae on pereopod V, carpus and propodus; L. left pereopod V, *in situ*, dactylus damaged.

pereonite. Dorsum of cephalon and pereonites 1–4 dense with simple setae. Pereonite 1 not embracing cephalon dorsolaterally. Pleotelson width at level of uropod insertion ¾ that of proximal end. Antenna I, second article length about 1.5× that of first article; number of articles known to vary from 6 to 8 in preparatory ♀, 12 to 23 in copulatory ♂. Mandibular incisor process with 6 teeth; palp apical article well developed in both sexes, number of setae varies from 6 to 16. Maxillipedal epipod short with blunt, rounded distal end; simple setae present on surface. Pereopods I–IV with undeveloped coxal plates; bases of unequal length: pereopods III and IV robust, $\approx ^3/_5$ length pereopod II; pereopod I more slender than pereopod II and ⅘ its length; pereopod II with row of stout setae along posterior margin of bases. Pereopod V carpus l/w 1.4. Female operculum pear-shaped; keel well developed, with setae; additional transverse row of extremely long, slender setae present on ventral surface just distal to end of keel. Male pleopod I well developed. Robust uropod with broad protopod and exopod; exopod approximately 1.5× endopod in width.

Additional description.—Body length 4.3–7.1 mm preparatory ♀, width 1.3 mm illustrated ♀; body length copulatory ♂ 3.1–5.0 mm, width 1.1 mm holotype ♂. Pereonite 2 l/w 0.3 in adults of both sexes. Antenna I second article l/w <4.0.

Remarks.—*Bellibos buzwilsoni* is easily recognized by its single pair of cephalic horns, the dense setation on the anterior half of the body, the unequal lengths of pereopod bases I–IV, and its robust uropod. This species is well sampled in the Atlantic Ocean; in particular, WHOI station 321 yielded 186 whole-bodied individuals. (Our work was already in progress when this sample was received. For this reason, the illustrated and diagnosed female is not from the type locality.) Such a large sample size permitted analysis of the size-frequency distribution of postmarsupial developmental stages (Fig. 14) and the variability of key morphological characters (Table 2). Developmental terminology follows Hessler (1970).

Size-frequency analysis indicates the presence of 3 manca stages; sex is undifferentiated in the first 2. Morphologically, manca 1 individuals are difficult to separate from the next stage. The anlage of pereopod VII is visible on manca 2 individuals; it can be developed to various degrees, presumably because the still soft limb continues to develop internally during the intermolt period. Manca 3 individuals possess a rudimentary seventh pereopod which varies from an unsegmented, wrinkled appendage to a partially segmented, firm limb. Sexes are now discernible: males exhibit rudimentary first pleopods, ⅓–½ the length of the opercular second pleopod; females possess an operculum of juvenile development, that is, with few setae and no keel. At least 2 more molts exist in males on morphological grounds, although the size-frequency analysis is inconclusive. Juvenile males possess a first pleopod equal in length to the second, although the rami of the distal end of the now paired first pleopods are not yet fully developed, and the second pelopodal stylet is short and blunt. Copulatory males exhibit a well-developed pleopod I and an elongate, tapering second pleopodal stylet bearing a complete duct. The large size range of these stage 5 males indicates that there may be more than one instar. Although the data are insufficient, size-frequency analysis suggests the existence of 3 female juvenile stages. Juvenile 2 is poorly documented, yet a consideration of likely instar size ranges indicates its existence. Morphologically, the first 2 stages are difficult to differentiate: juveniles 1 usually bear 2 setae whereas juveniles 2 bear approximately 5 setae on the apex of the opercular keel. Although the oostegites remain undeveloped in both stages, one of two juvenile 2 individuals has a distinct bud of tissue within its anterior coxae, presmably an oostegal anlage. In the third juvenile stage, the operculum is more heavily keeled and setose and preliminary oostegite buds are visible on the coxae of pereopods I–IV. There are 2 adult female stages: preparatory and brooding. Preparatory stage 7 females exhibit partially developed oostegites and a keeled, setiferous operculum. The 8 measured individuals range widely in size, suggesting that they reach the preparatory condition more than once in their lifetime, possibly alternating between the preparatory and brooding condition as seen in the Desmosomatidae (Hessler, 1970). Unfortunately, this hypothesis cannot be tested because no intact brooding females were sampled at this station.

TABLE 2. Range of variation of body length, number of articles in first antenna, number of setae on apical article of mandibular palp, and number of denticles on inner margin of fifth article of maxilliped is given for each of the apparent postmarsupial developmental stages, both ♂ and ♀, of *Bellibos buzwilsoni*. All specimens are from a single station, WHOI 321. **See text for discussion.**

Stage/sex	*N*	Mean body length ± 1 SD (mm)	No. articles antenna I (left, right)	No. setae apical article mandibular palp (left, right)	No. denticles fifth article maxilliped (left, right)
Manca 1 ♂♀	5	1.92 ± 0.08	(7, 7)	(5–6, 6)	(4, 4)
Manca 2 ♂♀	60	2.40 ± 0.09	(7, 7)	(5–6, 5–6)	(3–5, 3–5)
Manca 3 ♂	15	2.91 ± 0.11	(7–8, 7–8)	(6–8, 6–8)	(4–7, 4–6)
Manca 3 ♀	17	3.03 ± 0.26	(7, 7)	(4–8, 6–7)	(4–7, 4–6+)
Juvenile 1 ♂	43	3.30 ± 0.15	(9–12, 8–12)	(5–9, 5–8)	(5–7, 4–8)
Juvenile 1 ♀	21	3.53 ± 0.14	(7, 7)	(0–11, 7–11)	(5–10, 5–10)
Copulatory ♂	6	3.97 ± 0.74	(12–23, 14–23)	(9–15, 7–16)	(6–9, 7–9+)
Juvenile 2 ♀	2	4.20 ± 0.00	(–, 7)	(9–10, 9)	(8–10, 7)
Juvenile 3 ♀	5	5.55 ± 0.13	(7, 7)	(10–11, 10–11)	(9–10, 9–10)
Preparatory ♀	13	6.44 ± 0.59	(6–8, 6–8)	(6–12, 9–12)	(9–12, 10–14)

The morphological characters studied for variability include the number of articles in the first antenna, the number of setae on the apical article of the mandibular palp, and the number of denticles on the fifth article of the maxilliped. These characters are frequently used in the syneurycopine literature, usually without regard to their variability. The data are tabulated by stages in Table 2. The number of articles in the first antenna does not vary much in females from the earliest developmental stage to adulthood; the number increases with development in males, as does the variability. The number of setae on the apical article of the mandibular palp varies with sex in most syneurycopine species; *B. buzwilsoni* is an exception because both sexes possess well-developed mandibular palps with numerous setae. The number of setae increases allometrically, with individual variation. Lastly, the number of denticles on the inner edge of the third article of the maxillipedal palp also varies both allometrically and individually (see Table 2). The wide range of values found for each of the above characters indicates the low value of these meristic characters in diagnosing syneurycopine species. We continue the practice of presenting meristic counts and morphological measurements of single specimens in this paper because the sample sizes are usually too small to obtain significant ranges; one should regard the quoted value as a representative number, keeping in mind the potential for variability. However, in the diagnosis and additional description of *B. buzwilsoni*, we present the known range of a given character rather than a single type measurement because we have the variability data.

Characteristically, females are larger than the corresponding stage of males; the difference is amplified by increasing development. In both sexes, development progresses gradually; the final size discrepancy of adults is then a result of the greater number of female instars and possibly greater incremental growth of females. The *B. buzwilsoni* illustrated preparatory female (Fig. 7) is far smaller than the average size of preparatory females at WHOI 321, suggesting the possibility of geographical variation; WHOI 321 is in the northeastern Atlantic, the diagnosed female is from WHOI 66 on the Gay Head–Bermuda transect in the northwestern Atlantic Ocean. Two such distant populations, separated by the mid-Atlantic ridge may well diverge in certain characters.

Bellibos (Bellibos) dageti (Chardy), 1975
Figures 9 and 10

Synonymy.—*Syneurycope dageti* Chardy, 1975, pp. 695–698, Figs. 5–6.

Holotype.—Campagne Biogas IV Station 2 (47°31′N, 9°09.7′W): missing from National Museum of Natural History, Paris; ♀, 4.2 mm.

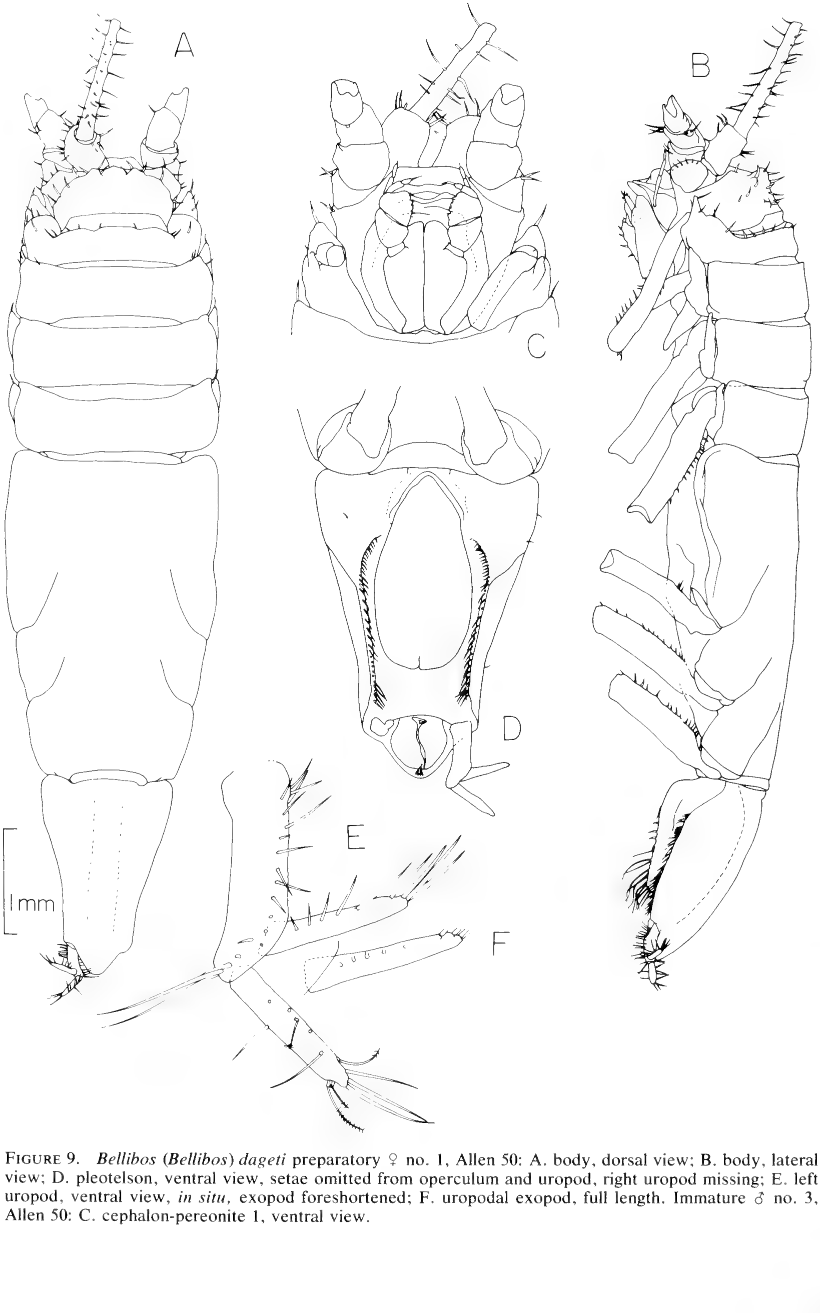

FIGURE 9. *Bellibos* (*Bellibos*) *dageti* preparatory ♀ no. 1, Allen 50: A. body, dorsal view; B. body, lateral view; D. pleotelson, ventral view, setae omitted from operculum and uropod, right uropod missing; E. left uropod, ventral view, *in situ*, exopod foreshortened; F. uropodal exopod, full length. Immature ♂ no. 3, Allen 50: C. cephalon-pereonite 1, ventral view.

Other material.—Present collection. WHOI stations 155 (6 individuals); 328 (31); 156 (7); 288 (4); 71 (1); 100 (1); 126 (12); 330 (2). J. Allen station 50 (21). Diagnosed preparatory ♀ no. 1 (Allen 50) USNM 173009; illustrated preparatory ♀ no. 2, immature ♂ no. 3, copulatory ♂ no. 4 (Allen 50) and copulatory ♂ no. 5 (WHOI 328), USNM 173010, USNM 173012, USNM 173011, and USNM 173013, respectively; preparatory ♀, ♂ fragment (WHOI 328) and juvenile ♀ (J. Allen 50) deposited at ZMUC.

Distribution.—Eastern and western Atlantic Ocean, 50°43.4′N to 0°46.0′S, 2379–4892 m.

Diagnosis.—*Bellibos* with flat, fusiform body; body length 3.8–4.1 (preparatory ♀), 3.9 (copulatory ♂) × tergal width of pereonite 2. Single pair of cephalic horns present, blunt-tipped and setose; cephalon not greatly expanded in length dorsally relative to first pereonite. Pereonite 1 embraces cephalon dorsolaterally; anterior edge fringed with simple setae. Pleotelson width at level of uropod insertion ½ that of proximal end. Antenna I, second article unusually elongate, up to 3× that of first, and setiferous; flagellum unknown. Mandibular incisor process may bear from 5 to 10 teeth; ♀ palp with reduced apical article bearing single seta; apical article ♂ palp well developed with 8 setae. Maxilliped with numerous large, unequally bifid setae on ventral surface of basipodite and along outer distal edge of epipodite; epipod pointed distally. Pereopods I–IV with well-developed coxal plates, pointed anteriorly each with an apical seta; bases of subequal length. Unequally bifid setae present along posterior edge of pereopod I–IV bases and anterior edge of pereopod V–VII bases. Pereopod VI carpus l/w 1.6. Main part, ♀ operculum oval; keel moderately developed with unequally bifid setae present along ridge. Pleopod I, ♂, outer ramus of distal end vestigial. Uropodal protopod elongate and slender; exopod subequal in width to endopod.

Additional description.—Body length 4.2–7.7 mm preparatory ♀, width 1.0–1.9 mm; body length copulatory ♂ 5.1 mm, width 1.3 mm. Body widest at pereonites 3 and 4. Pereonite 2 l/w 0.3 in adults of both sexes. Antenna I, second article l/w ≈8.

Remarks.—*Bellibos dageti* is characterized by a combination of unique traits: blunt and setiferous cephalic horns; first pereonite which laterally embraces cephalon; unusually elongate second article of first antenna; anteriorly pointed, well-developed pereopod I–IV coxal plates; uropodal rami of equal width. The large natasome in combination with the flat, fusiform body shape is unique within the subfamily.

The species was first described by Chardy (1975) on the basis of a single female specimen; unfortunately, this holotype was apparently lost in transfer to the Paris Museum (P. Chardy, *personal communication*). This loss is a real misfortune because, although our specimens (85 individuals of both sexes from 9 North Atlantic localities, 3 of which are in the vicinity of the type-locality) are very similar to the illustrations and description of the holotype, a close comparison reveals problematical differences.

The holotype is said to possess a mandible with a globular incisor process bearing "some ten denticles"; our described specimen (preparatory ♀ no. 1) bears 5 very distinct teeth. The holotype is 4.2 mm long and 1 mm wide at pereonite 4 (both measurements according to text of original description; use of scale line included with Chardy's figure yields a length of 1.5 mm). Our specimen is 7.7 mm long and 1.9 mm wide, almost twice as large as the holotype. This discrepancy may be due to ontogenetic variability. It is a preparatory female, but the maturity of the holotype is unknown. If the holotype is indeed an adult female, such a large size difference becomes as difficult to account for as the difference in the number of incisor teeth. These differences are not likely the result of geographical variability because both specimens come from the same ocean basin. The possibility exists that we are dealing with 2 discrete species characterized by size and the number of mandibular incisor teeth, but the reality of these differences is not well enough established to justify describing a new species at this time. Only one other difference was noted: the operculum of the holotype is illustrated without an apical cleft; all other syneurycopine specimens including the above specimen possess such a cleft. This character is, however, easily overlooked.

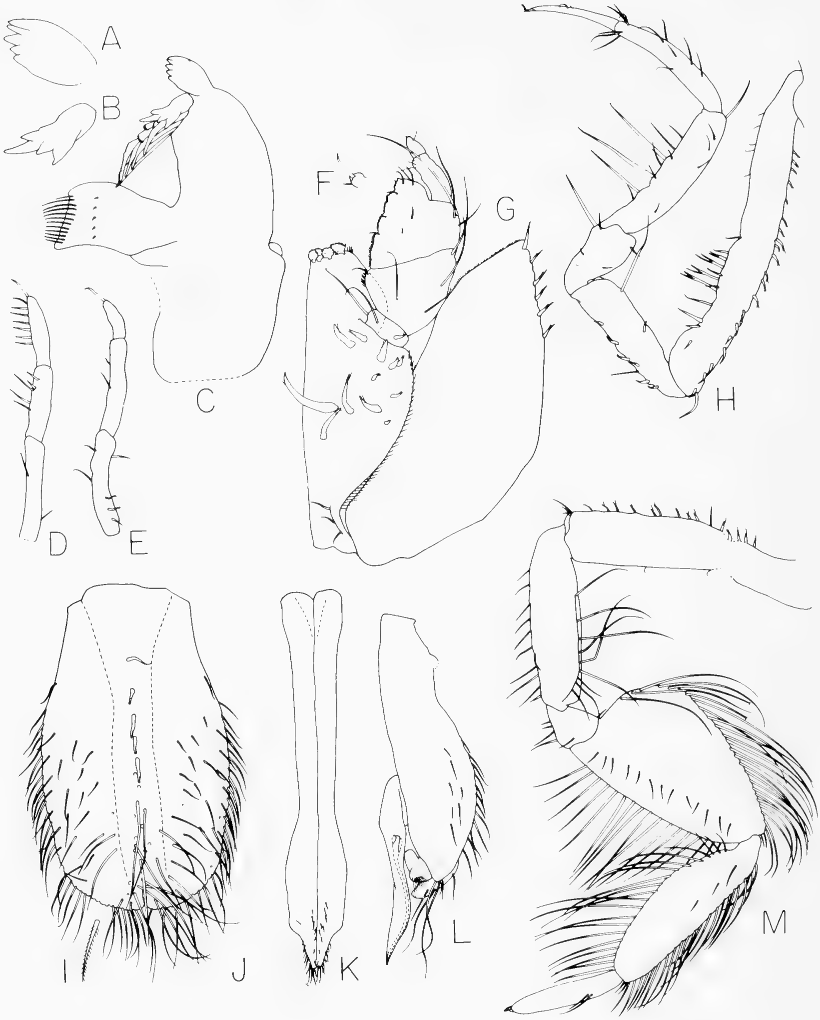

FIGURE 10. *Bellibos* (*Bellibos*) *dageti* preparatory ♀ no. 2, Allen 50: A. incisor process, mandible, plan view; B. lacinia mobilis, mandible, plan view; C. left mandible, mandibular palp obscured in this view; E. left mandibular palp; F. tip of distal joint of right maxillipedal palp; G. left maxilliped, distal joint of palp damaged; H. left pereopod I, *in situ*; M. left pereopod VI, *in situ*, long setae are all plumose, basis slightly damaged. Preparatory ♀ no. 1. Allen 50: I. plumose seta, enlarged view, typical of long, slender setae on operculum; J. operculum. Copulatory ♂ no. 5, WHOI 328: D. left mandibular palp. Copulatory male no. 4, Allen 50: K. pleopods I; L. left pleopod II, long setae are plumose.

The species is redescribed and illustrated from specimens in our working collection. From this material, it has been possible to describe a number of traits unrecorded in the original description, including the length of pereopod I–IV bases and the condition of males. Because there is no intact fifth pereopod on any of the mature speci-

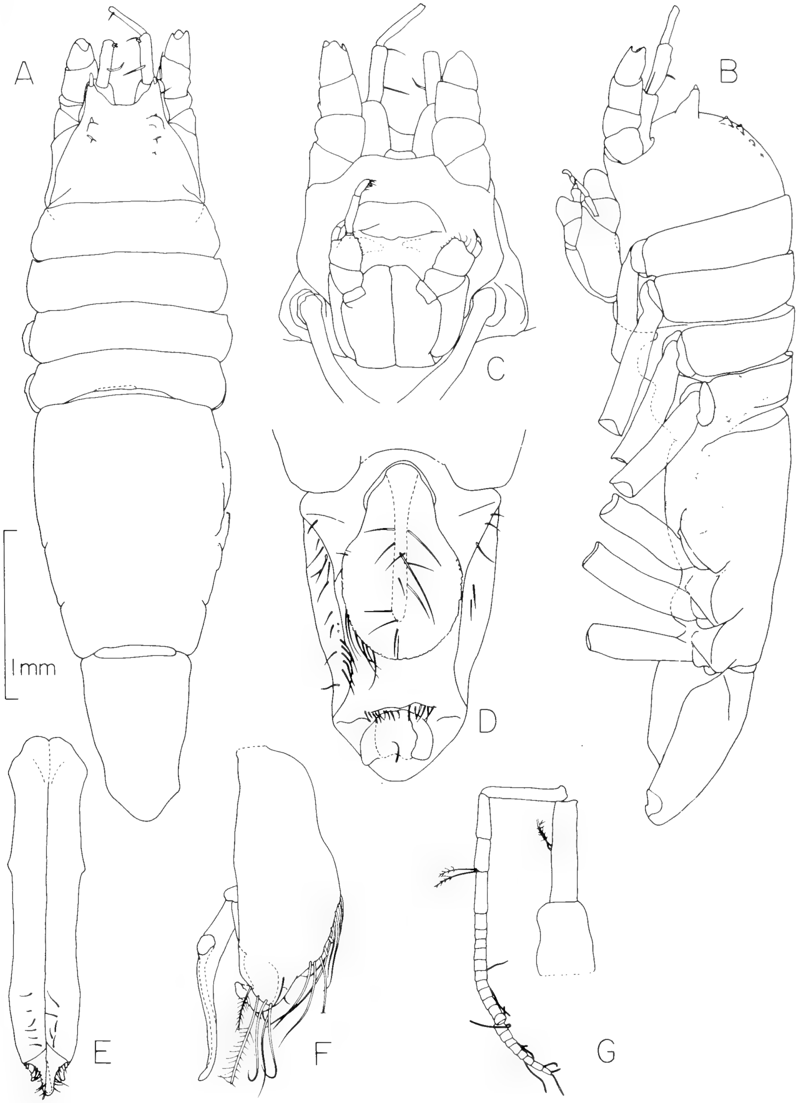

FIGURE 11. *Bellibos* (*Bellibos*) *multispina* nonpreparatory ♀, allotype (AMNH 12094): A. body, dorsal view, posterior pereonites damaged; B. body, lateral view, posterior pereonites damaged; C. cephalon-pereonite 1, ventral view; D. pleotelson, ventral view, marginal setae of operculum and left medial edge not illustrated, uropods absent. Paratype ♂ (AMNH 12095): E. pleopods I, *in situ*. Holotype ♂ (AMNH 12093): F. left pleopod II, *in situ*, all setae are plumose; G. left antenna I, *in situ*.

mens, the sixth is treated instead. Throughout the subfamily, the sixth pereopod is similar in shape to the fifth, although its dimensions are slighter.

Sexual dimorphism with respect to the antenna I flagellum remains unknown in *B. dageti*; the antenna is usually broken off at the junction between articles 2 and 3. However, the fact that the mandibular palp is sexually dimorphic suggests a parallel dimorphism for the first antenna.

Bellibos (*Bellibos*) *multispina* (Menzies), 1962
Figure 11

Synonymy.—*Syneurycope multispina* Menzies, 1962, pp. 151–153, Fig. 42E–K.

Holotype.—L.G.O. Biotrawl no. 52 (41°03′S, 07°49′E); AMNH 12093; ♂, 4.3 mm. Specimen in poor condition; head detached from body; right antenna I and pleopod II present; no pereopods or mandibular palp.

Other material.—Female allotype, 4.2 mm, AMNH 12094: fair specimen with some cuticular damage; without oostegites; pereopods, antennae missing. Male paratype, AMNH 12095: specimen without pleotelson; pleopods I and single pleopod II present; no pereopods or mandibular palp.

Distribution.—Southeastern Atlantic Ocean, 41°03′S, 4960 metres (known only from type locality).

Diagnosis.—*Bellibos* with anteriorly deep, robust body; body length 3.6 (♀, allotype), 3.4 (♂, holotype) × tergal width of pereonite 2. Cephalon greatly expanded in length dorsally, at least 2× length pereonite 1; longitudinal row of spines present on either side of midline: anteriormost spines largest, decreasing in size posteriorly; number of cephalic spines variable; each spine tipped with seta. Pereonite 1 not embracing cephalon dorsolaterally; pereonites 1–4 free of setae. Pleotelson width at level of uropod insertion ≈⅔ width at proximal end. Antenna I, second article <1.5× length first article, setae few; ♂ antenna I with ≈25 articles, number unknown for ♀. Female mandibular palp with robust apical article bearing 6 setae, unknown for ♂. Number of mandibular incisor teeth not recorded. Maxilliped with slender, simple setae; epipod unknown. Pereopods I–IV with undeveloped coxal plates; bases subequal in length, without stout setae; pereopods unknown beyond basis. Female operculum pear-shaped; moderately developed keel present with slender setae. Pleopod I, ♂, outer ramus of distal end well developed. Uropods unknown.

Additional description.—Body length ♀ (allotype) 4.2 mm, width 1.2 mm; body length ♂ (holotype) 4.3 mm, width 1.3 mm. Body widest at pereonites 2 and 3; pereonite 2 l/w 0.3 ♂ and ♀. Antenna I, second article l/w <4.0.

Remarks.—The most distinctive feature of *Bellibos multispina* is the double row of spines on the dorsal surface of the expanded cephalon (Figs. 11A and 11B). The number of spines does not appear to be fixed for the species, as the 3 type-specimens all exhibit different numbers of spines. Furthermore, on any single specimen the number of spines in the 2 rows need not be equal; the counts for the allotype, paratype, and the holotype are: 3L/5R, 4L/5R, 5L/6R, respectively (L = left, R = right).

This species is only known from the type-specimens. They comprise 2 adult males and 1 female whose maturity is difficult to ascertain because it does not possess oostegites. (Menzies incorrectly refers to 2 females and 1 male in the original description.) We have reillustrated certain views where helpful. The mandible and maxilliped, dissected presumably from the holotype and illustrated by Menzies, have been subsequently lost; no further dissection of the type-material was attempted. Unfortunately, the pereopods and uropods remain unknown.

Bemerria, subgen. nov.
Figures 12 and 13

Type species.—*Bellibos* (*Bemerria*) *monicae* (Chardy), 1975, pp. 698–701, Figs. 7–9.

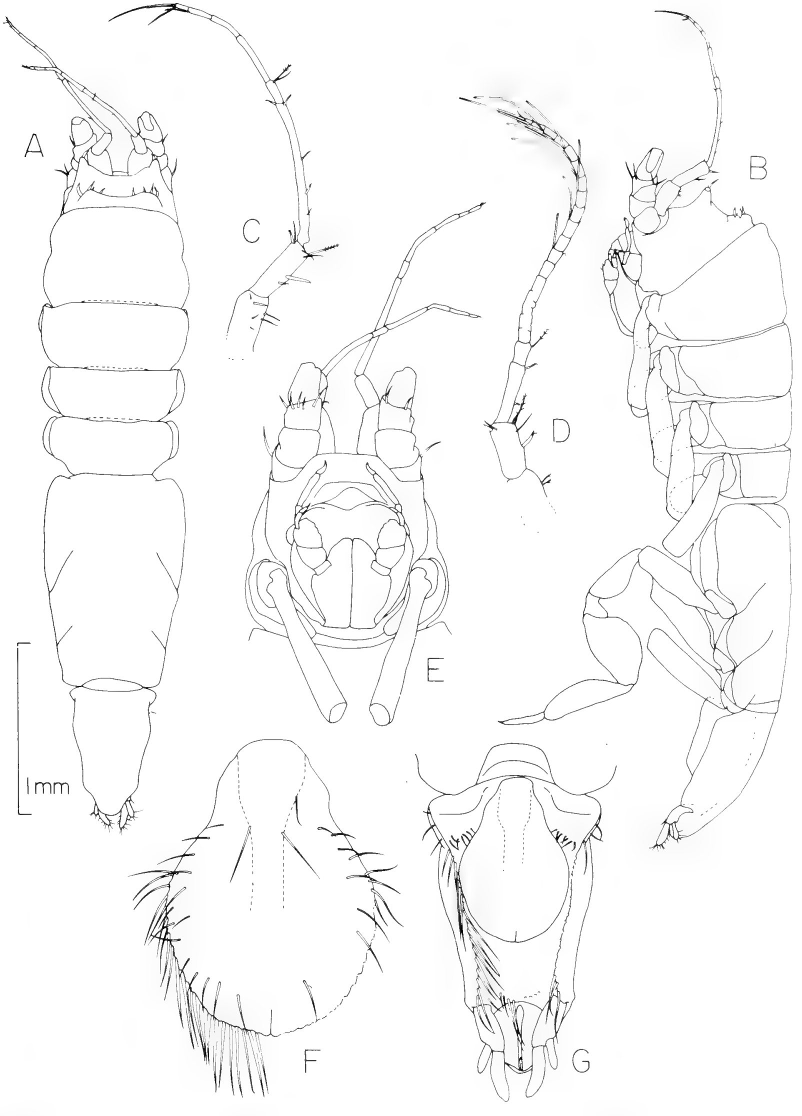

FIGURE 12. *Bellibos (Bemerria) monicae* preparatory ♀, WHOI 195: A. body, dorsal view; B. body, lateral view, setae omitted from appendages; C. left antenna I, lateral view, *in situ*; E. cephalon-pereonite 1, ventral view; F. operculum, setae omitted from left margin, all setae are plumose; G. pleotelson, ventral view, setae omitted from operculum, left medial edge of pleotelson and uropods, all setae are plumose. Copulatory ♂, WHOI 156: D. left antenna I, lateral view, *in situ*.

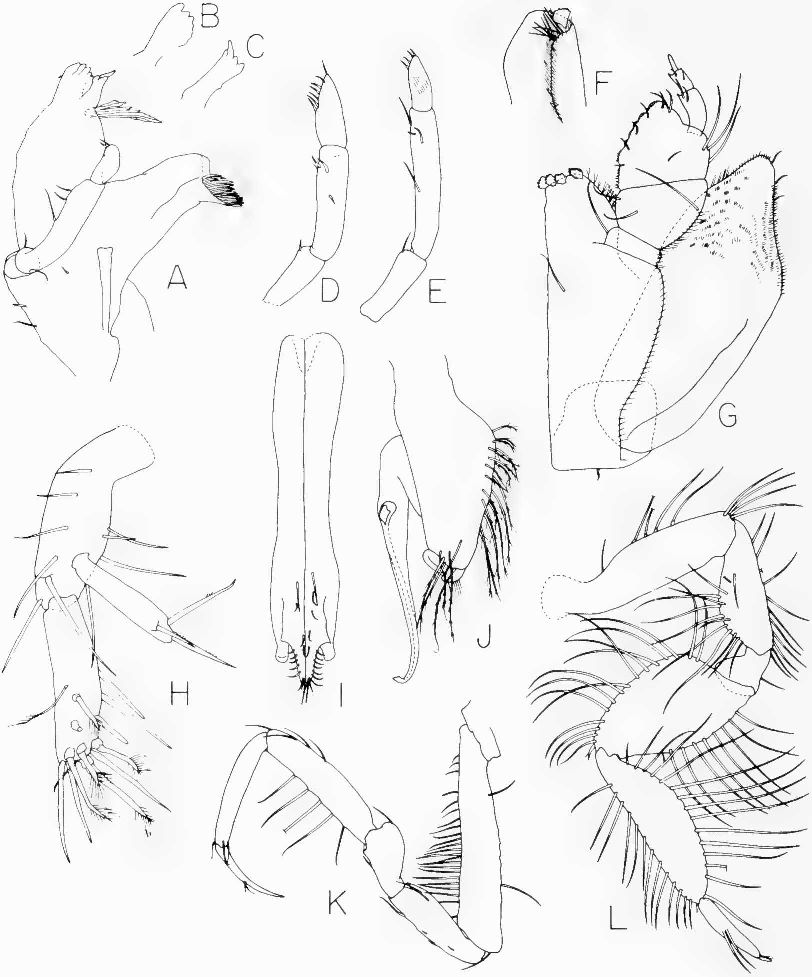

FIGURE 13. *Bellibos* (*Bemerria*) *monicae* preparatory ♀, WHOI 195: A. left mandible; B. incisor process, mandible, plan view; C. lacinia mobilis, mandible, plan view; E. left mandibular palp; F. distal edge, maxillipedal endite, dorsal view; G. left maxilliped; H. left uropod, lateral view, *in situ*, endopod foreshortened; L. right pereopod V, *in situ*. Copulatory ♂, WHOI 156: D. left mandibular palp, *in situ*; I. pleopods I; J. left pleopod II. Preparatory ♀, WHOI 72: K. left pereopod I, *in situ*.

Distribution.—Eastern and western Atlantic Ocean, 40°57′N to 72°47.6′S, 2864–4270 m.

Etymology.—In the spirit of the holiday season, during which time the manuscript was completed.

Diagnosis.—*Bellibos* with combined length pereonites 1–4 > pereonites 5–7. Articulation between cephalon and first pereonite reduced. Uropodal exopod ⅔ to ¾ length endopod.

Remarks.—*Bemerria* containing a single species, *Bellibos* (*Bemerria*) *monicae* (*see* ADDENDUM), shares similarities not only with its congeners but with *Syneurycope* as well. It presents a morphology intermediate to the 2 genera. The elongate, slender body shape with the anterior 4 pereonites longer than the posterior 3 is a trait of *Syneurycope*. The reduced articulation between cephalon and first pereonite is only a step away from the complete fusion of these segments exhibited by *Syneurycope*. *Bellibos monicae* is the only member of *Bellibos* in which the uropodal exopod is shorter than the endopod; in *Syneurycope*, this condition is carried to an extreme. The setation of the uropodal exopod is reduced in *Bemerria* to 5 apical setae (the uropod illustrated in Fig. 13H is unusual in bearing only 3 exopodal setae; all other examined specimens bear 5 such setae); *Syneurycope* has only 2. Although the above traits suggest affinity to *Syneurycope*, *Bemerria* possesses more traits in common with *Bellibos*: paired cephalic spines, a multiarticulated first antennal flagellum in both sexes, an expanded pereopod V carpus, a more pear-shaped female operculum, distal end of male pleopod I with shortened outer ramus, male pleopod II with a normally positioned exopod. Furthermore, the fusion of pereonite 1 to the cephalon is a diagnostic trait of *Syneurycope* in this revision, clearly excluding *B. monicae* from *Syneurycope*. Although we choose to include this species with the 3 remaining syneurycopine species in *Bellibos*, the intermediate status of *B. monicae* justifies its isolation in a separate subgenus.

Bellibos (*Bemerria*) *monicae* (Chardy), 1975
Figures 12 and 13

Synonymy.—*Syneurycope monicae* (Chardy), 1975, pp. 698–701, Figs. 7–9.

Holotype.—Campagne Biacores station 245 (40°57′N, 22°16′W): missing from the National Museum of Natural History, Paris; ♂, 4.0 mm.

Other material.—Present collection. WHOI station 195 (2 individuals), 71 (16), 156 (2). Rankin station 1969 no. 23 (1). Illustrated preparatory ♀ (WHOI 195) USNM 173015; illustrated copulatory ♂ (WHOI 156) USNM 173014; illustrated preparatory ♀ (WHOI 72) USNM 173016; ♂ and preparatory ♀ (WHOI 72) deposited at ZMUC.

Distribution.—See subgenus.

Diagnosis.—*Bellibos* with body length 4.5 (preparatory ♀), 3.8–4.8 (copulatory ♂) × tergal width of pereonite 2; anterior half of body deep. Single pair of cephalic horns present, tipped with an apical seta; transverse dorsal ridge poorly to well developed at posterior edge of cephalon, may bear setae. Dorsal length, first pereonite approximately 1.5× that of pereonite 2. Antenna I with ≈8 articles preparatory ♀, 19 articles copulatory ♂. Mandibular incisor process bears a few main teeth and an indistinctly serrated posterior edge; apical article of palp with ≈4 setae in adult ♀, up to 7 in adult ♂. Maxillipedal epipod narrow distally. Coxal plates undeveloped on pereopods I–IV; bases subequal in length. Pereopod V carpus l/w 1.4–1.5. Main part ♀ operculum nearly round; keel poorly developed. Male pleopod I, outer ramus of distal end well developed. Uropodal exopod width ≈½ that of endopod.

Additional description.—Body length preparatory ♀ (WHOI 195) 3.7 mm, width 0.8 mm; body length copulatory ♂ 2.7–4.1 mm, width 0.6–1.1 mm. Body widest at pereonite 2; l/w 0.4 preparatory ♀, 0.3–0.4 copulatory ♂.

Remarks.—*Bellibos* (*Bemerria*) *monicae* is best characterized by the expanded first pereonite. Other traits which are unique to this species are: a uropodal exopod approximately ⅔ the length of the endopod; a cephalic ridge which can be developed to various extents. This species was originally diagnosed by Chardy (1975) on the basis of a single male individual taken from the northeastern Atlantic Ocean; unfortunately, this holotype specimen was also lost enroute to the Paris Museum (P. Chardy, *personal communication*). We have redescribed and illustrated the species from a collection of 21 individuals of both sexes which were sampled at 4 stations in the northwestern and southern Atlantic. Although these individuals closely resemble *B. monicae*, comparison to Chardy's literature description and illustrations of the holotype reveal some

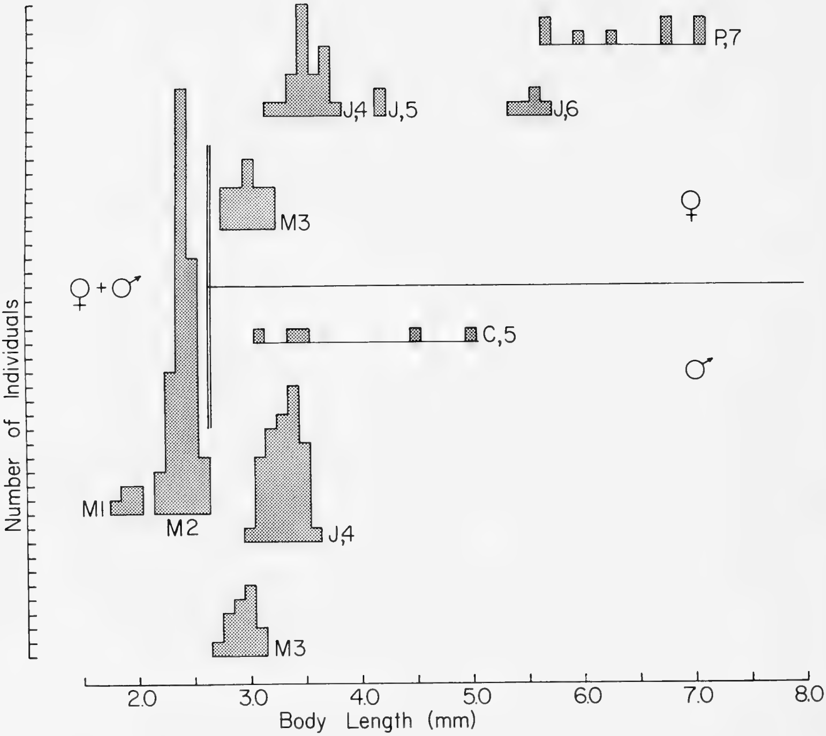

FIGURE 14. Size-frequency histogram of the postmarsupial developmental stages of *Bellibos buzwilsoni* from WHOI station 321. Stages are numbered separately for ♂♂ and ♀♀ and proceed from manca stage 1 (M1) through either preparatory ♀, stage 7 (P,7) or copulatory ♂, stage 5 (C,5). Sexes are first differentiated morphologically at manca stage 3 (M3). See text for discussion. Abbreviations: C, copulatory; J, juvenile; M, manca; P, preparatory. Each unit on vertical frequency scale = 1 individual.

differences which must be considered. Chardy describes the cephalon as fused with the first thoracic segment, yet he illustrates a complete suture line between the 2 segments. Our specimens also exhibit a complete suture line between the cephalon and first pereonite (Figs. 12A and 12B), although the flexibility at this joint appears reduced due to the loss of the arthrodial membrane. In actuality, this joint may be nonfunctional, but the fusion of the 2 segments is not complete because a suture line still separates them. In contrast, *Syneurycope* demonstrates complete fusion of this joint.

The sculpturing on the cephalon and the shape of the expanded first pereonite also differ from Chardy's description and illustration. The illustrated holotype lacks a cephalic ridge; a cephalic ridge may be poorly to well developed as a posterior continuation of the topography of the cephalic spines on our working specimens. The holotype is illustrated with a central anterior projection of pereonite 1; this projection is not evident on our specimens.

We find it premature to diagnose another species on the basis of these differences. It is possible that the holotype possesses a poorly developed cephalic ridge, overlooked by Chardy; and the shape of the anterior edge of the first pereonite could be an artifact of artistic interpretation.

The dentition of the mandibular incisor process and lacinia mobilis of a representative specimen from our collection may differ from the holotype. Chardy cites an incisor process with 4 teeth and lacinia mobilis with 3; our specimen exhibits a lacinia mobilis with the usual 4 teeth and at least 6 incisor teeth: 3 prominent ones followed by a posterior series of bumps which progressively diminish in size, the number of which is difficult to count. Although these could be diagnostic differences, the indistinct nature of the posterior edge of the incisor process, and the fact that Chardy's illustration shows 6 incisor teeth as opposed to the 4 that he cites in the description, make this difference suspect. Furthermore, the lacinia mobilis is illustrated by Chardy in side view, from which angle only 3 of the 4 teeth present would be visible anyway.

The male first pleopod of the holotype appears to differ from our illustration (*see* Fig. 13I; Chardy, 1975, Fig. 9D), but the difference is largely a result of Chardy illustrating the dorsal (inner) surface of the pleopod, while we illustrate the ventral (outer) surface.

The only remaining difference between Chardy's specimen and ours is body size. The holotype is 4.1 mm long and 1.1 mm wide at pereonite 2; body l/w is 3.8; pereonite 2 l/w is 0.3. The copulatory male which we illustrate is only 2.7 mm long and 0.6 mm wide; body l/w is 4.8; pereonite 2 l/w is 0.4. Both specimens appear to be copulatory by the form of the first and second pleopods. The holotype is 1½× larger than our specimen, the latter also appears more slender than the holotype. This size difference is perhaps the most difficult discrepancy to account for because size can be a diagnostic trait if consistent. Unfortunately, our collection (2 males) is too small to substantiate this difference.

Clearly, the loss of the *B. monicae* holotype has created a real problem. The species was described on the basis of a single male, without knowledge of the female or of individual variation. For this reason our samples are very important; they contain representatives of both sexes. The possibility exists that we are dealing with a new Atlantic species apart from Chardy's, but the data are inconclusive. Should the holotype ever be relocated, it would be a simple task to put this uncertainty to rest.

Addendum

We have recently sampled *Bellibos* (*Bemerria*) in the Pacific Ocean. A single brooding female was collected in the eastern equatorial Pacific (9°25.3′N, 151°10.0′W) from a depth of 5175 metres. Although the specimen is damaged, preliminary examination indicates that it is indeed a new species, closely related to *B.* (*B.*) *monicae*. Its overall morphology, including the dorsally expanded first pereonite, resembles *B. monicae* closely. There is a suite of differences, though, that should prove diagnostic of the new Pacific species. The cephalon differs from that of *B. monicae* in several ways: the cephalic horns are smaller in relative size and they are placed further anteriorly on the cephalon; the cephalic ridge is lacking; the maxillipedal epipod is now short and distally rounded, as if to accommodate a change in the shape of the face. Other differences include a more pointed distal end on the pleotelson, a mandibular incisor process bearing some 9 teeth, and a uropodal exopod with 8 setae.

Unfortunately, we did not receive this specimen until our manuscript was nearing completion. Because the specimen is both damaged and a brooding female, we have set it aside until additional material is collected. The existence of a new *Bellibos* (*Bemerria*) species supports the taxonomic scheme presented herein.

Unlike the majority of our material, the Pacific specimen retains its third and fourth pereopods; they are extremely slender and elongate, of similar proportions to those of *Syneurycope*. This is a significant find, and indicates that the presence of extremely elongate pereopods III and IV is a diagnostic feature of Syneurycopinae.

Acknowledgments

We thank H. L. Sanders and J. F. Grassle, Woods Hole Oceanographic Institution; J. A. Allen, University of Newcastle-upon-Tyne; and J. S. Rankin, University of Connecticut for providing us with sample material. H. S. Feinberg, American Museum of Natural History, New York; B. F. Kensley, South African Museum, Cape Town; and T. Wolff, University Zoological Museum, University of Copenhagen, Denmark kindly made type specimens available for our examination. Pierre Chardy generously advised us on matters relating to the species that he described. G. D. Wilson and J. F. Siebenaller read and commented on the manuscript. This research was supported by National Science Foundation Grant DES 74-21506.

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KEY TO KNOWN GENERA AND SPECIES OF SYNEURYCOPINAE

1a. Cephalic horns absent; cephalon fused to first pereonite; uropodal exopod minute, < ½ length endopod . . . . ***Syneurycope*** spp. 2

b. One or more pairs of cephalic horns present; cephalon not fused to first pereonite; uropodal exopod well developed, >½ length endopod . . . . ***Bellibos*** spp., gen. nov. 4

2a. Molar process of mandible curved, lacking setae, modified as a grinding surface . . . . *Syneurycope affinis* Birstein

b. Molar process of mandible truncate with marginal row of setae 3

3a. Narrow body; pleotelson complexly contoured, surface topography exaggerated; antenna I, ♀, first article not expanded in width, not fused to second article; uropodal endopod with 2 large apical setae and 2 stout lateral setae . . . . *Syneurycope parallela* Hansen

b. Broad body; pleotelson contouring less complex; antenna I, ♀, first article expanded in width relative to second, fused to second article; uropodal endopod with 3 large apical setae and 3 stout lateral setae . . . . *Syneurycope heezeni* Menzies

4a. Combined length of pereonites 1–4 > that of pereonites 5–7; uropodal exopod shorter than endopod; first pereonite expanded in length dorsally . . . . *Bellibos* (*Bemerria*) *monicae* (Chardy)

b. Combined length of pereonites 1–4 < that of pereonites 5–7; uropodal rami subequal in length; first pereonite not expanded dorsally . . . . *Bellibos* (*Bellibos*) spp. 5

5a. Cephalon expanded in length dorsally; multiple paired horns on dorsal surface of cephalon . . . . *Bellibos* (*Bellibos*) *multispina* (Menzies)

b. Cephalon not expanded; single pair of cephalic horns 6

6a. Flat, fusiform body; cephalic horns blunt, setose; pereonite 1 embraces cephalon dorsolaterally; second article, first antenna unusually elongate, >2× length of first article; anteriorly pointed coxal plates present on pereopods I–IV; pereopod I–IV bases subequal in length; uropodal rami subequal in width . . . . *Bellibos* (*Bellibos*) *dageti* (Chardy)

b. Robust, deep body; cephalic horns sharp, lacking apical setae; pereonite 1 not embracing cephalon dorsolaterally; second article, first antenna <2× length first article; pereopodal coxal plates undeveloped; bases of pereopods III and IV substantially shorter than bases of pereopods I and II; uropodal exopod nearly twice the width of endopod . . . . *Bellibos* (*Bellibos*) *buzwilsoni*, sp. nov.

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A new scalpellid (Cirripedia); a Mesozoic relic living near an abyssal hydrothermal spring*

William A. Newman

Abstract. A large stalked barnacle, *Neolepas zevinae* gen. et sp. nov., has been discovered living attached to ferriferous crust of a hydrothermal spring at 2600 metres on the crest of the East Pacific Rise. Comparisons with fossil and extant genera place the new genus as intermediate between the levels of organization found in *Eolepas* (Upper Triassic) and *Calantica* (Upper Jurassic–Holocene). Comparison with the ontogenetic stages of the advanced genus *Pollicipes* (? Upper Jurassic/lower Eocene–Holocene) indicates that *Neolepas* is represented by an 8-plated ontogenetic stage between the 6- and 13-plated stages of development. From these morphological and ontogenetic comparisons it is inferred that *Neolepas* represents the most primitive living scalpellid, a relic of Mesozoic age.

Habitat also favors the interpretation that *Neolepas* is a relic form, having found refuge near deep, hydrothermal springs. Such a refuge may have been attained in the late Mesozoic when predation pressures on sessile organisms are inferred to have dramatically increased. Though immigration into the hydrothermal environment by deep-sea stocks is a distinct possibility, in the present case, the route appears more likely to have been from relatively shallow waters of warm and tropical seas where tectonically active rifts intersect continental crust, and perhaps where islands are forming along ridge crests.

INTRODUCTION

Unusual environments are often inhabited by novel organisms and submarine hydrothermal springs have proved no exception in this regard (*see* Corliss et al., 1979). Since the first photographs of animals from certain hydrothermal springs of the Galapagos Rift Zone became available several years ago, it was obvious that if barnacles were to be found there, they would likely be of some unusual type. Barnacles have exploited virtually all other marine environments, so it seemed likely that they would occur there. It was therefore especially exciting when a half dozen specimens of a most singular barnacle were recently recovered from a hydrothermal spring off central Mexico.

The specimens represent a new genus and species, *Neolepas zevinae. Neolepas* has important implications in interpretations of the evolution of the Scalpellidae. The Scalpellidae, the largest family of the Lepadomorpha, has recently been revised (Zevina 1978*a*, *b*). After the systematic position of *Neolepas* is established, it becomes possible to discuss the geologic time and evolutionary circumstances under which it or its immediate ancestors likely became adapted to the hydrothermal environment.

HABITAT AND BIOTA

The present material was taken from the crest of the East Pacific Rise off the west coast of Mexico. The general topography of the region has been documented by Normark (1976). Francheteau et al. (1979) provide an artist's view of the porous sulfide edifices constructed by hydrothermal activity there. The sulfides were of predominantly zinc, copper and iron. Hydrothermal environments of submarine continental crust must

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* Contribution of the Scripps Institution of Oceanography, new series.

vary widely in their chemistry (P. Lonsdale, *personal communication*). Oceanic hydrothermal environments, conversely, although varying somewhat from spring to spring along a rift and from rift to rift, are likely quite similar in their characteristics. However, the very low concentrations of manganese at 21°N, as compared to the Galapagos situation, is notable (Francheteau et al., 1979) and this will be taken up below concerning metals of the hydrothermal environment and the barnacle. Corliss et al. (1979) summarize the situation surrounding the Galapagos Rift zone, a few thousand kilometres south of the *Neolepas* site:

> "Analyses of water samples from hydrothermal vents reveal that hydrothermal activity provides significant or dominant sources and sinks for several components of sea water; studies of conductive and convective heat transfer suggest that two-thirds of the heat lost from new oceanic lithosphere at the Galapagos Rift in the first million years may be vented from thermal springs, predominantly along the axial ridge within the rift valley. The vent areas are populated by animal communities. They appear to utilize chemosynthesis by sulfur-oxidizing bacteria to derive their entire energy supply from reactions between the seawater and the rocks at high temperatures, rather than photosynthesis."

According to Corliss et al. (1979), the animals collected in the Galapagos Rift hydrothermal springs proved remarkable: clams resembling the unusual family Vesicomyidae, mussels belonging to a new genus of Mytilidae, limpets of a new family, and pogonophorans of a new genus of Vestimentifera. A fish and crab peculiar to the area have also been observed. Some of these animals, such as the vestimentiferan, apparently have their closest relatives in deep water whereas others such as the true crabs hold their closest affinities with shallow water forms. Radiometric dating of shells from around an apparently expired vent suggested they were not more than 10 to 20 years old, indicating the minimum age of thermal activity at the spring was of the same order. Population structure differed from vent to vent, but individuals within a population were much the same size suggesting single colonizations in various vent areas (Corliss et al., 1979).

Vents are ephemeral and the exact locations of new ones unpredictable in space and time. But active rift zones persist for millions of years, and hydrothermal springs must have existed since the earth cooled sufficiently to allow the oceans to form; that is, before the origin of life. Therefore, other things being equal, species with adequate means of dispersal could persist indefinitely. But hydrothermal activity along rifts must at times shift more rapidly than can be compensated for by dispersal, and extensive extinctions have likely occurred. Furthermore, new forms must occasionally become adapted to the hydrothermal environment and such immigrations would, on occasion, cause extinctions through competition or predation.

It is important to attempt to determine the geological time an animal or its ancestor first became adapted to the hydrothermal environment. It is already apparent that the hydrothermal animals themselves are highly endemic, and therefore the geologic age at the generic level should be correspondingly great (Ekman, 1953). It will be instructive to know the degree of endemic similarity between vent regions; if it is high, dispersal between vent regions is low and vice versa.

The barnacle described here is endemic at the generic level. But it is the first cirriped from a hydrothermal spring, so the problem of regional endemism cannot be addressed. On the other hand, the scalpellid barnacles have a fairly good fossil record (*see* Newman et al., 1969). Therefore, upon determining its systematic position, its probable geologic age can be inferred.

DESCRIPTION

Family SCALPELLIDAE Pilsbry, 1907:3
Subfamily LITHOTRYINAE Gruvel, 1905:8 & 96
(*nom. correct.* Zevina, 1978*a*: 1000, *pro* Lithotrynae Gruvel, 1905)

Diagnosis.—Scalpellids with 8 capitular plates (rostrum, carina, terga, scuta and one pair of latera); peduncle with numerous whorls of calcareous scales. Hitherto represented only by the genus *Lithotrya*.

FIGURE 1. *Neolepas zevinae* gen. et sp. nov.: The first paratype (British Museum; Nat. Hist.) reg. no. 1979·209. ×2.5.

Neolepas gen. nov.

Diagnosis.—A lithotryine with fully developed capitular plates and strong, imbricating peduncular scales in whorls of more than 8, which, once developed, are retained throughout life. Type of the genus: *N. zevinae* sp. nov.

Neolepas **zevinae** sp. nov.

Diagnosis.—As for the genus.

Material.—Attached to ferriferous crust from near hydrothermal springs on the crest of the East Pacific Rise (20°50′N; 109°W) at a depth of 2600 m. ALV 915, rock-4, 21 April 1979. Temperature field estimated to be from near ambient (1.5°C) to 5°C (R. Ballard, *personal communication*).

Deposition of types.—Holotype, USNM Cat. No. 172581; first paratype, British Museum (Natural History) Reg. No. 1979·209; ontogenetic stages, USNM Cat. No. 172582.

Description.—A hermaphrodite resembling *Pollicipes mitella* (Linné) in form, but having a capitulum formed of but 8 plates homologous to those of *Lithotrya* (Fig. 1). The animal is intrinsically white, with the surface of the plates marked only by faint growth lines beneath a transparent cuticle.

The capitular plates, and especially the older peduncular scales which increase in age towards the point of attachment, are stained brownish red by a thin, ferromanganese deposit. The surface of the capitulum of the 2 largest specimens was covered with randomly spaced folliculinid cases which, preserved in 80% ethanol, were blue green.

The imbricating, triangular, projecting, spine-like peduncular scales form as min-

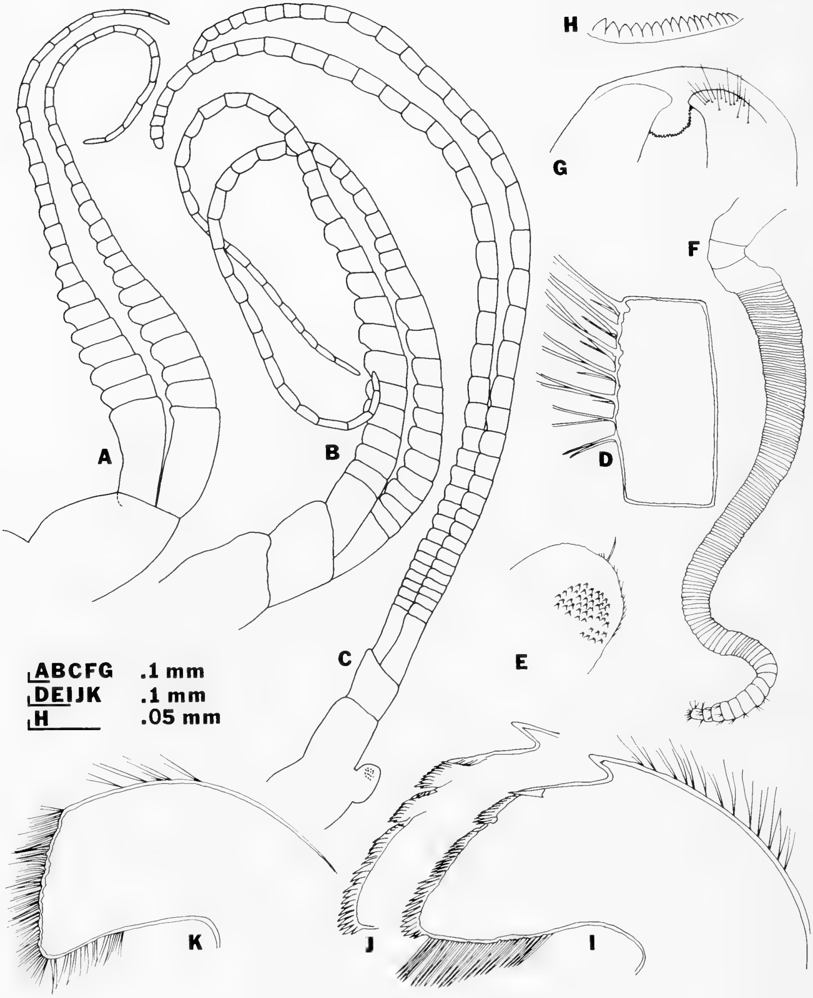

FIGURE 2. *Neolepas zevinae* gen. et sp. nov.: Arthropodal structures of first paratype: A, cirrus I; B, cirrus II; C, cirrus VI and caudal appendage; D, intermediate article of cirrus VI; E, caudal appendage enlarged; F, penis; G, labrum; H, crest of labrum; I, left mandible; J, cutting edge of right mandible; K, first maxilla.

iscule points in the growth zone immediately below the capitulum. These points grow longer and broader and become more projecting, as successive whorls are added. This process is the same as that described for scalpellids in general and is markedly different from the specialized situation in *Lithotrya*, where the scales are periodically shed (Darwin, 1851). In *Neolepas*, whorls so formed are somewhat irregular and difficult to follow around the circumference of the peduncle, but they appear to be composed of about 12 scales each in the paratype.

The 6 specimens ranged from approximately 3.5 to 58 mm in total length. In the

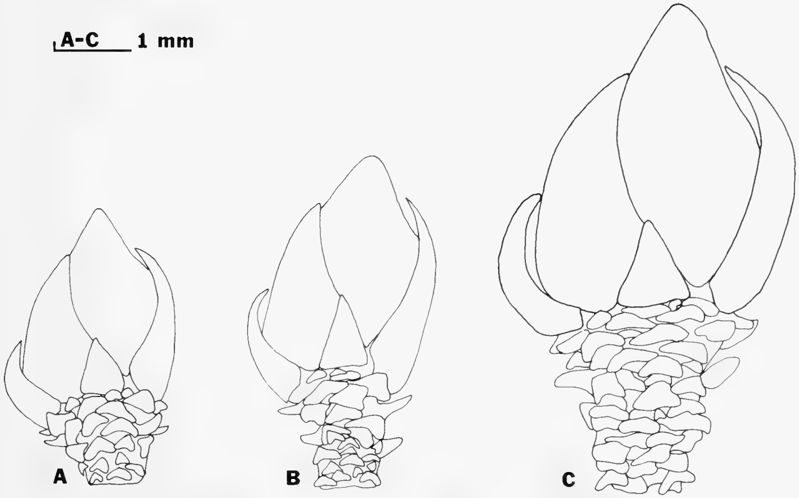

FIGURE 3. *Neolepas zevinae* gen. et sp. nov.: Juvenile stages in which the height of the capitulum exceeds the height of the peduncle (cf. Fig. 1).

3 smallest specimens the peduncle is less than half the height of the capitulum (Fig. 3). But this proportion reverses itself with further growth and in the paratype (Fig. 1) the peduncle is nearly twice, and in the holotype more than twice (41 to 17 mm), the height of the capitulum. This allometry accounts for the obvious addition of new peduncular scales compared to the less obvious growth increments in the capitular plates in the larger specimens. The result is that the capitulum comes to stand proportionately higher above the substratum with increasing age and, since the ovaries occupy the peduncle, there is more space for them. Placing the capitulum well above the substratum may be advantageous in insuring that the vital organs are well above the reach of some predators and that the trophic apparatus is in water of relatively undisturbed laminar flow.

The penis is well developed, the female genital apertures were observed at the bases of the first cirri and the holotype was brooding eggs. This indicates that the individuals are hermaphroditic. However, no complemental males were found between the occludent margins of the scuta, in the inner concave surface of the rostrum or, upon dissection, in the mantle cavity, and there are no pockets on the interior of the scuta. Thus the species appears to be purely hermaphroditic.

Trophi and cirri are designed for capture and manipulation of fine particles to an extraordinary degree (Fig. 2). The fragile nature of the cirri indicates that net casting must be extremely slow and then only into gentle currents.

The crest of the labrum, flanked by a pair of relatively small mandibular palps, bears a single row of minute, sharp teeth. The unique mandible is also provided with very fine denticles on the second and third tooth and along the very broad inferior angle. The combs formed by these fine teeth curve around onto the anterior surface of each mandible where they are in a position to scrape the crest and posterior (inner) surface of the labrum, as well as direct food pushed to them from behind by the maxillae, toward the mouth. Both the first and second pairs of maxillae are undistinguished, other than being simple and clad with very fine setae.

The cirri are uncommonly long, beginning with the first and second pairs in which the distal portions of the rami are antenniform. The third cirri resemble the remaining pairs. The uniarticulate caudal appendages are small. Cirral counts are:

First paratype

		I	II	III	IV	V	VI	c.a.
R	a	25	33	45	47	34	37	1
	p	30	34	40	39	34	40	
L	a	24	33	44	49	46	47	1
	p	30	35	?32	36	39	39	
Holotype								
R	a	31	35	47	54	58	60	1
	p	24	38	48	54	66	63	
L	a	30	36	47	56	?55	?54	1
	p	28	34	50	58	?59	?60	

Incubating eggs were found in the largest individual, as a single layer, in a pair of ovigerous lamellae of approximately 12 mm diameter. Each lamella was attached by a "Y"-shaped ovigerous frena on either side of the mantle cavity, and contained approximately 220 ellipsoidal eggs each measuring about 300 by 500 μm. Unfortunately, the eggs were at an early stage of development, and it could not be determined whether the larvae were to be released as nauplii or cyprids. If nauplii, it likely would have been possible to determine whether or not they would have been planktotrophic. Since this information is important in considerations of dispersal, it is regrettable that it was unavailable. But egg size in *Neolepas* is unusually large and this will be briefly considered in the discussion.

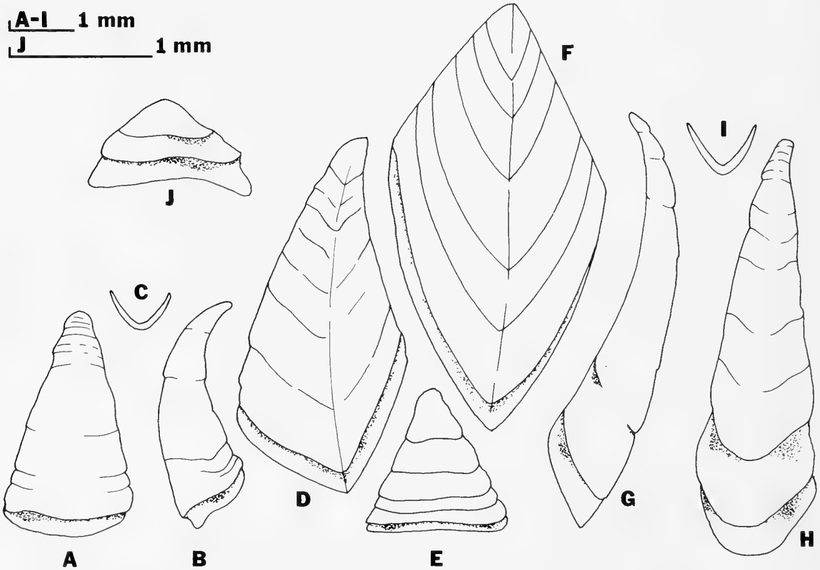

FIGURE 4. *Neolepas zevinae* gen. et sp. nov.: Disarticulated capitular valves and a peduncular scale of a paratype (lateral views are of right side): A–C, frontal, lateral and cross-sectional views of rostrum; D–F, lateral view of scutum, median latus and tergum respectively; G–I, lateral, dorsal and cross-sectional views of carina; J, lateral view of a peduncular scale.

The genus has been named *Neolepas*: Neo—Greek *neos* (recent) + lepas—Greek *lepas* (shellfish); a Recent (Holocene) form inferred to have stemmed from an ancient

(*Eolepas*/*Archaeolepas*) lepadomorph lineage. The species has been named for Dr. Galina B. Zevina, in appreciation of her numerous contributions to our knowledge of the thoracican cirripeds, and especially for her recent revision of the living Scalpellidae (1978*a*, *b*).

Discussion

Affinities

If one takes the structural data at face value, *Neolepas* must be assigned to the previously monotypic subfamily Lithotryinae. *Lithotrya* then is its closest relative and several species are found inhabiting primarily intertidal limestone in the western Atlantic and Indo-West Pacific. *Lithotrya* encompasses the only burrowing thoracican cirripeds, but this habitat alone is hardly grounds for erecting a new genus for the new form from the hydrothermal spring; there are a number of important structural differences.

Lithotrya is specialized for burrowing, as deduced by Darwin (1851). These specializations include (1) reduction of the rostrum and to some extent the single pair of latera, sometimes to mere rudiments, since the rostrum is no longer needed to protect the basal portion of the occludent scutal margin and the latera have become involved in forming, with the carina and terga, a plug in the burrow when the animal is withdrawn; (2) dimorphism in the peduncular scales, those surrounding the base of the capitulum being larger than those clothing the bulk of the peduncle; (3) small size and low profile of peduncular scales, forming a many-faceted calcitic grinding surface to attach primarily aragonitic limestone (chemical dissolution in burrowing may also be involved); (4) secretion of a calcareous cup or pad of cement attaching the animal near the base of the burrow; and (5) periodic molting and replacement of the peduncular cuticle and scales that totally replaces the grinding surface, a process unique to *Lithotrya*.

These characters readily separate *Lithotrya* from *Neolepas* at the generic level, but they do not preclude the two genera being in the same subfamily. The distinguishing features of *Lithotrya* are specializations to burrowing that are readily derivable from a *Neolepas*-like ancestor.

Position of the Lithotryinae

Broch (1922), without an appropriate explanation, placed *Lithotrya* as a derivative of the higher pollicipoid, *Protomitella*. This would require its being a reduced form having lost at least the subcarina and supplementary whorl of capitular plates. Broch, following Pilsbry (1908), was very much concerned with the structure and distribution of males among the scalpellids and came to the conclusion that they were absent in all higher forms. Males are absent in *Lithotrya* and this automatically made it a higher form. But the value of males in ranking genera is dubious since in the genus *Ibla* alone there is a pure hermaphrodite, a hermaphodite with complemental males and a species in which the female is accompanied by dwarf males. Furthermore, it has been discovered that complemental males are even found in certain relatively advanced balanomorph barnacles (McLaughlin and Henry, 1972).

Zevina (1978*a*) places the Lithotryinae as the first subfamily of the Scalpellidae in her important revision of the extant members of this family. She arranges the remaining genera essentially in ascending phylogenetic order of increasing complexity according to the criteria set forth by Drushchits and Zevina (1969). Foster (1978) independently came to the same conclusion and places *Lithotrya* at the stem of scalpellid evolution as far as living genera are concerned. However, in the second part of her revision of the scalpellids (Zevina, 1978*b*), apparently for the same reasons as Broch (1922), she places the Calanticinae rather than the Lithotryinae at the stem of her phylogenetic tree.

Broch (1922) took the fossil record into account in drawing phylogenetic conclusions, and he championed the fundamental nature of the 5 ontogenetically chitinous, primordial valves in cirriped evolution. However, the rather simple forms, *Cyprilepas* (Wills, 1963) with its bivalved chitinous carapace, *Praelepas* (Chernyshev, 1930) with its 5 chitinous valves and *Eolepas* (Withers, 1928) with its rostrum, had yet to be discovered. And, at the time, it was not realized that the Paleozoic Machareidia, with their numerous whorls of calcareous imbricating plates, were not barnacles (Withers, 1928). Furthermore, neither Broch (1922) nor Zevina (1978*a*, *b*) drew upon the ontogenetic data in *Pollicipes* that Broch (1922) had so carefully described and Drushchits and Zevina (1969) had recognized as important, in drawing phylogenetic inferences. Finally, neither Broch nor Zevina had *Neolepas* to ponder. What bearing then does fossil and ontogenetic evidence have in determining the position of the Lithotryinae in the evolution of the Scalpellidae?

Fossil and Ontogenetic Evidence

Pollicipes is considered the most advanced of the generalized members of the pollicipoid Scalpellidae (Broch, 1922; Zevina, 1978*b*), and the postlarval ontogenetic stages in extant *Pollicipes polymerus* Sowerby are described by Broch (1922). It is remarkable to observe that there is virtually a one-for-one correspondence between the appearance of fossil cirripeds through time and this ontogenetic sequence. Only the "*Neolepas* or 8-plated stage," recapitulated in the ontogeny of *Pollicipes*, is missing from the fossil record. By placing *Neolepas* in the open position (Fig. 5), we should be able to infer the geologic age of the *Neolepas* grade of evolution with considerable confidence, even though it is only known from the Holocene.

Figure 5 has been prepared to aid in the comparison between the extant and fossil genera involved here, and in visualizing their alignment with the ontogenetic stages in *Pollicipes*. The oldest fossil evidence for the Cirripedia is found in the Silurian lepadomorph *Cyprilepas* (Wills, 1963). However, the lepadomorphs descended from free-living ancestors at an ascothoracican level of organization (Newman et al., 1969; Newman, 1974). Unfortunately ascothoracicans are known only as far back as the Cretaceous, and then by fossil traces made by the more specialized wholly parasitic type, like *Ulophysema* (Madsen and Wolff, 1965). But one cannot distinguish the bivalved carapace of generalized ascothoracicans from some forms referred to the archaeocopid ostracods (Lower Cambrian–?Lower Ordovician; Sylvester-Bradley, 1961). Therefore, because the ascothoracican level of organization cannot have been less than Silurian, and because fossils that could represent them have been found in the Cambrian, the latter age is inferred here. The important point for present purposes is, however, that the ancestral free-living form, represented for the most part by the generalized characteristics of an extant ascothoracican such as *Synagoga*, is passed through in the ontogeny of all cirripeds as the cyprid stage, as illustrated in Fig. 5.

The cyprid larva, when first attached to the substratum, can be considered representative of the "*Cyprilepas* stage" in the evolution of barnacles as well as in the ontogeny of *Pollicipes*, because it is the closest living approximation of that level of organization in all cirripeds above the Ascothoracica. Indeed, if an attached cyprid capable of feeding and reproduction were found, and there were no contrary evidence, it should be assigned to the Silurian family Cyprilepadidae.

The next, or what can be referred to as the "*Praelepas* stage" in the ontogeny of *Pollicipes*, has the formerly bivalved carapace divided up into 5 plates; the paired terga and scuta of each side and the carina protecting the dorsal articulation. At this stage, all 5 plates are of a prismatic chitinous construction; the so-called primordial valves of Darwin (1851:22). The bivalved carapace of *Cyprilepas* is prismatic chitin (Wills, 1963), and this is the condition in the 5-plated stage in the ontogeny of higher cirripeds (Lepadomorpha and Verrucomorpha; Darwin, 1851).

While *Praelepas* of the Carboniferous retained chitinous valves throughout life, and the peduncle was unarmored (Schram, 1975), in extant 5-plated lepadiform barnacles (*Oxynaspis*, *Lepas*, *Poecilasma*, etc.), these same plates are calcified. Darwin (1851) noted that *Oxynaspis*, with its tendency to form subcentral scutal and carinal

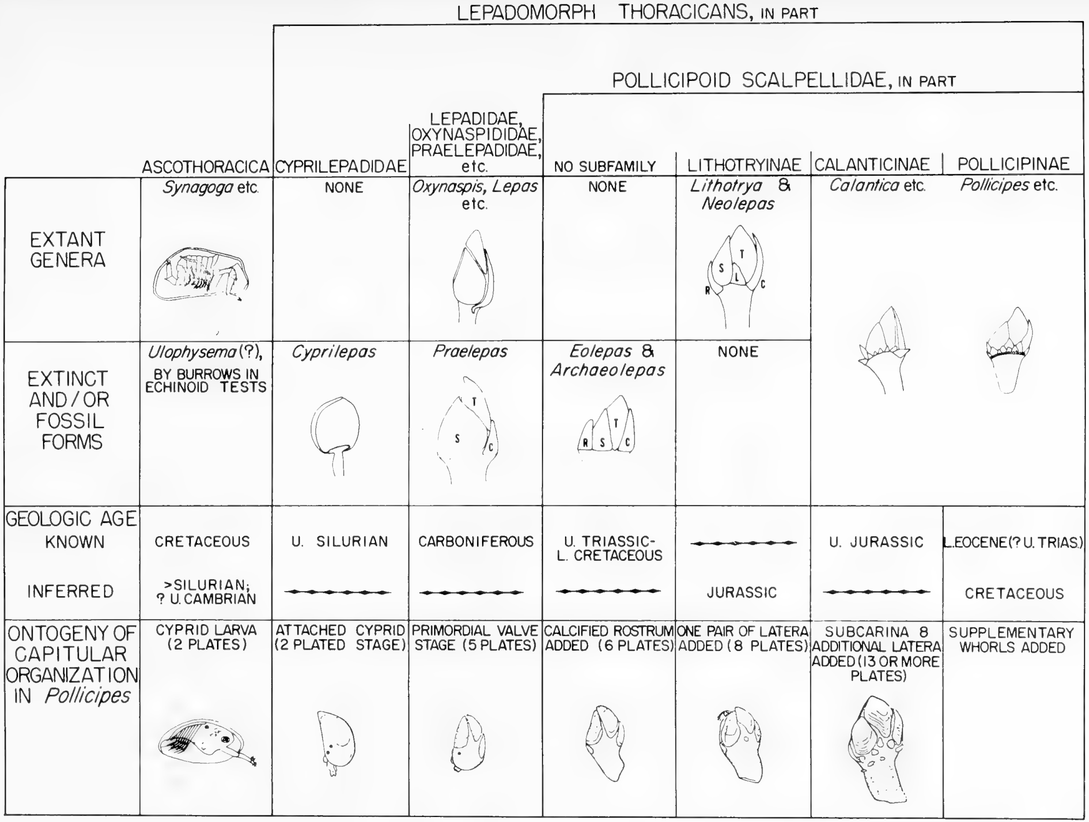

FIGURE 5. The ontogeny of *Pollicipes polymerus* (Linné), as described by Broch (1922), compared to extant and extinct cirriped taxa. Capitular ontogeny has a part for part correspondence with the phylogenetic sequence. From the phylogeny, a Jurassic age for the Lithotryinae can be inferred.

umbones, was intermediate between lepadiforms and scalpelliforms. It is noteworthy that in *Praelepas* the carinal umbo is already apical in position, as it is in all generalized scalpellids.

The next, or "*Eolepas* stage" in the ontogeny of *Pollicipes*, corresponds to the oldest fossil scalpellid, *Eolepas*. In this stage the calcareous rostrum has been added, bringing the number of capitular plates to 6. The lack of a chitinous primordium for the rostrum led Broch (1922) to consider the 5 chitinous valves as the primitive condition, a view subsequently substantiated from the fossil record by *Praelepas*.

The *Eolepas/Archaeolepas* level of organization, which spanned most of the Mesozoic, included a peduncle armed with calcified denticles. It is from peduncular denticles that the additional capitular valves were phylogenetically derived. The capitular organization of *Eolepas* is passed through in the ontogeny of *Pollicipes*, but the peduncle at this stage is unarmored.

In the next or "*Neolepas* stage" in the ontogeny of *Pollicipes*, a pair of median lateral plates is added. This brings the capitular count to 8. There are no recognized fossil representatives of this 8-plated stage, but the *Neolepas* level of capitular organization fills the gap between the *Eolepas* (6-plated) and the *Calantica* (13-plated) stages in ontogeny.

In the next, or "*Calantica* stage," in the ontogeny of *Pollicipes*, a subcarina and 2 pairs of latera have been added thereby duplicating the level of organization in scalpellids reached in the late Mesozoic, a level that has persisted into the Holocene in members of the Calanticinae (Zevina, 1978; Foster, 1978). Many elaborate variations occurred, but no forms representing them survived much beyond the Jurassic or Cretaceous (Newman et al., 1969; Hatton, 1977).

The addition of one or more whorls of numerous small plates around the base of the capitulum completes the ontogeny of *Pollicipes*. This level of organization is known from the fossil record with certainty from the lower Eocene, but it is likely to have been achieved at least by the Cretaceous. Some populations of *Pollicipes* persisted as dominant high intertidal lepadomorphs in the eastern Atlantic, eastern Pacific and Indo-West Pacific today, although Foster (1978) points out that the last species, *P. mitella*, is quite distinct from *Calantica* and *Pollicipes* and should be assigned to the genus *Capitulum* Gray, as proposed by Withers (1928). This is very interesting because *Capitulum* could readily be derived from *Neolepas* by the elevation of a single whorl of peduncular scales to the capitulum.

Comparing the orderly increase in capitular complexity, in the evolution of the lepadomorphs, with the ontogentic stages in the postlarval development of *Pollicipes*, supports the decision to insert the *Neolepas* level of organization between that of *Eolepas* and *Calantica*. The *Neolepas* stage is also seen following the *Eolepas* stage in the ontogeny of some species of *Calantica* described by Foster (1978).

The purpose of the aforegoing exercise has been to interpret the phylogenetic position of the Lithotryinae in the Scalpellidae and thereby to estimate the probable age of the *Neolepas* level of organization, because it may have no counterpart known in the fossil record. Placing *Neolepas* in the open position between the *Eolepas* and *Calantica* levels of organization in the fossil sequence, allows one to infer an age for the Lithotryinae of at least Jurassic. However, there are specimens referred to *Blastolepas orlovi* Drushchits and Zevina, described by the same authors (1969; figs. 2d (128/11 and 4 (128/15)) from an ammonite from the Lower Cretaceous of the northern Caucasus, that appear to be a lithotryine since they are figured as lacking the carinal latus and subcarina of stramentines such as *Blastolepas*. Drushchits and Zevina infer that these specimens are ontogenetic stages of *Blastolepas*, but the peduncular scales are already formed. Therefore it is very unlikely that they are an ontogenetic stage because addition of plates to the capitulum after the peduncular scales have appeared, is unknown in extant scalpelliforms. If, upon reexamination of this material, it turns out that the carinal latus and subcarina are actually lacking, the existence of the Lithotryinae in the Lower Cretaceous would appear to have been established. The new form would be neither *Lithotrya* nor *Neolepas* because the peduncular whorls are each composed of but 8 plates, as in the archaeolepadidine *Archaeolepas* and the stramentines *Stramentum, Loricula, Squama* and *Blastolepas*.

Specter of Progenesis

A well-preserved ontogenetic sequence has its pitfalls in drawing inferences concerning progressive evolution because there is the possibility of regressive evolution in the form of paedomorphosis (progenesis; Gould, 1977). In the present case, *Pollicipes* could conceivably retrogress to the *Eolepas* level of capitular organization, because it is at this stage in its ontogeny that cirral feeding begins. This is more than far enough back for present purposes because it is a stage below the level of *Neolepas*. Thus, the *Neolepas* level of organization could be achieved through progenesis. Was it?

The capitular and peduncular armament of *Neolepas* is fully developed. All capitular plates are fully approximate and as heavy in construction as in any shallow water or intertidal scalpellid, and much more so than in any abyssal scalpellid. The carina guards the entire dorsal region, from the base to the occludent portion of the tergal margin, and the rostrum does likewise up to the occludent portion of the scutal margin. The large latera fully guard the basal junction between the scuta and terga, where the capitulum joins the peduncle. Peduncular scales fit as closely as possible around the base of the capitulum, in the peduncular growth region, and as successive whorls enlarge as the capitulum moves upwards, they immediately take on a strongly spined imbricating form. All available plates are arranged to optimize fully their protective capabilities and there are no indications that any have been lost in the optimization process. There is no evidence then to suggest that *Neolepas* is progenetic.

This is in contrast to the situation in *Lithotrya* whose identical capitular organization shows retrogression in the rudimentary nature of the rostrum and latera. The cause of the retrogression is its adaptations to burrowing. However, retrogression in some plates leads to the distinct possibility of loss of others in this genus, and a study of its ontogenetic stages might shed some light on the matter. But there is presently no evidence that *Lithotrya* has lost any capitular plates, as far as adult morphology is concerned, and I can only conclude that *Lithotrya* has descended from a pre-*Calantica, Neolepas*-like form.

The dwarf, parasitic males of *Calantica* are another matter (*see descriptions by* Foster, 1978) because many progress no further than the *Eolepas* or *Neolepas* ontogenetic stage. But their capitular plates are barely approximate and their peduncles are scaleless, all of which suggests that progenesis is responsible for their reduced form.

In the final analysis, there is no way of proving whether or not Lithotryinae consists of progenetic forms. Even the discovery of a fossil of a *Neolepas*-like species of the appropriate geologic age would not be proof of the matter. But all the evidence we do have strongly favors the conclusion that *Lithotrya* and *Neolepas* are relics of a late Mesozoic radiation.

EGG SIZE, SEASONALITY AND RECRUITMENT

Barnes and Barnes (1968) have noted that the number of eggs produced by barnacles is in good part a function of individual size, that frequency of brood production is apparently greatest under optimal conditions and that size of eggs appears to decrease with decreasing latitude. These generalities are based mainly on high and mid-latitude species having planktotrophic nauplius larvae. They have been correlated primarily with the parceling of adult metabolic resources to larvae and the productivity of the waters into which they will be released, particularly along latitudinal gradients. No consideration has been made of the broader issues of biogeography concerned with differences in dispersal requirements for continental, insular and pelagic species. Furthermore, no attention has been paid to deep-sea barnacle species, other than to note that deep-sea barnacles generally hatch as cyprids (Hoek, 1883; Newman and Ross, 1971). Any correlation between what has been observed in *Neolepas* with what is known in cirripeds in general will be tenuous at best because all we have to work with is the number and size of eggs from a single brood taken from the largest specimen and the range in size of juveniles in the single sample.

In a recent paper, Achituv and Barnes (1978) tout the eggs of a western Indian Ocean intertidal species, *Tetraclita rufotincta* (Pilsbry), as being exceptionally large. They are nearly 19× the volume of those of other species of *Tetraclita* (a subtropical/tropical genus), and >3.5× that of relatively high latitude forms such as *Balanus balanus* (Linné) and *Semibalanus balanoides* (Linné). The eggs of *T. rufotincta* are ellipsoids, as cirriped eggs usually are. They measure about 464 by 316 μm when first laid and 477 by 362 μm when eyed or approaching hatching. It appears that the nauplii of *T. rufotincta* are planktotrophic (Y. Achituv, *personal communication*).

The newly laid eggs of *Neolepas* measured approximately 500 by 300 μm. Therefore *Neolepas* is comparable to *T. rufotincta* in having exceptionally large eggs. Number of eggs per brood is not comparable, however, and we know neither the form nor the trophic capabilities of the larva that hatches. Achituv and Barnes (1978) report the number of eggs per brood in *T. rufotincta* over a wide range of sizes. The count increases from approximately 1000 per brood in the smallest individuals to nearly an order of magnitude more in the largest. The number of eggs in the largest and only specimen of *Neolepas* having them was approximately 440, half that of the smallest *T. rufotincta*. However, *T. rufotincta,* at least on the shores of Elat, has a breeding season of but 2 months a year. It is therefore tempting to suggest that breeding in *Neolepas* is likely seasonless, as has been noted in some other deep-sea invertebrates (Rokop, 1974). By producing numerous broods per year *Neolepas* would be in a position to make up for its relatively small clutch size.

That larval availability is continuous throughout the year is strongly supported by the wide range of sizes (3.5 to 58 mm high) observed in the single sample of 6 specimens of *Neolepas*. Recruitment must be, if not continuous, at least over a long period of time. This is contrary to the conclusion reached by Corliss et al. (1979) who, because of the distinctly different populations of uniformly sized individuals at different vents, suggested that colonization was often effectively a single event. This may be the case for some of the community dominants, but it does not appear to be so for *Neolepas*.

It is important to note that *T. rufotincta,* in addition to producing large eggs, is also unusual for a *Tetraclita* in being distributed on numerous islands of the western Indian Ocean as well as continental shores. Large eggs in this case, and consequently large larvae, may be an adaptation to long-range dispersal, rather than simply to relatively sterile tropical waters as suggested by Achituv and Barnes (1978). If so, this may be in good part the explanation for the exceptionally large egg size in *Neolepas* whose "islands" are apparently hydrothermal springs.

NEOLEPAS AND THE HYDROTHERMAL ENVIRONMENT

Immigration into Hydrothermal Environments

An interesting question concerns how species or their ancestors first became adapted to the hydrothermal regime. It seems there are but 2 possibilities: (1) they either entered from shallow water in situations such as where islands are forming along ridge crests and rift zones intersect continental crust. Under such conditions they could first become adapted to the hydrothermal environment and then to the deep sea, or (2) they have been derived from deep-sea forms that became further adapted to the hydrothermal regime. The first option is the most parsimonious because there is a greater diversity of relatively eurytopic forms in shallow water to choose from and, in terms of gradients, the transition is less severe. But the deep-sea route is open and it is unlikely that nothing has taken advantage of it.

The new barnacle, *Neolepas*, is a scalpellid and the pollicipoid section of the family (Lithotryinae, Calanticinae and Pollicipinae; Zevina, 1978) is represented by 9 extant genera. Although 5 of these are exclusively intertidal or shallow water, 3 have wide bathymetric ranges, from less than 500 metres into abyssal depths (Zevina, 1978*a*). However, the latter are at a higher level of organization than the Lithotryinae. Therefore, because *Lithotrya* is intertidal and was likely derived from a shallow-water form comparable to *Neolepas*, it seems most probably that *Neolepas* was derived from a shallow-water lithotryine radiation of which *Lithotrya* is the sole surviving shallow-water representative.

Lithotrya, in inhabiting intertidal limestone in the western Atlantic and Indo-West Pacific, and in having no surviving shallow-water relatives, is apparently a relic that has escaped predation pressures of the reef environment by burrowing (Newman, 1960). This view, that *Lithotrya* is a relic, is shared with Foster (1978:122) who wrote: "The tropical rock-boring genus *Lithotrya* may . . . be an intertidal refugee of early scalpellid evolution, finding protection by boring into coral boulders. The few capitular plates . . . in addition to the basic five, may be a pre-pollicipoid condition in scalpellid evolution." Interestingly, appropriate predation pressures are inferred to have dramatically increased in the late Mesozoic (Vermeij, 1977), a time when the lithotryines are inferred to have evolved from the now wholly extinct *Eolepas* level or organization. It seems likely that it was during this late Mesozoic revolution that *Lithotrya* found its refugium in burrowing and *Neolepas* found refuge near hydrothermal springs in relatively shallow water.

Neolepas *and some Metals of the Hydrothermal Environment*

Rock-5, the substratum from which the sample of specimens of *Neolepas* was taken, was not clearly associated with an active hydrothermal vent. Unfortunately, there are no temperature data for this particular site, but the temperature field was estimated to range from near ambient (1.5°C) to as high as 5°C (R. Ballard, *personal communication*). The rock itself consisted of a clump of thickly encrusted empty worm tubes. The crust, at least that to which the largest barnacles were attached, proved to be a ferriferous deposit having a metallic composition of Fe, Si, Ca, Mn and Mg, in order of decreasing abundance. Aluminum was nearly equal in relative concentration to Mg, but Na, P, K, Cu and Zn were in trace amounts (Analytical Facility, SIO: Cambridge [S-4] SEM and Ortec Energy Dispersive X-ray Analyzer). The deposition of largely Fe rather than other metals such as Zn and Cu would be expected at the cooler end of the hydrothermal spectrum (R. Ballard, *personal communication*).

A similar appearing deposit was already noted as occurring on the shell of the barnacles, there being more on the older than the younger parts. The peduncular scales are particularly appropriate in this regard because they are graded in age. A series of scales was therefore sampled for SEM/X-ray analysis. A single scale was taken at intervals of 1 cm along the holotype specimen, beginning in the growth zone just below the capitulum and ending near the point of attachment to the substratum. The first scale, from the growth zone and therefore the youngest in the series, had a composition of Ca, S and Si, P and Fe, 5 of the 8 elements analyzed for. Iron moved up in relative concentration over the next 3 (older) intervals. Interestingly Mn appeared and then increased along with Fe so that the metallic composition of the crust on the older scales was commonly Fe, Mn, Ca, Si and Mg; a ferromanganese deposit. As noted above and by Francheteau et al. (1979), Mn is in relatively low abundances at 21°N. The high concentrations that develop on the scales of *Neolepas* are therefore curious. They may be due to bacterial activity because the scales of *Neolepas* are calcite (J. Hawkins, *personal communication*) and it has recently been demonstrated that calcite is required for Mn oxidation by pure cultures of marine bacteria (Nealson and Ford, *in press*).

The barnacles were being incrusted with ferromanganese deposits rather than salts or oxides rich in Zn and Cu reported from the high end of the hydrothermal temperature spectrum. Therefore the chemistry of the animals themselves was examined. Three samples were taken from the holotype of *Neolepas*—the left scutum (not destroyed in the process), the scutal adductor muscle and a slice of the prosomal region including a portion of the digestive gland. These same structures were also sampled from *Pollicipes polymerus*, a local intertidal relative of *Neolepas*. While scanning for metals, the proportions of Mg, and S to Ca were determined. The two species were quite similar except that Mg was higher in *Neolepas* than in *Pollicipes*, but Mg was higher than S only in the digestive gland and adductor muscle of *Neolepas*. Zinc was detected only in the digestive gland of *Neolepas*. Thus it appears that while *Neolepas* is ingesting and assimilating some Mg from the hydrothermal environment, it is ingesting but not assimilating Zn because there were no significant amounts in the musculature and exoskeleton.

The source of the Zn found in the digestive gland must be from ingested material from the surrounding water, presumably inorganic particles and the food, because there are only traces in the immediate substratum. The food is probably in good part bacteria that may be clinging to and extracting free energy from suspended zinc sulfide and similar oxidizable particles (K. H. Nealson, *personal communication*). Bacteria utilizing H_2S may also be involved (Corliss et al., 1979). It is notable that the filter feeding appendages and mouthparts of *Neolepas* are especially adapted to handle extremely fine particles.

ACKNOWLEDGMENTS

Thanks are due to Drs. F. Grassle and R. Hessler for allowing me to work on this material. I am most grateful to Dr. R. Ballard for collecting the specimens of *Neolepas*; to Drs. J. Hawkins, P. Lonsdale and K. Nealson for discussions about hydrothermal environments; to R. La Borde (Analytical Facility, SIO) for advice on the chemical analyses; to Drs. F. Schram and R. Hessler for helpful criticisms of the first draft of the manuscript; and to Drs. R. Scheltema and R. Strathmann for general discussions on reproductive strategies in marine invertebrates. The photo (Fig. 1) of *Neolepas* was taken by Mr. Larry Ford (Photographic Laboratory, SIO), and the drawings were prepared by Ms. Nancy Freres. Thanks are also due the Rise Project Group, supported by National Science Foundation grants OCE 78-01664, 78-21082 and 79-00984, for bringing together the technology and expertise that made the collection of the specimens of *Neolepas* possible. Support from the National Science Foundation (DEB 78-15052) for work on the systematics of cirripeds is gratefully acknowledged.

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ADDENDUM:

Three interesting pieces of lore bearing on cirriped evolution came to my attention after this article went to press. The first, thanks to Dr. F. Schram (San Diego Natural History Museum), is a paper by M. A. Whyte (1976, A Carboniferous pedunculate barnacle. Proceedings of the Yorkshire Geological Society *41*, part 1, (1):1–12 + pls. 1 & 2), describing what appears to be the first Paleozoic scalpelliform lepadomorph. Whyte interprets it to be at the *Eolepas/Archaeolepas* level of scalpellid organization, including peduncular scales as well as a capitulum of 6 plates (the basic 5 plus the rostrum; Table 1 herein). This places the origin of the scalpelliforms some 50 million years earlier than previously recognized and then virtually contemporaneous with the more primitive lepadiform *Praelepas* (5 capitular plates and naked peduncle). However, with the more generalized Cyprilepadidae (one pair of capitular plates and naked peduncle) appearing in the Silurian, there is at least a 100-million-year span in which the lepadiforms can make their appearance before the scalpelliforms, as indeed they must have.

Actually there appears to have been even more time available than this (Silurian to Carboniferous) for the lepadiforms to appear, since the second piece of lore concerns an apparent pedunculate barnacle from the Burgess Shale being described by Desmond Collins and David Rudkin (Royal Ontario Museum). Dr. Collins, at the suggestion of Dr. A. J. Southward (Plymouth), kindly allowed me to see pictures of what I cannot fault as a pedunculate barnacle. Thus the origin of the cirripeds must have been in the earliest Paleozoic as inferred herein (Table 1).

The third piece of lore further heightens appreciation of the ancient roots of the cirripeds. Mr. Mark Grygier (Scripps Institution of Oceanography) has discovered that an ascothoracican, *Dendrogaster* sp. from the Ross Sea, has a generalized flagellated spermatozoan otherwise unknown to the Crustacea, and he has since received a personal communication from Dr. K. G. Wingstrand (Copenhagen) that another ascothoracican, *Ulophysema* from the North Atlantic, likewise has flagellated sperm. Thus the cirripeds are not only very old but they must have stemmed from a reproductively unspecialized stock.

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Four species of *Pterynotus* and *Favartia* (Mollusca: Gastropoda: Muricidae) from the Philippine Islands

Anthony D'Attilio and Hans Bertsch

Abstract. Four species of muricid gastropods from the Philippine Islands are discussed and figured. Three of the species are described as new.

INTRODUCTION

During the past several years collectors and fishermen in the Philippines have obtained many new or otherwise interesting specimens of marine mollusks. Some of this valuable material has been given by collectors and dealers to museums in this country for study and identification, resulting in the publication of several new taxa (*see* Emerson & D'Attilio, 1979).

Through the courtesy of several shell dealers cited below, we have recently obtained for the collection of the San Diego Natural History Museum specimens of 4 species of muricid gastropods. These were obtained mostly by native Philippine fishermen using tangle nets laid out overnight in depths of 150 metres and less. One of these species was recently described by Dr. Kosuge in a new Japanese journal devoted to malacology; the other 3 are new species we describe herein.

Muricidae Rafinesque, 1815
Muricinae Rafinesque, 1815
Pterynotus Swainson, 1833

Type species *Murex pinnatus* Swainson, 1822 (=*Purpura alata* Röding, 1798) by subsequent designation, Swainson, 1833 (text to plate 122).

The genus *Pterynotus* encompasses Muricinae shells having 3 or more varical flanges or flanges developing into spines. Several subgenera have been proposed for this genus, especially by Jousseaume, 1880. These subgeneric taxa have been variously accepted or rejected or at times raised to full generic rank. The present species are referable to *Pterynotus* sensu stricto based on their alate trivaricate morphology and dentate labrum (as in the generic type species). A variable characteristic of the genus is the presence or absence of denticles on the columella. The new species described here as *Pterynotus aparrii* has columellar denticles, whereas *Pterynotus miyokoae* lacks denticles.

Pterynotus miyokoae Kosuge, 1979
(Figures 1a, b, c, d)

Original reference.—*Pterynotus miyokoae* Kosuge, 1979, pp. 1–2, plt. 1, figs. 1–7.

Supplementary description.—The shell of the largest specimen we examined is 67 mm high, broadly fusiform, protoconch of 1½ polished rounded whorls; spire of moderate height, strongly convex and possessing 7 whorls; suture deeply impressed. The

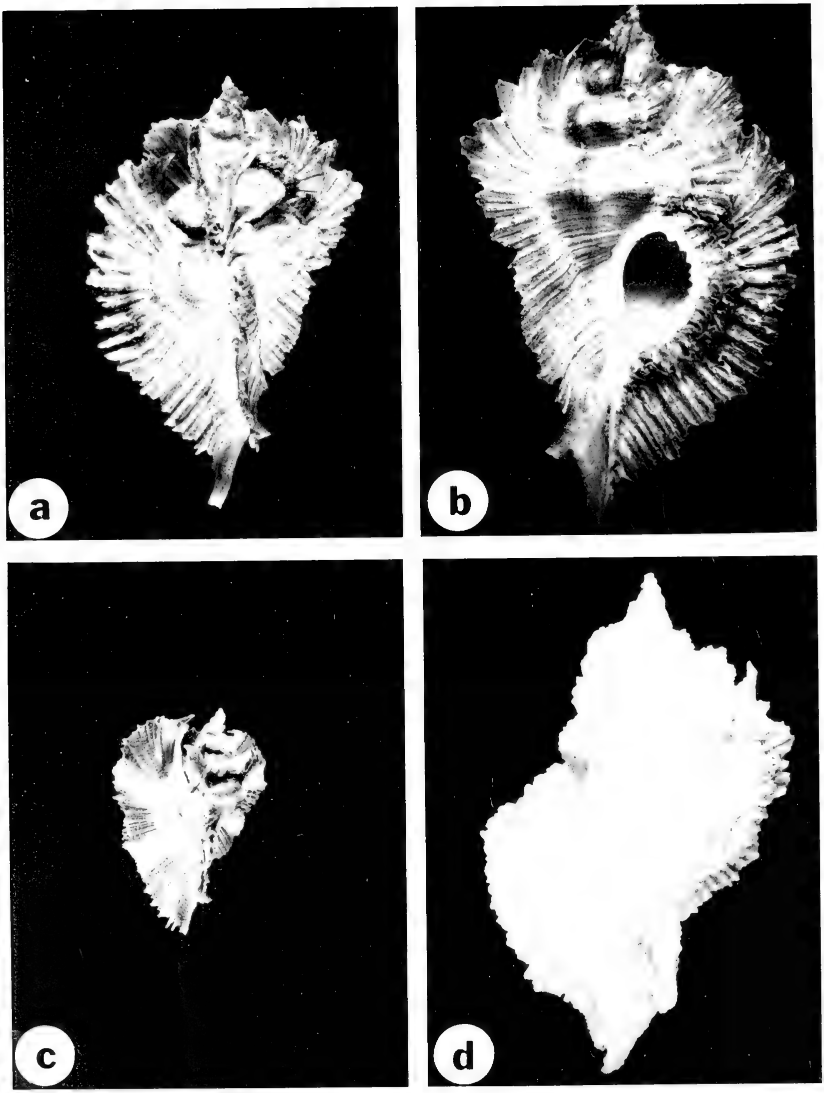

FIG. 1. *Pterynotus miyokoae* Kosuge, 1979. a. Dorsal view of shell, 67-mm-long specimen; Clifford and Clifton Martin Collection. b. Apertural view of shell of specimen illustrated in Fig. 1a. c. Dorsal view, 36-mm-long specimen; Ben and Ruth Purdy Collection. d. Dorsal view, 65-mm-long specimen, collected at Russell Island in the Solomons; AMNH 196014.

body is of moderate size relative to spire; canal moderately long, terminally attenuated, and recurved with a sinuous narrow opening. Aperture is broadly ovate, the anal sulcus is bracketed by a denticle on either side; immediately below the small denticle at the sulcus the entire outer crenulate lip has a continuous series of strong elongate denticles arranged singly posteriorly and in pairs anteriorly; closer to the apertural margin the major denticles have smaller swellings on either side which may become terminally bifurcate; the arcuate columella is simple.

Axial sculpture consists of 3 broad, wing-like varices which expand continuously from the lower portion of the canal to their termination at the suture. In addition the elongated varical wing is decidely recurved over the shoulder. The varices are aligned slightly oblique to the axis, and the flanges overlap on the spire with each new flange on the receding side of the earlier one; the margins of the varices terminate in short fine, spiny extensions varying slightly in length according to the strength of the spiral cords, but increasing in length so that the longest spine is near the preceding whorl. On the final and central varix there is a strong axial swelling which is the result of a strong depression between the varix and body and another lengthy depression on the forward side of the varical flange.

Two nearly equally-sized knobby costae are found intervarically on the shoulder and fading before the base of body whorl. Spiral sculpture consists of numerous primary cords (about 26) extending from the suture to the lower portion of the canal; the interspaces between the primary cords contain secondary or lesser cords; all spiral sculpture is scabrously ornamented except that when the scales are abraded the thickened bases of the scales remain in the form of knobs. The fluted leading (ventral) sides of the varical wings are scabrously laminate heavily below, lightly above where the surface displays strong fluting.

The shell is a medium shade of rust or rust brown; with one slightly paler band at the shoulder, one at the base of the body, and a much weaker one is perceptible on the canal. In light-colored specimens the shell appears white with pale brown bands. There is a narrow whitish band at the suture, the aperture is off white. Some specimens differ in the intensity of the brown color which is chocolate brown in one specimen.

The operculum is typically unguiculate muricine with the nucleus at the base and concentric ridges radiating from the nucleus.

Type locality.—Off Mactan Island, Cebu, Philippines, in 200 m.

Material examined.—1) One shell, 67 mm long; collected in the Philippine Islands, March 1979, from fishermen's nets, depth unknown; in the collection of Clifford and Clifton Martin.

2) Two specimens, 62 mm and 36 mm; dredged at Vaval, in the Philippine Islands, depth unknown. These specimens are in the collection of Ben and Ruth Purdy.

3) Two shells, 65 mm (AMNH collection 196014) and 53 mm (Robert and Dorothy Janowsky collection) long; collected at Russell Island in the Solomons (slightly southeast of 9° S; 159° E), January 1977, dredged from 600 feet (off a fine sand bottom with coral rubble). These specimens constitute a southeastward range extension for *Pterynotus miyokoae* of ≈4000 km from the Philippines.

Discussion.—As suggested by Kosuge, this species is most closely related to *Pterynotus loebbeckei* (Kobelt in Löbbecke and Kobelt, 1879), a species previously known from the area of Cebu and Bohol Islands in the Philippines as well as from the type locality in southeastern Japan. Through the courtesy of R. and D. Janowsky, we have examined specimens of *P. loebbeckei* (which establish a westward range extenstion of more than 8000 km) collected at Reunion Island in the Indian Ocean.

Pterynotus loebbeckei lacks the strongly sculptured characters of *P. miyokoae*, in that the axial costae are weak and form no prominent feature of the shell; the heavy ridge forms a conspicuous feature of the varical base in *P. miyokoae* but is lacking in *P. loebbeckei*; the varical margin is only weakly recurved; the strongly recurved portion of the varical flange over the shoulder on *P. miyokoae* but wanting in *P. loebbeckei,* being reduced in a descending manner towards the previous whorl. The columella of *P. miyokoae* in the 5 examples we examined is smooth and does not possess the characteristic strong denticles on the upper and lower portion which occur in *P. loebbeckei*; the outer (labrum) apertural denticles in *P. loebbeckei* are of simple form showing no other sculptural elaboration as in the new species. In contrast to the banded brown over whitish coloration of the new species, *P. loebbeckei* has an apricot orange or orange pink coloration within the outer portions of the aperture, and on the columella callous as well as over the remaining shell.

Pterynotus ***aparrii*** D'Attilio & Bertsch, sp. nov.
(Figures 2a, b, c, d)

Description.—Shell reaches approximately 35 mm high; narrowly fusiform, protoconch not preserved; spire relatively low of fine moderately convex whorls; suture weakly impressed; body whorl weakly convex and moderate in size; canal long, terminally tube-like and strongly recurved and narrowly open. Aperture is of a tear-drop shape, pointed anteriorly; anal sulcus u-shaped with a large knobby denticle on the outer side; the outer lip is wavy with crenulations reflecting the spiral sculpture and there are 5 short elongate denticles within the lower portion of the apertural margin; between these denticles and the large posterior one delimiting the anal sulcus there is a gap which has only one small denticle; the inner lip is adherent above, erect below and possesses 3 denticles on the lower half of the columella. The canal possesses the extension of a varical flange on its right side; a prominent recurved canal from a previous whorl is on its left side.

Axial sculpture consists of 3 blade-like varices which cross the shoulder strongly, diagonal to axis; the last and intermediate blade only is well developed; the varical blades are undulating and the margins have large lobe-like extensions at the shoulder, a secondary one at the base of body whorl and a lesser one on the canal; a single weak costa is found intervarically.

The spiral sculpture consists of numerous cords of minor or major character with the stronger cords extending the varical blade into a spiny-edged lobe; there are 3 major cords at the shoulder lobe, 2 to 3 major cords at the base of the body whorl and 2 on the canal; finer cords occur between the major cords to form a continuous varical blade from above the recurved portion of the canal to a termination of the blade against the preceding whorl; the entire surface of the intervarical area and the dorsal side of the varical blades are crossed by close set raised growth striae which are in addition scabrous when not abraded. The leading side of the varical blades are scabrously laminate below on the thickened varix, and less so on the fluted area of the blades as they project above the thickened varix.

Color of shell is pale orange; aperture is a deeper orange especially rich in the area of the denticles.

Operculum not known.

Material examined.—1) Holotype, San Diego Natural History Museum, Department of Marine Invertebrates, Type Series: SDNHM T.S. 518. Shell is 35 mm long; collected at Punta Engaño, Cebu Island, in the Bohol Straits, Philippine Islands, 1978, from fishermen's nets in approximately 75–100 metres of water.

2) Two specimens, 32 mm and 27 mm long; collected at Punta Engaño, Cebu, 1978, fishermen's nets. These specimens are in the collection of Ben and Ruth Purdy.

3) One specimen, 37 mm long; collected at Panglao, Bohol, Philippine Islands. This shell has a golden yellow coloration, and is in the collection of Gene Everson.

Type locality.—Punta Engaño, Cebu Island, Bohol Straits, Philippine Islands (approximately 10° 20′ N; 124° E).

Etymology.—The patronym honors a knowledgeable shell fisherman, Mr. Rudolpho O. Aparri of Cebu City, Philippine Islands (the -ii suffix results from adding the genitive singular case-ending to the entire surname).

Discussion.—This new species has a smaller shell than *Pterynotus loebbeckei* which it resembles superficially because of its color. It also resembles both in color and in size *Pterynotus bibbeyi* (Radwin and D'Attilio, 1976), known mostly from southeastern Japan.

The new species differs in having 3 varices, whereas in *P. bibbeyi* all specimens examined have 4 varices. *Pterynotus aparrii* also resembles *Pterynotus laqueatus* (Sowerby, 1841) which has a similar size and somewhat similar coloration. However,

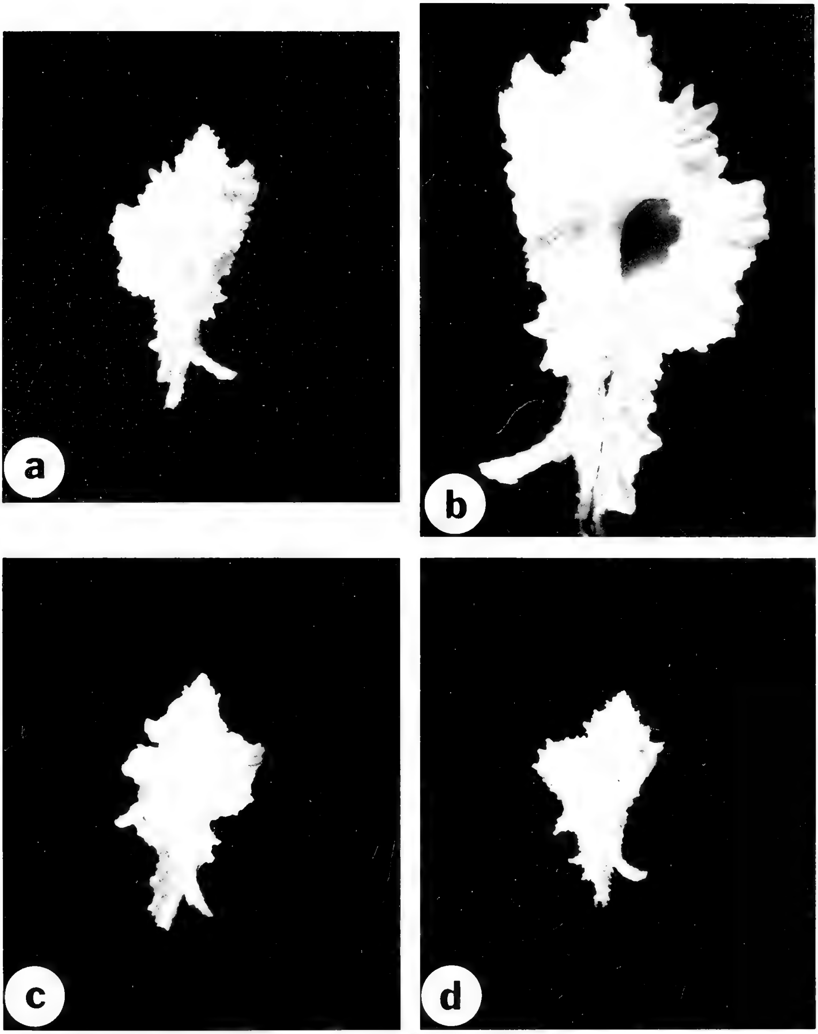

FIG. 2. *Pterynotus* ***aparrii*** D'Attilio & Bertsch, sp. nov. a. Dorsal view, holotype specimen, SDNHM T.S. 518 (shell is 35 mm long). b. Apertural view, holotype specimen, SDNHM T.S. 518. c. Dorsal view, 32-mm-long specimen; Ben and Ruth Purdy Collection. d. Dorsal view, 27-mm-long specimen; Ben and Ruth Purdy Collection.

P. laqueatus has not yet been discovered elsewhere than at Guam in depths accessible to scuba diving, in about 25 to 30 metres. *Pterynotus laqueatus* differs by its regular subcircular aperture, proportionately higher spire, coarser spiral sculpture, a strong intervarical costa, an additional costa at base of receding side of the varix, and its color which is variably shaded pink, pink-violet and pale orange.

Muricidae Rafinesque, 1815
Muricopsinae Radwin & D'Attilio, 1971
Favartia Jousseaume, 1880

Type species, *Murex breviculus* Sowerby, 1834, by original designation. Recent workers have treated the species referable to *Favartia* and *Murexiella* Clench and Perez Farfante, 1945, at differing generic–subgeneric levels. Radwin and D'Attilio (1976:144–161) recognized these genus-group taxa as full genera. Ponder (1972) virtually synonymized the 2 taxa, giving only a token subgeneric status to *Murexiella,* because the "shell features are not consistently different in species ascribed to both groups."

It is true that the species of *Favartia/Murexiella* show a range of variation for a number of characteristics, which appears diverse and inconsistent. A clear example of the range of shell morphology can be seen by comparing sculpture, spine length, and varical flange development of various species of *Favartia*: *F. humilis* (Broderip, 1833), *F. macgintyi* (M. Smith, 1938), *F. salmonea* (Melvill and Standen, 1899), *F. confusa* (Brazier, 1877), *F. cellulosa* (Conrad, 1846), and *F. brevicula* (Sowerby, 1834).

We agree with Ponder that justification does not exist for both *Favartia* and *Murexiella* to be recognized at the generic rank. We afford *Murexiella* subgeneric recognition and restrict to this taxon, species that have the long spines connected by varical webbing that is characteristic of *Favartia* (*Murexiella*) *hidalgoi* (Crosse, 1869), the type species, including also: *F.* (*M.*) *bojadorensis* (Locard, 1897?), *F.* (*M.*) *radwini* (Emerson and D'Attilio, 1970), *F.* (*M.*) *diomedaea* (Dall, 1908), *F.* (*M.*) *mactanensis* (Emerson and D'Attilio, 1979), and *F.* (*M.*) *martini* (Shikama, 1977).

Regardless of the different generic interpretations, the 2 new species described here are referable to *Favartia* (sensu stricto).

Favartia ***pelepili*** D'Attilio & Bertsch, sp. nov.
(Figures 3a, b, c)

Description.—This species has a shell attaining over 30 mm in height; is biconically fusiform, an indeterminate protoconch, a high spire of 5 weakly shouldered whorls, suture weakly defined; body moderately broad; canal broad above, below tapering tubelike and terminally strongly recurved, very narrowly opened, and bearing 3 previous terminal portions of the canals on its left side; aperture ovate moderately small with the margin strongly erect; the outer lip undulated into 5 troughs or grooves extending within for a short distance; no appreciable anal sulcus discernible.

Axial sculpture consists of 5 varices raised above into spiny extensions; the varices are aligned moderately diagonal relative to the axis of the shell, and over the shoulder the notable varical margin arches very strongly to the following varix, in part obscuring the suture; very fine growth striae are found intervarically.

Spiral sculpture consists of 5 rounded cords, the uppermost one at the shoulder, the interspaces between the cords diminish progressively to the fifth cord at base of body. The cords develop into recurved spines above (at apex) the varix, the shoulder one is longest and less recurved than the following 3, the last spine (5th) is much less recurved and is pointed in the growing direction. The spine on the canal is forward projecting and otherwise similar to the lowest spine on the body. Terminally these spines spread out into 2 or 3 folded lobes. Spinelets are distributed one each between the spines on the body and the canal spine. Two or 3 overlapping spinelets constitute the ornamentation on the varix across the shoulder. The spines are weakly opened or fold inwardly to touch centrally. On their leading side a 2nd smaller set of similar spines is nested between the lower portion of the major spines; below these secondary spines there are yet smaller similar spines. Between the last spines and the varical margin there are a few weak scabrous lamellae. The structure of secondary spines forms in effect a low webbing between the spines.

The shell is a light umber brown and a paler lighter umber suffuses the aperture.

The holotype is 33 mm long. The paratype is smaller (18 mm in length) and is

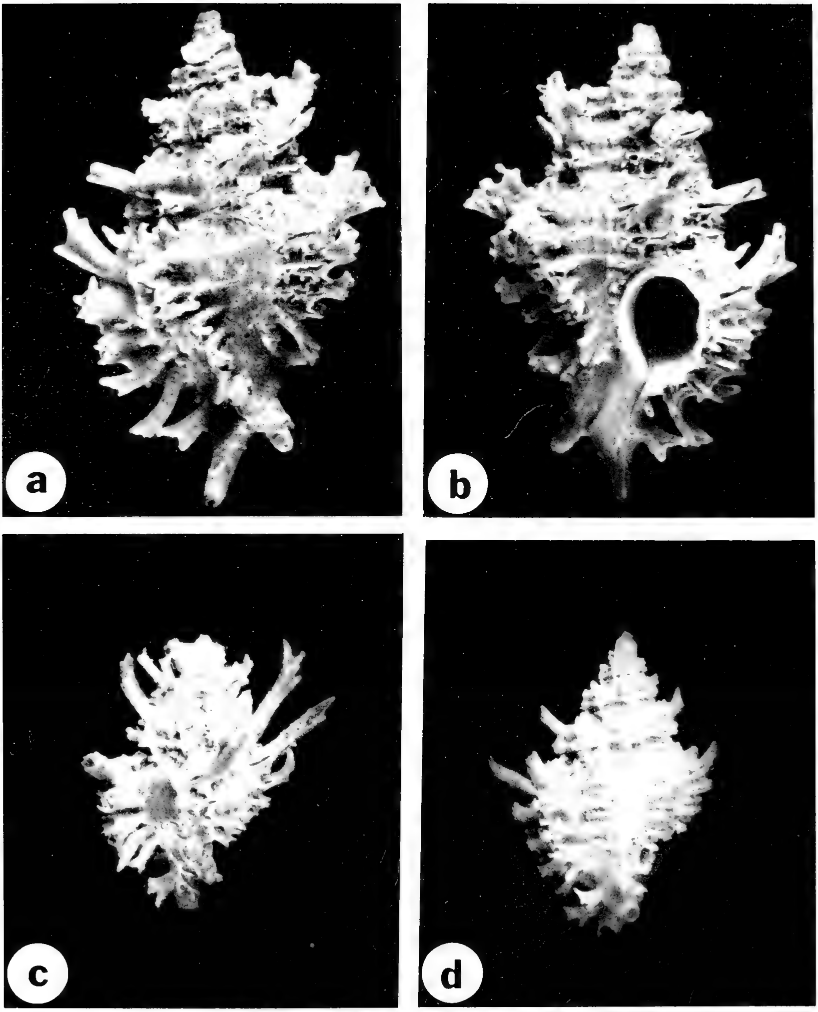

FIG. 3. *Favartia* ***pelepili*** D'Attilio & Bertsch, sp. nov. a. Dorsal view, holotype specimen, SDNHM T.S. 519 (shell is 31 mm long). b. Apertural view, holotype specimen, SDNHM T.S. 519. c. Dorsal view, paratype specimen, SDNHM T.S. 520 (shell is 18 mm long). *Favartia* ***judithae*** D'Attilio & Bertsch, sp. nov. d. Dorsal view, 20-mm-long shell; Judith Bertsch Collection.

distinguished from the holotype by the comparatively extreme length of the shoulder spines which are not bent and project diagonally upward as high as the spire. Color of paratype similar to holotype.

Material examined.—Two specimens; Holotype, SDNHM T.S. 519; shell is 33 mm long. Paratype, SDNHM T.S. 520; shell is 18 mm long. Both specimens collected in the Bohol Straits, between Bohol and Cebu Islands, Philippine Islands, early in 1979, by fishermen's nets in approximately 75 to 100 metres of water.

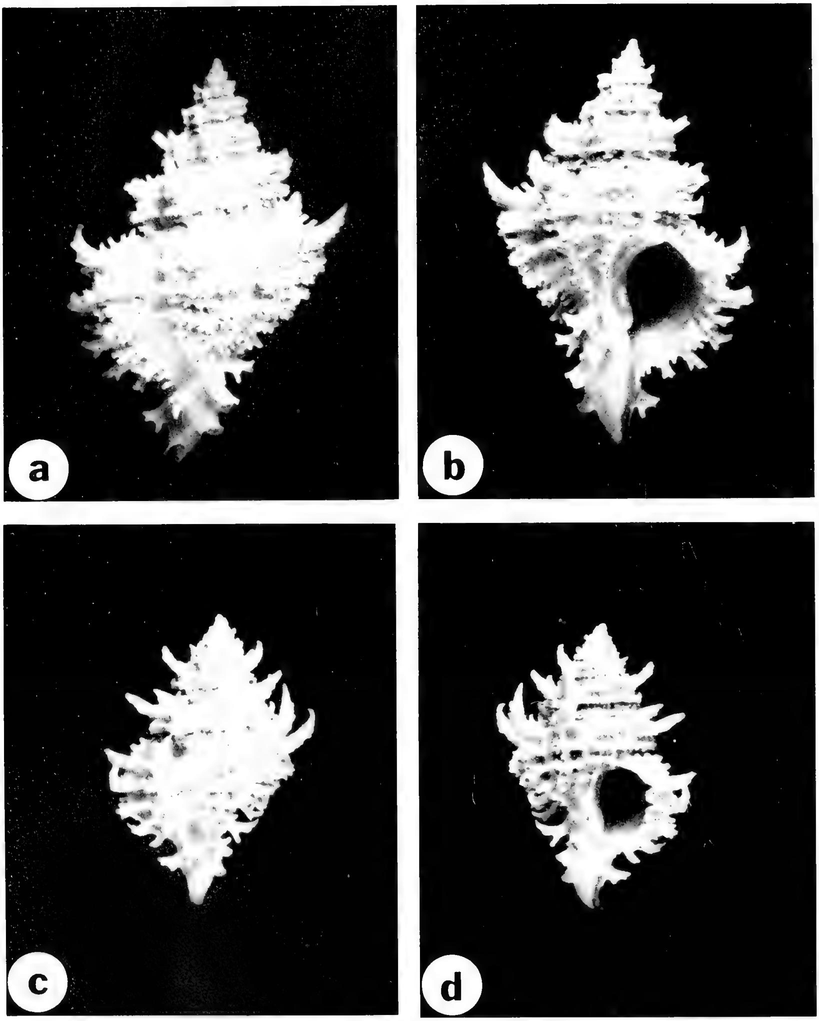

FIG. 4. *Favartia* ***judithae*** D'Attilio & Bertsch, sp. nov. a. Dorsal view, holotype specimen, SDNHM T.S. 521 (shell is 25 mm long). b. Apertural view, holotype specimen, SDNHM T.S. 521. c. Dorsal view, paratype specimen, SDNHM T.S. 522 (shell is 19 mm long). d. Apertural view, paratype specimen, SDNHM T.S. 522.

Type locality.—Bohol Straits, Philippine Islands (approximately 10° 20′ N; 124° E).

Etymology.—The species name means Pele's hair (a combination of Pele—Hawaiian volcano goddess, and *pili*—Latin plural, hairs; used as a noun in apposition; the genitive ending has been omitted from Pele for the sake of euphony), a term in vulcanology that indicates volcanic glass spun out into hairlike form. The shell with its long spines resembles a small piece of lava with wind-blown "hair" streaming behind.

Discussion.—This species differs from other Indo-Pacific species of *Favartia* by its larger size and longer spines on the varices. *Favartia salmonea* (Melvill and Standen, 1899) represents the opposite end of this type of shell development with varices having poorly developed scale-like spines; it also has a richly variable coloration from pink to orange or red. An intermediately related form is *Favartia balteata* (Sowerby, 1841), easily recognized by its flesh colored shell, rosy aperture, and short, burnt-brown, foliose scaley spines. Two other related species are *Favartia voorwindei* Ponder, 1972 and *Favartia striasquamosa* Ponder, 1972, which differ in having uncolored smaller shells of ≈10 mm and relatively lower spined varices numbering 6 to 7.

Favartia ***judithae*** D'Attilio & Bertsch, sp. nov.

(Figures 3d, and 4a, b, c, d)

Description.—This species reaches a length of ≈25 mm. The shell is broadly biconically fusiform, the protoconch (Fig. 4c–d) has 2½ rounded whorls, the spire is moderately high and consists of 5 convex whorls; the suture is weakly defined; the body whorl is broad and convex; the ovate aperture is moderate in size; the margin of the inner lip is adherent above and weakly erect below, the outer lip has an undulate margin that is a reflection of the external spiral sculpture; no anal sulcus discernible; the barely open canal is broad above with the tube-like recurving distal portion bent at a right angle, this character is best seen when this portion of the canal is preserved; in the holotype the canal ends shortly after starting to recurve. The terminal portions of 4 former canals are preserved on the siphonal fasciole.

Axial sculpture consists of 7 varices, the varices are broad with relatively narrow intervarical spaces; the varices are continuous over the shoulder from whorl to whorl and aligned diagonally to axis of the shell; the varical margins arch to the preceding whorl thereby obscuring the suture.

Spiral sculpture consists of 5 rounded cords situated from shoulder to base of body and progressively diminishing in strength in that direction; transverse striae are very fine. After crossing the intervarical spaces the cords terminate as spines above the crest of the varix. The shoulder spine is strongest but weakly recurved relative to the 2nd and 3rd which are more strongly recurved and in addition are twisted posteriorly; the 4th and 5th spines diminish in size and degree of recurving. All spines are open with their forward directed margins strongly undulate. Three progressively shorter similar spines are nestled below and within each main spine; the remaining varical area between the spines and the margin is ornamented with a few rows of scaly laminae. There is a strong spine on the canal preceding its recurved distal portion, additional single spinelets occur between the major spines, and 3 or 4 spinelets are situated between the spine on the canal and that on the body whorl. The varix above the shoulder has 4 or 5 marginally scabrous spinelets.

Shell color is a relatively rich flesh pink; the aperture ranges from a deeper pink to light red.

Material examined.—Three specimens. Holotype, SDNHM T.S. 521; shell is 25 mm in length. Paratype, SDNHM T.S. 522; shell is 19 mm in length. One specimen, shell length 20 mm, in the collection of Judith Bertsch. All 3 specimens were collected by tangle nets (in about 75 to 100 metres depth) off the north end of Mactan Island, Bohol Straits, Philippine Islands.

Type locality.—Bohol Straits, between Cebu and Bohol Islands, Philippine Islands (approximately 10° 20′ N; 124° E).

Etymology.—This species is named for Judith Bertsch, wife, fellow diver, and field assistant.

Discussion.—This species has a compact shell, richly scabrous in sculpture, and of similar morphology to *Favartia pelepili.* It differs from that species in the number of varices (7 as against 5 for *F. pelepili*), its smaller size and the reddish coloration in place of light brown. In contrast to the present taxon, most species of *Favartia* have smaller shells (except *F. breviculus*) and are commonly colored some shade of white or grey white. It is distinguishable from other Indo-Pacific species for the same reasons specified in the discussion of *F. pelepili.*

In both *Favartia pelepili* and *F. judithae*, the leading (adapertural or growing) side of the spines is exceedingly complex and bristly, bearing many smaller spines jammed up against each other. The receding (abapertural) edge, by comparison, is almost smooth. This extreme development of spines upon spines, and the great length of the major spines that recurve almost to 180°, are more characteristic of these two new species than other *Favartia* species in which these traits are less pronounced.

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A revision of the species of *Cafius* Curtis from the west coast of North America with notes of the east coast species (Coleoptera: Staphylinidae)

R.E. Orth and Ian Moore

Abstract. Ten west coast species of *Cafius* are described in detail. Lectotypes have been selected and are recorded for 8 of them. *Cafius bistriatus* (Erichson) and *Cafius caribeanus* Bierig are reported for the first time from western North America. Five east coast species are discussed. *Cafius sericeus* Holme does not occur in North America. The species previously reported under that name is *Cafius aguayoi* Bierig. Separate keys are presented for the west coast and east coast species. Drawings of the dorsal aspect and of the aedeagus of each species are given.

INTRODUCTION

Members of genus *Cafius* are generally restricted to seashores and the margins of rivers near the sea throughout the world. These insects are highly mobile, both on sandy beaches and in the air.

This study was undertaken because of the difficulty of distinguishing members of 2 Pacific coast species, *Cafius sulcicollis* (LeConte) and *Cafius decipiens* (LeConte), from the existing literature. Examination of type specimens has resolved that problem and indicated the presence of 2 species not previously reported from the west coast of North America.

According to Blackwelder (1952), the name *Cafius* was validated by Curtis in 1829 by "virtual monotypy." He said, "Curtis listed three species in 1829, but two of these are nomina nuda." The type species is *Cafius xantholoma* (Gravenhorst), a European species.

A few species of genus *Philonthus* were originally described in *Cafius* because of their seashore habitat, including one, *Philonthus nudus* (Sharp), from the west coast of North America. Members of *Philonthus* do not have the pronotal side margin deflexed, so that in *Philonthus* the large setigerous central puncture is on the marginal carina or removed from it by no more than the width of the puncture. In *Cafius,* and most other genera of the subfamily Staphylininae, the pronotal side margin is strongly deflexed in front so that the large central setigerous puncture is removed from the lateral carina by a least 3 × the width of the puncture. This is an excellent character for separating members of *Cafius* from those of *Philonthus. Philonthus nudus* (Sharp) (= *Philonthus johnsoni* [Fall]) was treated as a *Cafius* by Sharp (1874), Fall (1916) and Koch (1936); but it is obviously a *Philonthus,* as pointed out by Moore (1965). Another character useful in separating members of the 2 genera is dilation of the anterior tarsus. In *Cafius,* the anterior tarsus of both sexes is usually broadly dilated. In *Philonthus nudus,* the anterior tarsus is dilated very feebly in males and not at all in females.

Fifty-three species of *Cafius* are presently recognized. The majority of these are from temperate regions, although several species are widespread in the tropics. Four species are known from Europe, 4 from Japan, 12 from Australia, Tasmania and New Zealand, and

13 from North America. Of the North American species, 10 are found on the Pacific coast, 5 on the east coast and the West Indies, 2 of the species being common to both regions.

The first 2 species to be described from Pacific North America, *Cafius femoralis* and *Cafius canescens,* described by Mäklin (1852), were from Alaska. In 1863, LeConte described *Cafius opacus, Cafius dubius* (a synonym of *C. opacus*), *Cafius lithocharinus, Cafius decipiens,* and *Cafius sulcicollis* all from San Diego, California. Horn revised the North American species in 1884 and added 2 new species from California, *Cafius seminitens* and *Cafius luteipennis.* Fall (1916) described an insect from Washington as *Cafius johnsoni.* This species was treated as a subspecies of *Cafius nudus* (Sharp) from Japan by Koch (1936), and later removed to *Philonthus* by Moore (1965). Koch (1936) revised the world species of *Cafius,* but described no new North American species. Hatch (1957) treated the 5 *Cafius* species known from the Pacific Northwest and included good illustrations of them. The present study adds 2 species to the list of Pacific North American species.

Cafius has been divided into a number of subgenera. The North American species have been assigned to several of these subgenera. We feel that the subgenera which have been applied are poorly conceived and do not reflect phylogeny. Consequently we have not used the subgeneric category in this study.

Descriptions of larvae and pupae and notes on ecology have been provided for 4 of these species by James et al. (1971) and for 1 by Moore (1975). They observed that both larvae and adults are predaceous. Orth et al. (1978) found noxious beach flies to be less abundant when large numbers of staphylinids, mostly species of *Cafius,* were present in wrack where these flies were breeding. When staphylinids were scarce or absent, fly larvae were present in great numbers in the wrack and adult flies swarmed on the beach. They speculated that, under normal conditions, beach flies were under good natural biological control by wrack-inhabitating staphylinids.

METHODS

All measurements refer to greatest width or length of a given part. Length of the tempora is from the bottom of the eye to a line tangential to the base of the head. Suture of the elytra is measured from the posterior tip of the scutellum to a line tangential to the apices of the elytra.

Male genitalia, particularly the shape and relative lengths of the aedeagus and paramere, offer good characters for separating members of some of the species. When viewed from the side, the paramere usually touches or closely approaches the aedeagus at 2 points besides its basal attachment to the aedeagus, one near its middle and the other near its apex. These are raised areas on the aedeagus; so we have called them the **middle tumescence** and the **apical tumescence.** The relative distance of these 2 points from the basal attachment, from one another, and from the apex of the paramere are useful characters in distinguishing some species.

We have examined type material in the LeConte and Horn collections in the Museum of Comparative Zoology (MCZ), Harvard University. These collections consist of series of various numbers of specimens described by the above persons, as well as specimens of *Cafius canescens* and *Cafius femoralis* from Mäklin's type series.

Because there is some question as to which specimens constitute the original type series of some of these species, and to justify our choice of lectotypes, we have listed in full the data present on all specimens from both the LeConte and Horn collections.

In a letter written by John L. LeConte to Alexander Agassiz in 1875 and later published in the Coleopterist's Bulletin (LeConte, 1961), LeConte stated, in reference to his collection, "It has been enriched by the extreme liberality and courtesy of many distinguished European entomologists who have sent me even the second specimens of many North American species, which were otherwise unobtainable at that time. I have thus nearly a complete series of the species described from the West Coast by Eschscholtz, Mannerheim and Mäklin." This information was taken into consideration in selecting lectotypes for Mäklin's species from the LeConte collection.

A single specimen (usually the first in each series) in the LeConte and the Horn collection bears a red label reading "Type" and a number. These were apparently affixed by N. Banks, but never published, so they are not lectotypes. In most cases, we have selected specimens which we felt were more suitable as lectotypes than those specimens with the red "Type" labels.

The following abbreviations of names of repositories have been used: (CAS)-California Academy of Sciences, San Francisco; (ERIC)-Entomological Research Institute of Canada, Ottawa; (FMNH)-Field Museum of Natural History, Chicago; (MCZ)-Museum of Comparative Zoology, Harvard; (UCR)-University of California, Riverside; (USNM)-United States National Museum, Washington, D.C.

KEY FOR IDENTIFICATION OF *CAFIUS* OF WESTERN NORTH AMERICA

A. Pubescence of each abdominal tergite arranged on each side in the form of a cowlick so that outer hairs lie diagonal to lateral margin.
B. Two terminal sternites contrastingly more densely pubescent than preceding sternites .... 1. *C. seminitens* Horn
BB. Two terminal sternites not more densely pubescent than preceding sternites .... 2. *C. canescens* (Mäklin)
AA. Pubescence of abdominal tergites entirely longitudinal.
C. Tenth antennomere longer than wide.
D. Suture of elytra shorter than pronotum .... 3. *C. opacus* (LeConte)
DD. Suture of elytra not shorter than pronotum .... 4. *C. femoralis* (Mäklin)
CC. Tenth antennomere not longer than wide.
E. Punctures of undersurface of head partly coalescent .... 5. *C. lithocharinus* (LeConte)
EE. Punctures of undersurface of head not coalescent.
F. Elytra bright buff .... 6. *C. luteipennis* Horn
FF. Elytra reddish-brown to piceus.
G. Head reddish-brown .... 7. *C. decipiens* (LeConte)
GG. Head black.
H. Disc of pronotum strongly reticulate, dull .... 8. *C. sulcicollis* (LeConte)
HH. Disc of pronotum feebly or not reticulate, shining.
I. Gula strongly reticulate and granulate .... 9. *C. bistriatus* (Erichson)
II. Gula with fine wavy lines .... 10. *C. caribeanus* Bierig

1. *Cafius seminitens* Horn
Figs. 1A, 5A, 6A-C.

Cafius seminitens Horn, 1884, Trans. Amer. Ent. Soc. 11:235; Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:183; Dvořák, 1957, Ent. News, 68:15 Fig. 1-2 (♂); Hatch, 1957, Univ. Wash. Publ. Biol. 16:211; Moore, 1965, Coleopt. Bull. 19:98 Fig. 7 (pt.); James, Moore and Legner, 1971, Trans. San Diego Soc. Nat. Hist. 16:282 (larva), 283 Fig. 2 (larva), 285 (larva), 286 Fig. 6 (pupa); Moore, 1975, Pan-Pac. Ent. 51:140 (larva); Orth, Moore and Fisher, 1978, Wasmann Jour. Biol. 35:175 Fig. 5 (toto), 181, 182, 186 (ecology).

Description of lectotype.— ♂

This male from the Horn collection in MCZ is labeled as follows: "Cal", "Horn coll/H2259", "*seminitens/*_____[?] Calif." and "Lectotype/*Cafius seminitens*/Horn desig. '78/ R.E. Orth, I. Moore."

Type locality.—"California sea coast."

The lectotype is the only specimen in the Horn collection. The following specimens are in the LeConte collection: 1 female with a gold disc (California), a red label reading "Type 7328" and white labels reading "*P. seminitens* Hn." and "LeConte collection"; a male with a gold disc, a "♂" symbol and "LeConte collection"; a specimen with a "♂" symbol, "Cal." and "LeConte collection" labels; and 1 with "♂", "Cala." and "LeConte collection" labels.

Length.—9.1 mm.

Color.—Largely dark brown, with head piceus and lower edge of elytral epipleura and humerus infuscate to yellow.

Head.—Quadrate, wider than long, slightly wider than pronotum, widest near middle of tempora which are noticeably bulbous; eye slightly more than half as long as tempora; disc of head with a short central longitudinal impression, with 6 to 8 large widely spaced punctures on each side of midline and several more closely placed punctures behind eye; surface with very faint strigulose ground sculpture in impressions, otherwise polished; undersurface almost impunctate, with distinct strigulose ground sculpture; gula densely reticulate; antenna hardly longer than head; 10th segment wider than long.

Pronotum.—Wider than long, widest near apical angles; front margin nearly straight, apical angles narrowly rounded, sides gently arcuate into broadly rounded basal angles and arcuate base; disc with a shallow central longitudinal impression and a series of irregularly spaced punctures on each side of midline, with a few scattered punctures at sides; surface without ground sculpture except very faintly in the 2 rows of discal punctures.

Elytra.—With suture somewhat shorter than length of pronotum; each elytron slightly narrower than sutural length; surface very densely and uniformly punctured throughout.

Abdomen.—With acrocostal sutures of basal tergites wavy, with a central wide shallow blunt posteriorly directed cusp; more sparsely but as coarsely punctured as elytra, reticulate between punctures; pubescence coarse, silver colored, diagonally arranged near midline and at sides, the latter somewhat in the manner of a cowlick. First 5 visible tergites with a large impressed puncture centrally on each side of midline. Sternites 5 and 6 almost twice as densely punctured and pubescent as preceding sternites. Apical margin of 6th sternite with a triangular emargination about as deep as wide, without a membranous margin. In ventral view, aedeagus quite blunt at its apex as in *Cafius decipiens* males; but paramere much shorter relative to the aedeagus, than that of *C. decipiens* males and has more pegs on its inner face.

Male characters.—First 4 segments of the anterior tarsus broadly dilated. Head sometimes proportionately much wider than in female. Apical margin of 6th sternite with a triangular emargination.

Female characters.—Anterior tarsus almost as broadly dilated as in male. Head uniformly small. Apical margin of 6th sternite entire.

Variation.—Head and pronotum discs are, in most adults, more shiny than in those of *Cafius canescens.* The 2 rows of longitudinal punctures on the pronotal disc are not consistent. One specimen which we have seen has only a single puncture on each side near the apical margin. Most specimens have 6 to 8 punctures on each side; one has as many as 13; the rows always seem to be interrupted in the middle. In some specimens the pale color of the elytral humerus extends along the basal margin and also includes part of the scutellum.

Notes.—Members of this species closely resemble those of *Cafius canescens* but can be distinguished from the latter by their silvery pubescent, short antennae, wavy acrocostal suture and, particularly their densely pubescent 5th and 6th sternites.

The larva and pupa were described and notes on ecology were provided by James et al. (1971).

We have examined 870 specimens.

Distribution.—This species is known from British Columbia to Rosario, Baja California del Norte, Mexico, and undoubtedly extends farther south along the unexplored coast of Baja California, probably at least as far as Punta Eugenia, Baja California Sur. According to Orth et al. (1978), it was abundant at Refugio State Beach, Santa

Barbara County, California, in the spring and summer and was present there in most other months, but only rarely encountered during midwinter. Besides the type specimens, we have seen the following:

BRITISH COLUMBIA. Queen Charlotte Island, Keen (1; ERIC); Masset, Graham Island, Mrs. Clark (1; MCZ); Courtenay, 15 June 35 (1; ERIC); Metchosin, W. Victoria, 29 May 58, Lindroth (1; ERIC).

WASHINGTON. Seattle, King County, 30 June 66, L. Russell (2; UCR).

OREGON. Newport, Lincoln County, 17-21 July, Wickham (1; MCZ); Glenada, Lane County, 20 Aug. 41, B. Malkin (1; FMNH); Glenada, Lane County, 8 June 46, B. Malkin (3; FMNH); Coos Bay, Coos County, 6 Aug. 23, H. Notman (1; ERIC).

CALIFORNIA. Samoa Beach, Humboldt County, 27 Jan. 56, P.S. Bartholomew (8; CAS); San Miguel Island, Santa Barbara County, 20 June 10, V.W. Owen (3; CAS); many specimens from many localities from Marin County to San Diego County throughout the year but mostly from May to August.

MEXICO, BAJA CALIFORNIA NORTE. Many specimens from north of Ensenada mostly in July and August (UCR, ERIC); Ensenada, 31 Mar. 47, B. Malkin (1; FMNH); Ensenada, 3-5 June 05, F.X. Williams (1; CAS); Ensenada, 18 June 19, J.R. Sleven (13; CAS); Ensenada, 5 July 65, E. Schlinger (1; UCR); Ensenada, 16 Aug. 50, I. Moore (1; ERIC); Estero Beach, 20 July 60, I. Moore (1; ERIC); Colonia Guerrero, 28 May 50, I. Moore (5; ERIC); Laguna Santa Maria, 7 Sep. 55, I. Moore (2; ERIC); 15 mi N. Rosario, 1 Aug. 38, Ross & Michelbacher (8; CAS).

2. *Cafius canescens* (Mäklin)

Figs. 1B, 5B, 6D-E.

Philonthus canescens Mäklin, 1852, Bull. Soc. Imp. Moscow, 25:313.

Cafius canescens (Mäklin), Horn, 1884, Trans. Amer. Ent. Soc. 11:235; Casey, 1885, Bull. Calif. Acad. Sci. 1:337 Fig. 4 (pt.); Koch, 1936, Publ. Mus. Ent. Pietro Rossi 1:181 Fig. 2c (pt.), 183; Hatch, 1957, Univ. Wash. Publ. Biol. 16:211, Pl. 27 Fig. 5 (toto); Dvořák, 1957, Ent. News 68:18 Fig. 3-4 (♂); James, Moore and Legner, 1971, Trans. San Diego Soc. Nat. Hist. 16:281 Fig. 1 (larva), 282 (larva), 284 (larva), 285 Fig. 5 (pupa), 288 (pupa); Moore, 1975, Pan-Pac. Ent. 51:140; Orth, Moore and Fisher, 1978, Wasmann Jour. Biol. 35:175 Fig. 4 (toto), 181, 182, 185 (ecology).

Description of lectotype.— ♀

Length.—8.1 mm.

Color.—Largely piceus, with lower edge of elytral epipleura and humeral region pale.

Head.—Quadrate, slightly wider than long, lateral basal angles broadly rounded; eye a little longer than tempora; disc of head impunctate; area behind eyes and narrowly along base with large umbilicate punctures separated by their own diameters or less; disc of head with a shallow central longitudinal impression and a broad shallow circular impression on each side between eye and central groove; densely reticulate throughout; undersurface sparsely and coarsely punctured and densely reticulate; gula densely reticulate; antenna distinctly longer than head, 10th segment distinctly transverse.

Pronotum.—Wider than long; apex straight, apical angles rounded, sides nearly straight to broadly rounded basal angles, base gently arcuate; disc largely impunctate except for a longitudinal row of about 15 moderate-sized punctures in a groove on each side of midline; with rather dense setigerous punctures along side margins, particularly anteriorly; surface densely reticulate throughout.

Elytra.—With suture slightly shorter than length of pronotum; each elytron slightly wider than half of sutural length; surface very densely and uniformly punctured throughout.

Abdomen.—More sparsely but as coarsely punctured as elytra; reticulate between punctures, with acrocostal suture straight; pubescence coarse, golden, diagonally arranged near midline and at sides, the latter somewhat in the manner of a cowlick. First 5 visible tergites each with a large impressed puncture centrally on each side of midline.

Sternites uniformly punctured and pubescent throughout.

This female from the LeConte collection at MCZ has the right antenna missing beyond the 7th segment and is labeled as follows: "*canescens* Mäklin/Kodiak", "J. LeConte/collection", "lectotype/*Cafius canescens*/Mäklin desig. '78/R.E. Orth, I. Moore."

Type locality.—The original description gives the type locality as "Insula Edgecombe sub fuscis rejectis" (Edgecome Island, beneath wrack.) Because this is the only specimen in the LeConte collection which could be one of Mäklin's cotypes, we have chosen it as the lectotype. In the LeConte collection, there is also 1 male with a gold disc (California), a red label reading "*P. canescens* Mäklin."; another male with a gold disc; a male labeled "Cal." with a prominent ink dot under the C; and a male labeled "Cala."

Male characters.—First 4 segments of anterior tarsus broadly dilated. Apical margin of 6th sternite with a large triangular emargination as deep as wide, bottom of the emargination with a membrane with an oval margin. Head of most males larger than in females, in some males also wider than pronotum. Aedeagus differs from that of males of other Pacific coast species in being acutely pointed at its apex. Paramere relatively shorter than in males of other species, being hardly more than ½ the length of the aedeagus.

Female characters.—Anterior tarsus about as widely dilated as in male. Apical margin of 6th sternite entire.

Variation.—The extent of the pale humeral and elytral epipleural area varies slightly. In some specimens, reticulation of the disc of the head and pronotum is not strong.

Notes.—Adults of *Cafius canescens* and *C. seminitens* are easily recognized among the Pacific coast species of *Cafius* by the irregular arrangement of pubescence on the abdomen. In the other species, pubescence is regular and strictly longitudinal. In these 2, the pronotum is wider than long, a condition which occurs otherwise only in some males of *C. lithocharinus. Cafius canescens* adults differ from *C. seminitens* adults particularly in the lack of dense pubescence on the 2 terminal sternites, in the shorter antennae, reticulate disc of the head and pronotum, and the straight acrocostal suture.

Description of larva and pupae and notes on ecology were provided by James et al. (1971).

We have seen 5197 specimens.

Distribution.—This species is known from Kodiak, Alaska, to El Tomatal, Baja California Norte, Mexico. Its range undoubtedly extends much farther south along the unexplored coast of Baja California, probably at least to Punta Eugenia, Baja California Sur. It is the commonest species of *Cafius* in the spring and summer on southern California beaches. Adults are abundant in wrack, but can also be seen flying along the beach and alighting on sand. Orth et al. (1978) reported adults at Refugio State Beach, Santa Barbara County, California, in all months of the year except January, but most abundantly in the spring. Besides the type specimens, we have seen the following:

ALASKA. Kukal Bay, 5 July 99, T. Kincaid (7; USNM); Mt. Pariat, Alaska Peninsula, 7 Sep. 13, E.C. Van Dyke (1; ERIC); Propoff Island, 5 July 99, T. Kincaid (11; USNM); Sitka, Liebeck (1; MCZ).

BRITISH COLUMBIA. Courtenay, Gregson (1; CAS); Kyle Bay, 6 May 32, Gregson (3; ERIC); Q[ueen] C[harlotte] Isl[ands], J.H. Keen (1; ERIC); Masset, Graham Island, Mrs. Clark (1; MCZ); Tofino, July 26, Spencer (1; CAS); Vancouver, 23 July 32, H.B. Leech (8; ERIC); Victoria, Hubbard & Schwartz (1; USNM).

WASHINGTON. Many localities mostly in the warm months.

OREGON. Many localities mostly in the warm months.

CALIFORNIA. West Cove, Catalina Island, Los Angeles County, 11-14 July 71, J. Pinto (1; UCR). Many localities, the majority from Marin County to San Diego County, mostly in the warm months.

MEXICO, BAJA CALIFORNIA NORTE. La Misión de San Miguel, May-Aug. 50, I. Moore (257; ERIC); La Salina, July-Aug. 71, I. Moore (1117; UCR); Colonia Guerrero, 28 May 50, I. Moore (71; ERIC); Colonia Guerrero, 16 Aug. 50, I. Moore (8; ERIC); El Tomatal, 18 June 74, V. Lee (1; CAS).

3. *Cafius opacus* (LeConte)

Figs. 1C, 5C, 6F-G.

Philonthus opacus LeConte, 1863, Smith. Misc. Coll. VI, No. 140:40.
Cafius opacus (LeConte), Horn, 1884, Trans. Amer. Ent. Soc. 11:235,239; Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:192; Orth, Moore and Fisher, 1978, Wasmann Jour. Biol. 35:176 Fig. 8 (toto), 182, 187 (ecology).
Philonthus dubius LeConte, 1863, Smith. Misc. Coll. VI, No. 140:39.
Cafius dubius (LeConte), Horn, 1884, Trans. Amer. Ent. Soc. 11:244.

Description of lectotype. — ♂

Color.—Largely bright reddish-brown with an indistinctly darker area on disc of head near each eye, entire disc of each elytron darker with margins pale, and basal abdominal segments nebulously darker.

Head.—Quadrate, somewhat wider than long, lateral basal angles broadly rounded; eye small, about ⅖ as long as tempora; punctures of upper surface relatively small, simple, separated mostly by more than their diameters, with a very narrow inconspicuous impunctate strip through middle; ground sculpture finely, densely reticulate throughout; undersurface with puncturation and ground sculpture very similar to that above; gula finely and densely reticulate; antenna about ⅓ longer than combined lengths of head and pronotum, 10th segment ⅙ longer than wide.

Pronotum.—About ⅕ longer than wide, apex arcuate, widest near broadly rounded apical angles, sides almost straight but just perceptibly concave before broadly rounded basal angles, base arcuate; surface with simple punctures very similar in size to those of head, regularly arranged from impunctate central area to lateral margin, central impunctate area clearly defined and slightly elevated above rest of surface; surface densely and finely reticulate throughout.

Elytra.—With suture about ⅔ length of pronotum; each elytron about ¾ as wide as sutural length; surface very finely and densely sculptured, punctures hardly noticeable.

Abdomen.—With acrocostal suture straight; surface finely rather densely punctured and reticulate; pubescence fine, longitudinal throughout.

This male in the LeConte collection in MCZ has a gold disc (California) and a small ♂ symbol, beneath which is a red label reading "Type 6291" and a white label reading "*P. opacus* LeC. S.D." We have affixed a yellow label reading "Lectotype/*Cafius opacus*/LeConte desig. '78/R.E. Orth, I. Moore."

Type locality.—San Diego, California.

Besides the lectotype, there are 2 males and a female bearing gold discs in the LeConte collection, the males each with a small ♂ symbol. There are also 2 females with "Cala." labels, each with a small check in ink under the letter C. Another pin carries 2 cards, each of which has 2 specimens glued to it and a "Cal." label with a conspicuous ink dot under the letter C. These last 6 specimens may or may not be a part of the original series.

Male characters.—First 4 segments of anterior tarsus broadly dilated; apical margin of 6th sternite with a large oval emargination surrounded by a narrow membranous margin. Genitalia similar to those of *C. bistriatus* males but pegs on inner face of paramere more numerous and tightly clustered at apex of paramere than in the latter.

Female characters.—Anterior tarsus about as broadly dilated as in male; apical margin of 6th sternite is entire.

Variation.—Color, particularly of the head, abdomen and sometimes the elytra, varies from bright reddish-brown to dark reddish-brown.

The single male specimen labeled *C. dubius* LeConte in the LeConte collection has a gold disc (California), a white label reading "*P. dubius* LeC. S.D." and a red label reading "Type 6292." It is a dark specimen of *C. opacus*. The genitalia have been dissected and are in glycerine in a plastic capsule on the pin. The type locality is "San Diego, California," LeConte 1863.

Notes.—Adults of this species are easily distinguished from those of all other Pacific coast species of *Cafius*, except *C. femoralis*, by their elongate 10th antennomere. They differ from *C. femoralis* adults in having shorter elytra in which the suture is shorter than the pronotum. In the latter species, the elytral suture is as long as the pronotum.

The immature stages have not been described.

We have seen 214 specimens.

Distribution.—This species is known from Refugio State Beach, Santa Barbara County, California, to Socorro Dunes, Baja California Norte. Orth et al. (1978) reported adults from Santa Barbara County, California, from September to May. Besides the type specimens, we have seen the following:

CALIFORNIA. Refugio State Beach, Santa Barbara County, R.E. Orth (6) 15 Oct. 76, (2) 8 Nov. 76, (1) 6 Dec. 76, (14) 17 Jan. 77, (9) 7 Feb. 77, (3) 14 Apr. 77, (65) 17 May 77 (UCR); San Pedro, Los Angeles County, Aug., E.C. Van Dyke (1; CAS); San Pedro, Los Angeles County, E.C. Van Dyke (9; CAS); San Pedro, Los Angeles County, 8-11-03, Blanchard (1; MCZ); San Pedro, Los Angeles County, Aug., Wickham (1; USNM); Torrey Pines, San Diego County, 7 Apr. 34 (1; ERIC); Torrey Pines, San Diego County, 15 Nov. 50, I. Moore (1; ERIC); La Jolla, San Diego County, 22 Nov. 50, I. Moore (1; ERIC); Point Loma, San Diego County, 28 Dec. 28, E.C. Van Dyke (19; CAS); San Diego, San Diego County, F.E. Blaisdell (11; CAS); San Diego, San Diego County, 23 May 27 (1; CAS); Coronado, San Diego County, 7 June 90, F.E. Blaisdell (1; CAS).

MEXICO, BAJA CALIFORNIA NORTE. Rio San Telmo, 16 June 38, Ross & Michelbacher (70; CAS); Socorro Dunes, 17 July 74, R.M. Haradon, V. Lee & W.E. Savary (1; UCR).

4. *Cafius femoralis* (Mäklin)

Figs. 1D, 5D, 7A-B.

Philonthus femoralis Mäklin, 1852, Bull. Soc. Imp. Moscow 25:189.

Cafius femoralis (Mäklin), Horn, 1884, Trans. Amer. Ent. Soc. 11:235, 238; Casey, 1885, Bull. Calif. Acad. Sci. 1:337 Fig. 5 (pt.); Koch, 1936, Publ. Mus. Ent. Pietro Rossi 1:199; Hatch, 1957, Univ. Wash. Publ. Biol. 16:210, 355 Pl. 27 Fig. 2 (toto).

Cafius mutatus Gemminger and Harold, 1868, Cat. Coleopt. 2:590.

Description of lectotype.— ♂

Length.—5.8 mm.

Color.—Head black, pronotum and abdomen dark brown, elytra slightly paler, femora and tarsi pale brown, tibiae dark brown, mouth parts and base of antenna dark brown, antenna progressively paler toward apex.

Head.—Quadrate, about as long as wide, basal angles broadly rounded; eye more than half as long as tempora; punctures of upper surface small, separated by about their diameters, with a central longitudinal impunctate area along length of head; ground sculpture finely, densely reticulate; undersurface finely and densely punctured and reticulate; gula densely reticulate; antennae distinctly longer than combined lengths of head and pronotum; 10th segment ¹⁄₁₀ longer than wide (contrary to statements by Horn 1884, pp. 235, 238).

Pronotum.—Longer than wide; apex broadly rounded; widest near broadly rounded apical angles, thence narrowed with sides nearly straight to the somewhat narrowly rounded basal angles; base arcuate; surface with evenly placed dense small punctures except for central longitudinal impunctate area, densely reticulate except for a small tumid area in middle at base.

Elytra.—With suture a little shorter than length of pronotum; surface so finely and densely sculptured that punctures hardly visible.

Abdomen.—With acrocostal suture nearly straight; finely rather densely punctured and reticulate; pubescence fine, longitudinal throughout; undersurface uniformly punctured and pubescent. Apex of 6th sternite with a triangular emargination which is about as wide as deep, the base of which has a membrane with an oval emargination.

This male has a gray disc, a male symbol, a white square reading "177", a red label reading "Type 7330", a large white label reading "*Philonthus femoralis*/Mäklin/Kodiak", a label reading "LeConte/collection", and one reading "Lectotype/*Cafius* *femoralis*/Mäklin desg. '78/R.E. Orth, I. Moore." One other specimen, a female, in the LeConte collection has a label reading "*maritimus* Mots. Kodjak" and a "LeConte collection" label.

Type locality.—Kodiak Island, Alaska.

Male characters.—Anterior tarsus broadly dilated. Apical margin of 6th sternite with deep triangular emargination with a membrane at its bottom. Genitalia similar to those of *Cafius luteipennis* males; but paramere with 10 pegs on its inner face rather than 6 as in members of the latter species.

Female characters.—Anterior tarsus almost as broadly dilated as in male. Apical margin of 6th sternite entire.

Variation.—There is little variation among the specimens seen by us.

Notes.—*Cafius femoralis* and *C. opacus* are unique among Pacific coast species in having the 10th antennal segment longer than wide. In *C. opacus* adults, the elytral suture is distinctly shorter than the pronotum, whereas in *C. femoralis* adults, it is fully as long as the pronotum.

The immature stages have not been described.

We have examined 239 specimens.

Distribution.—This species is known from Alaska to Carmel, Monterey County, California. Besides the type specimens, we have seen the following:

ALASKA. Haines, 3 June 68, Campbell & Smetana (30; ERIC); Kodiak (1; MCZ).

BRITISH COLUMBIA. Q[ueen] C[harlotte] I[sland], [Keen], (4; ERIC); Masset, Graham Island (1; MCZ); Bowser, 12 June 55, W.J. Brown (25; ERIC); Pacific Rim, N.P. Michigan Cr., 12 July 75, M. & B. A. Campbell (23; ERIC); Metchosin, West Victoria, 29 May 58, Lindroth (1; ERIC); Victoria, Hubbard & Schwarz (1; USNM).

WASHINGTON. Port Angelus, Clallam County, 28 May 07, E.C. Van Dyke (18; CAS).

OREGON. Cannon Beach, Clatsop County, 15 June 27, E.C. Van Dyke (1; CAS).

CALIFORNIA. Bear Harbor, Mendocino County, D. Giuliani (6; ERIC); Needle Rock, Mendocino County, 6 Oct. 74, D. Giuliani (4; UCR); Mouth of Russian River, Sonoma County, Jan. 70, D. Giuliani (1; UCR); Carmel, Monterey County, 4 Feb. 17, L.S. Slevin (1; CAS); Carmel, 28 Mar. 22, (22; CAS); Carmel, 13 Apr. 13, L.S. Slevin (1; CAS); Carmel, 21 May 11, E.C. Van Dyke (1; CAS).

5. *Cafius lithocharinus* (LeConte)

Figs. 2A, 7C-D.

Philonthus lithocharinus LeConte, 1863, Smith. Misc. Coll. VI, No. 140:38.

Cafius lithocharinus (LeConte), Horn, 1884, Trans. Amer. Ent. Soc. 11:23, 236; Koch, 1936, Publ. Mus. Ent. Pietro Rossi 1:193; Hatch, 1957, Univ. Wash. Publ. Biol. 16:210, 235 Pl. 27 Fig. 2 (toto); James, Moore and Legner, 1971, Trans. San Diego Soc. Nat. Hist. 16:282 (larva), 288 (pupa); Leech and Moore, 1971, Wasmann Jour. Biol. 29:66 (ecology); Mòore, 1975, Pan-Pac. Ent. 51:140 (larva); Orth, Moore and Fisher, 1978, Wasmann Jour. Biol. 35:175, Fig. 6 (toto), 182, 183, 186 (ecology).

Description of lectotype.— ♂

Color.—Largely piceous with, near inner apical angle of each elytron, a buff to reddish-brown nearly circular spot extended to apical margin but not to suture. Sixth and 7th visible tergites and cerci reddish-brown; 4th sternite with a small reddish-brown area on each side near base and a similar transverse band near apical margin, 5th sternite largely reddish-brown with lateral and apical margins piceous, 6th and 7th sternites reddish-brown. Elytral epipleura buff colored. Legs reddish-brown.

Head.—Quadrate, slightly wider than long, lateral basal angles broadly rounded; eye ½ length of tempora; punctures of upper surface large, umbilicate, largely separated by about their diameters, somewhat more crowded at base; with an impunctate area adjacent to clypeal margin connected narrowly with a broad central impunctate area; ground sculpture finely, densely reticulate throughout; undersurface roughly sculptured with large coarse coalescent punctures arranged in diagonal rows; gula densely and finely reticulate; antenna slightly shorter than combined lengths of head and pronotum, 10th segment slightly wider than long.

Pronotum.—About as wide as long; apex broadly rounded; widest near broadly rounded apical angles, thence narrowed with lateral margins slightly concave to the broadly rounded basal angles; base arcuate; surface with simple punctures separated by less than their diameters, somewhat smaller and more crowded than those of head; central impunctate area clearly defined; not elevated except very slightly in a small area near base; surface densely reticulate and dull throughout except for small, somewhat shiny basal area.

Elytra.—With suture slightly shorter than length of pronotum; each elytron ¾ as long as sutural length; surface very finely, uniformly densely, somewhat roughly punctured; finely reticulate between punctures.

Abdomen.—Finely and more sparsely punctured than elytra; finely reticulate between punctures. Acrocostal sutures straight. Pubescence fine, longitudinal throughout. Undersurface uniformly punctured and pubescent throughout.

This large male in the LeConte collection at MCZ has the left antenna missing beyond the 3rd segment. Below the specimen, a gold disc (California) and a small ♂ symbol are attached. We have added a label reading "Lectotype/*Cafius lithocharinus*/ LeConte desig. '78/R.E. Orth, I. Moore."

Type locality.—San Diego, California.

Besides the lectotype, there are 2 males and 1 female in the LeConte collection bearing gold discs. One of the males has a white label reading "*P. lithocharinus* LeC. S.D." and a red label reading "Type 6288." The LeConte collection also includes 2 males and 3 females labeled "Cal" and 1 female labeled "Cal" with a conspicuous ink dot under the C. These last 6 specimens may not be part of the original type series.

Male characters.—First 4 segments of anterior tarsus broadly dilated. Apical margin of 6th sternite with triangular emargination about as deep as wide, emargination partly filled by membrane with an oval emargination. Genitalia most similar to those of *C. femoralis* males. However, aedeagus not as strongly tapered at apex and paramere somewhat longer in relation to aedeagus than in *C. femoralis* males.

Female characters.—Head about as wide as pronotum, anterior tarsus almost as broadly dilated as in male and 6th sternite simple.

Variation.—Color, particularly that of the elytra, is variable. Rarely is the disc of the elytra entirely piceous. The buff colored spot may be variously enlarged or may extend across the entire apex of the elytra, or, in few specimens, even forward to cover the entire elytron. In the latter case, the specimen will resemble *Cafius luteipennis* adults; but the elytra have a more reddish cast compared with the yellowish cast of *C. luteipennis* adult elytra. The legs and abdomen are variably darker in some specimens. Size of the head and pronotum of males varies considerably. In some males, such as the lectotype, the head is much wider than the pronotum, in which case, the pronotum is also wider than usual, about as wide as long. In other males, the head is variably narrow until it may be no wider than pronotum in which case the pronotum is longer than wide. In females, the head is always about as wide as the pronotum, which is longer than wide. In some females, the punctures on the undersurface of the head are not strongly coalescent.

Notes.—Most specimens of *Cafius lithocharinus* can be recognized by the pale apical margin of the elytra; but, as mentioned above, some individuals have the elytra entirely piceous or entirely pale. The sculpture of the undersurface of the head readily distinguishes members of this species from all other Pacific coast species; the punctures are very large, deeply impressed and crowded in diagonally arranged short rows of coelescing punctures. The sculpture of the undersurface of the head is coarse and rough.

The larvae, pupae and ecology were described by James et al. (1971).

We have examined 5506 specimens.

Distribution.—This species is known from British Columbia to Cedros Island, Baja California del Norte, Mexico. According to Orth et al. (1978), adults were abundant in wrack at Refugio State Beach, Santa Barbara County, California, from September through March but not from April to August. They said, "It is known to fly in swarms along the beach in winter probably on dispersal flights (Leech and Moore 1971); and at such times can be found under almost every bit of debris on the beach. Flights look deceptively like swarms of flies." Besides the type series, we have seen the following specimens:

BRITISH COLUMBIA. Pacific Rim, Klanawa River, 14 July 75, J.M. & B.A. Campbell (117; ERIC).

WASHINGTON. 2 mi. n. La Push, Clallam County, 17 Oct. 74, D. Giuliani (1; UCR); Kaloloch, 3 Sept. 34, A.L. Melander (1; MCZ).

CALIFORNIA. Sonoma, Sonoma County, June 27, Ricksecker (1; FMNH); many spms., many localities from Marin County to San Diego County, mostly from Sep. to May.

MEXICO, BAJA CALIFORNIA NORTE. Rosarito Beach, 27 May 50, I. Moore (34; ERIC); Descanso Bay, 29 May 50, I. Moore (1; ERIC); La Misión de San Miguel, 27 May 50, I. Moore (3; ERIC); La Salina, var. dates June-Aug. 71, I. Moore (35; UCR); Ensenada, 16 Aug. 50, I. Moore (1; ERIC); Rio San Telmo, 15 June 38, Ross & Michelbacher (1; CAS); Camalú Point, San Ramón Bay, 19 June 39, Harbison & Bildebeck (2; UCR); Colonia Guerrero, 28 May 50, I. Moore (15; ERIC); 15 m. n. Rosario, 1 Aug. 38, Ross & Michelbacher (14; CAS); Estero Rosario, 25 Apr. 68, P. Arnaud (95; CAS); n. end Cedros Island, 27 Mar. 53, J. Figg-Hoblyn (1; ERIC.)

6. *Cafius luteipennis* Horn
Figs. 2B, 7E-F

Cafius luteipennis Horn, 1884, Trans. Amer. Ent. Soc. 11:235, 237; Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:191; Hatch, 1957, Univ. Wash. Publ. Biol. 16:211, 355 Pl. 27 Fig. 3 (toto); James, Moore and Legner, 1971, Trans. San Diego Soc. Nat. Hist. 16:282 (larva), 284 Fig. 3 (larva), 287 Fig. 7 (pupa); Moore, 1975, Pan-Pac. Ent. 51:140 (larva); Orth, Moore and Fisher, 1978, Wasmann Jour. Biol. 35:175 Fig. 7 (toto), 182, 183, 186 (ecology).

Description of lectotype.— ♂

Color.—Piceus with elytra bright buff.

Head.—Quadrate, about as wide as long, lateral basal angles broadly rounded; eye about ¾ as long as tempora; punctures large umbilicate, mostly separated by their diameters or less; disc with a small irregularly defined impunctate area; reticulate between punctures; undersurface with large evenly spaced weakly impressed punctures throughout; antennae almost as long as combined lengths of head and pronotum, 10th segment a little wider than long.

Pronotum.—Somewhat longer than wide; apex nearly straight, widest near broadly rounded apical angles, thence narrowed with lateral margin very slightly concave to broadly rounded basal angles; base arcuate; surface with simple punctures mostly spaced about as on head, with a broad central longitudinal impunctate area and a small irregularly shaped impunctate area on each side near the apex adjacent to line of punctures which delimits the central impunctate space; surface densely reticulate throughout.

Elytra.—With suture shorter than length of pronotum; each elytron ½ as wide as sutural length; surface finely, densely punctured, reticulate between punctures.

Abdomen.—With acrocostal sutures straight; finely and more sparsely punctured than elytra, finely reticulate; pubescence fine, longitudinal throughout. Sternites uniformly punctured and pubescent.

This male from the Horn collection in MCZ bears the following labels: "Cal", "Horn coll/H2261" and "Lectotype/*Cafius luteipennis*/Horn desig. '78/R.E. Orth, I. Moore."

Besides the lectotype, there are 9 specimens with the same data as the lectotype in the Horn collection, 1 of which also bears a label reading "*Ph. luteipennis* LeC." (Sic!). The LeConte collection also contains the following specimens: 1 female with labels reading "Cal" underlined in red ink, a red label reading "Type/7329" and a "*C. luteipennis* J.

LeC.'' (Sic!) label; a male with a ''Cal'' label with an ink dot under the C; a female with a ''Cala.'' label and a female with a ''Cal'' label underlined with red ink.

Male characters.—First 4 segments of anterior tarsus broadly dilated. Apical margin of 6th sternite with a shallow oval emargination with a membranous border. Aedeagus most similar to that of *C. femoralis* males, but differs particularly in having only 6 pegs at inner apex of paramere instead of 10 as in the latter.

Female characters.—Anterior tarsus about as broadly dilated as in male. Apical margin of 6th sternite entire.

Variation.—There appears to be very little variation among the specimens examined. A few males have the head a little larger than that of females.

Notes.—Adults of this species are easily recognized among Pacific coast *Cafius* by their bright buff colored elytra. A few specimens of *C. lithocharinus* have clear, bright golden elytra; but in these, the punctures on the underside of the head are large and coalescent in diagonal rows. In *C. luteipennis* adults, the punctures of the undersurface of the head are always discrete.

Description of larvae and pupae and notes on ecology were provided by James et al. (1971).

We have examined 885 specimens.

Distribution.—This species is known from British Columbia, Canada, to El Tomatal, Baja California del Norte, Mexico; but undoubtedly it will eventually be found to extend farther south along the unexplored coast of Baja California. Orth et al. (1978) reported it from Refugio State Beach, Santa Barbara County, California, as most abundant from September through May. Besides the type specimens, we have seen the following:

BRITISH COLUMBIA. Masset, Graham Island, 1918, Mrs. Clark (1; MCZ); Q[ueen] C[harlotte] I[slands], [Keen] (7; ERIC); Miracle Beach, Vancouver Island, 22 Aug. 75, J.M. & B.A. Campbell (3; ERIC); Parkville, 23 Nov. 38, H. Andison (2; ERIC); Victoria, Coquillett (3; USNM).

WASHINGTON. 2 mi. n. La Push, Clallam County, 17 Oct. 74, D. Giuliani (1; UCR).

OREGON. Whitehead Beach, Curry County, 6 July 74, A. Newton & M. Thayer (2; MCZ).

CALIFORNIA. Haversneck, Mendocino County, D. Giuliani (1; ERIC); Mouth of Russian River, 4 July 08, Van Dyke (1; ERIC); Avalon, Santa Catalina Island, Los Angeles County, KWH (1; USNM); many specimens, many localities between Marin and San Diego counties, mostly from October to April.

MEXICO, BAJA CALIFORNIA NORTE. Descanso Bay, 27 May 50, I. Moore (3; ERIC); La Salina, 22 July 71, I. Moore (2; UCR); Colonia Guerrero, 16 Aug. 50, I. Moore (4; ERIC); Socorro Dunes, 17 July 74, R.M. Haradon, V. Lee and W.E. Savary (1; UCR); Rosario, 1 Aug. 38, Ross & Michelbacher (2; CAS); Arroyo Rosario, 25 Apr. 63, P. Arnaud (3; CAS); El Tomatal, 18 July 74, R.M. Haradon, V. Lee and W.E. Savary (5; UCR).

7. *Cafius decipiens* (LeConte)

Figs. 2C, 7G-H.

Philonthus decipiens LeConte, 1863, Smith. Misc. Coll. VI, No. 140:40.

Cafius decipiens (LeConte), Horn, 1884, Trans. Amer. Ent. Soc. 11:235, 239; Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:190.

Description of lectotype.— ♂

Length.—7.7 mm.

Color.—Head dark reddish brown, remainder of body and appendages a paler uniform reddish brown.

Head.—Quadrate, slightly wider than long, basal angles broadly rounded; eye ½ length of tempora; punctures of upper surface moderate sized, not conspicuously umbilicate, separated mostly by about their own diameters; with a central impunctate area extending from clypeal margin to near base; ground sculpture densely reticulate throughout; undersurface with punctures and ground sculpture very much like that above; gula densely reticulate; antennae a little longer than combined lengths of head and pronotum; 10th segment slightly wider than long.

Pronotum.—Somewhat longer than wide; apex broadly rounded, widest near broadly rounded apical angles, thence narrowed and straight to broadly rounded basal angles; base arcuate; surface with simple punctures about same size as those of head, separated by about their own diameters; central impunctate area clearly defined and hardly elevated except for a small basal tumid area; surface densely reticulate and dull throughout.

Elytra.—With suture about ⅕ shorter than pronotum; each elytron ¾ as wide as sutural length; surface very finely densely sculptured, punctures hardly distinguishable.

Abdomen.—Finely, rather sparsely punctured and finely reticulate, with acrocostal suture straight. Pubescence fine, longitudinal throughout.

This male in the LeConte collection at MCZ bears a gold disc (California) and a small ♂ symbol. Beneath this is a plastic capsule containing the genitalia in glycerine. We have attached a label reading "*Lectotype* desg. *Cafius decipiens*/LeConte 1978, Orth and Moore."

Type locality.—San Diego, California.

Besides the lectotype, 1 male (with sex symbol attached) and 1 female, both with gold discs are in the LeConte collection. The female also has a white label reading "*P. decipiens* LeC. S.D." and a red label reading "Type 6290." There are also 1 male and 3 females, each with a white label reading "Cal.", the male also with a small sex symbol. These last 5 specimens may not be part of the original type series.

Male characters.—First 4 segments of anterior tarsus somewhat broadly dilated. Apical margin of 6th sternite with a broad deep oval emargination surrounded by a fairly wide membranous border. Genitalia most similar to those of *Cafius sulcicollis* males, but aedeagus strongly constricted in apical third, then abruptly widened, resembling shoulders. In *C. sulicollis* males, aedeagus slipper-shaped, without a trace of shoulders at apical third.

Female characters.—First 4 segments of anterior tarsus about as broadly dilated as in male. Apical margin of 6th sternite entire.

Variation.—The specimens seen by us show little variation.

Notes.—Members of this species closely resemble those of *C. sulcicollis* but can be distinguished by their reddish-brown head, which is black in *C. sulcicollis* adults. The eye is almost exactly ½ the length of the tempora whereas in *C. sulciocollis* adults the eye is noticeably longer than ½ the length of the tempora. Males of this species differ strikingly from those of the other Pacific coast *Cafius* species in the shape of the aedeagus, which is strongly constricted in its apical third. Male genitalia are relatively larger than those of the other Pacific coast species.

Nothing is known of the life history or ecology of this species.

We have seen 34 specimens.

Distribution.—This species is known from San Pedro, Los Angeles County, California, to 24 kilometres north of Rosario, Baja California Norte, Mexico. The single specimen listed below from Mexico is the only one with a collection date. All California specimens were probably collected near or before the turn of the century. Besides the type series we have seen the following specimens:

CALIFORNIA. Cal., F.A. Eddy (2; MCZ); Cal., Hubbard & Schwarz (3; USNM); San Pedro, Los Angeles County, July, A. Fenyes (2; CAS); San Pedro, Los Angeles County, Aug., A. Fenyes (1; CAS); San Diego County, F.E. Blaisdell (1; CAS); San Diego, San Diego County (1; MCZ); [San Diego Bay, Spring], T.L. Casey (see Casey 1885:312) (10; USNM); San Diego, Hubbard & Schwarz (5; USNM).

MEXICO, BAJA CALIFORNIA NORTE. 15 mi. n. Rosario, 1 Aug. 38, Ross & Michelbacher (1; CAS).

8. *Cafius sulcicollis* (LeConte)
Figs. 2D, 8A-B.

Philonthus sulcicollis LeConte, 1863, Smith. Misc. Coll. VI, No. 140:40.
Cafius sulcicollis (LeConte), Horn, 1884, Trans. Amer. Ent. Soc. 11:235, 237; Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:191; Leech and Moore, 1971, Wasmann Jour. Biol. 29:65 (ecology); Orth, Moore and Fisher, 1978, Wasmann Jour. Biol. 35:176 Fig. 9 (toto), 182, 187 (ecology).

Description of lectotype.— ♂

Length.—5.8 mm.

Color.—Head and metasternum black, remainder of body and appendages reddish-brown.

Head.—Quadrate, slightly wider than long, lateral basal angles broadly rounded; eye distinctly more than ½ as long as tempora; puncturation of upper surface just discernably umbilicate, most punctures separated by about their own diameters, slightly more crowded at base, with an impunctate area adjacent to clypeal margin and a small impunctate central area; ground sculpture densely reticulate throughout; undersurface with puncturation and ground sculpture very similar to that above; gula densely, finely reticulate; antenna very slightly shorter than combined lengths of head and pronotum; 10th segment slightly wider than long.

Pronotum.—Distinctly longer than wide, apex arcuate, widest near broadly rounded apical angles, sides slightly concave before broadly rounded basal angles, base arcuate; surface with simple punctures evenly placed, about same size as those of head; central impunctate area somewhat irregularly defined by punctures but demarked on each side by a shallow sulcus; surface densely reticulate throughout except for a very small shining area in middle near base.

Elytra.—With suture as long as pronotum; each elytron about ¾ as wide as sutural length. Surface very finely, densely, and asperately punctured.

Abdomen.—Finely, sparsely punctured, finely reticulate between punctures, with acrocostal suture straight. Pubescence fine, longitudinal throughout.

This male in the LeConte collection at MCZ has beneath it a gold disc (California) and a small ♂ symbol. Below this is a plastic capsule containing the genitalia in glycerine and a label reading "Lectotype/*Cafius sulcicollis*/LeConte desig. '78/R.E. Orth, I. Moore."

Type locality.—San Diego, California.

Besides the lectotype, there are 3 females with gold discs in the LeConte collection, one of which also bears a white label reading "*P. sulcicollis* LeC., S.D.", and a red label reading "Type 6289." One male in the LeConte collection, but possibly not part of the original type series, has a white label reading, "Cal." underlined in red ink; and another male has a "Cal." label with a distinct ink dot below the C.

Male characters.—First 4 segments of anterior tarsus broadly dilated. Apical margin of 6th sternite with an oval emargination, about as deep as wide and nearly filled with membrane. Genitalia most similar to those of *C. luteipennis* males. They differ most noticeably from the latter in that the middle tumescence is distinctly closer to the basal attachment of the paramere than to the apex of the paramere; whereas, in the latter it is very nearly centrally placed.

Female characters.—First 4 segments of anterior tarsus are about as broadly dilated as in male and apical margin of 6th sternite entire.

Variation.—Very little variation has been detected.

Notes.—Adults of this species are easily distinguished from those of other Pacific coast *Cafius* species except *C. decipiens* by the combination of the transverse 10th antennomere, the longitudinal abdominal pubescence, the simple puncturation of the undersurface of the head and the uniformly punctured sides of the pronotum. They differ from *C. decipiens* adults in having a black head and longer eye. The eye is more than ½ the length of the tempora. In *C. decipiens* adults, the head is reddish-brown and the eye is almost exactly ½ as long as the tempora.

The immature stages have not been described. Larva described as belonging to this species and records of this species from the Salton Sea, Imperial County, California, and Sonora, Mexico, by Moore (1974, 1975) and Moore and Legner (1973) actually represent *Cafius bistriatus* (Erichson).

We have examined 213 specimens.

Distribution.—This species has been reported from Refugio State Beach, Santa Barbara County, California (Orth et al. 1978) to Magdalena Island, Baja California Sur, Mexico (Horn 1894). The Magdalena Island specimen has not been seen by us. There is a single female in the collection of the University of California, Riverside, which we doubtfully place here, collected by Derham Giuliani 3.2 kilometres north of La Puch, Clallam County, Washington, 17 October 1974. Orth et al. (1978) reported this as the least abundant of the *Cafius* species found at Refugio State Beach, Santa Barbara County, California, but only slightly less so than *C. opacus.* Furthermore, it is a winter species found chiefly from October to May. Leech and Moore (1971) reported adults in flight on the beach in Baja California and San Diego, California.

Besides the type series we have seen the following specimens:

CALIFORNIA. Gaviota, Santa Barbara County, 20 Sept. 50, I. Moore (1; ERIC); Refugio State Beach, Santa Barbara County, R.E. Orth, (4) 8 Nov. 76, (9) 6 Dec. 76, (5) 17 Jan. 77, (6) 7 Feb. 77, (2) 14 Mar. 77, (4) 12 Apr. 77. (1) 17 May 77, (1) 2 Aug. 77, (1) 8 Sept. 77 (UCR); Frazier Point, Santa Cruz Island, 8 Jan. 71, J. Pinto, Chearey, R. Somerby (1; UCR); Santa Barbara, Santa Barbara County, June, A. Fenyes (1; CAS); Redondo, Los Angeles County, Apr., A. Fenyes (1; CAS); Redondo, Los Angeles County, July, A. Fenyes (1; CAS); San Pedro, Los Angeles County, Aug., A. Fenyes (2; CAS); San Pedro, Los Angeles County (1; FMNH); Los Angeles, Los Angeles County, Coquillett (1; USNM); Laguna Beach, Orange County, Baker (1; FMNH); Cardiff, San Diego County, 21 Aug. 71, G. Olton & I. Moore (1; UCR); Torrey Pines, San Diego County, 22 May 55, I. Moore (1; UCR); La Jolla, San Diego County, 11 Apr. 34, I. Moore (1; CAS); La Jolla, 22 Apr. 51, I. Moore (30; ERIC); La Jolla, 29 Aug. 50, I. Moore (29; ERIC); La Jolla, 22 Sept. 53, I. Moore (2; ERIC); La Jolla, 22 Oct. 50, I. Moore (1; ERIC); La Jolla, 22 Nov. 50, I. Moore (84; ERIC); Sunset Cliffs, San Diego County, 23 Aug. 50, I. Moore (1; ERIC); Sunset Cliffs, San Diego County, 5 Oct. 53, I. Moore (1; ERIC); Ocean Beach, San Diego County, 2 Sept. 50, I. Moore (3; ERIC); Mission Bay, San Diego County, 25 Sept. 53, I. Moore (1; ERIC); San Diego Bay, San Diego County, 2 Sept. 50, I. Moore (26; ERIC); Point Loma, San Diego County, 28 Dec. 28, E.C. Van Dyke (1; ERIC); San Diego, San Diego County, May, A. Fenyes (1; ERIC); San Diego, A. Watson (1; ERIC); North Island, San Diego County, 2 Mar. 30, I. Moore (1; ERIC); North Island, San Diego County, 6 Apr. 38, I. Moore (1; ERIC).

MEXICO, BAJA CALIFORNIA NORTE. Colonia Guerrero, 28 May 50, I. Moore (10; ERIC); 15 mi. n. Rosario, 1 Aug. 35, Ross & Michelbacher (1; CAS); Arroyo Rosario, 25 Apr. 63, P. Arnaud, (1; CAS).

9. *Cafius bistriatus* (Erichson)

Figs. 3A, 5E, 8C-D, 10

Philonthus bistriatus Erichson, 1840, Gen. Spec. Staph. 502.

Philonthus bilineatus Erichson, 1840, Gen. Spec. Staph. 503.

Cafius bistriatus (Erichson), Horn, 1884, Trans. Amer. Ent. Soc. 11:235, 237; Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:175, 187; Blackwelder, 1943, Bull. U.S. Nat. Mus. 182:436, 438.

Cafius bilineatus (Erichson), Koch, 1936, Publ. Mus. Ent. Pietro Rossi 1:176, 187.

Cafius sulcicollis (LeConte), Moore, 1975, Pan-Pac. Ent. 51:140 (larva), Fig. 1-4 (larva), 142 (larva).

Description of male.—From El Desemboque, Sonora, Mexico.

Length.—6.5 mm.

Color.—Head black, remainder of body dark reddish-brown with antenna gradually paler to apex.

Head.—Quadrate, about as wide as long, lateral basal angles broadly rounded; eye distinctly shorter than tempora; punctures of upper surface moderate-sized, umbilicate, separated by more than their own diameters, with an irregular impunctate central area the length of head; surface densely reticulate at sides, weakly so in very center of disc; undersurface uniformly punctured with ground sculpture very similar to that above; gula densely reticulate; antennae a little shorter than combined lengths of head and pronotum, 10th segment slightly wider than long.

Pronotum.—Longer than wide, apex broadly rounded, widest near broadly rounded apical angles, thence narrowed and nearly straight to the broadly rounded basal angles, base arcuate; surface with a broad longitudinal impunctate area bounded on each side by a row of 16 or 17 large equidistant punctures, and with a narrow irregular impunctate area lateral to same almost as long as pronotum; sides somewhat evenly punctured to lateral margin; surface reticulate at sides, reticulation becoming very feeble in central impunctate area.

Elytra.—With suture slightly longer than pronotum; each elytron ⅔ as wide as sutural length; surface distinctly and very densely punctured, punctures separated by less than their own diameter, very finely reticulate between punctures.

Abdomen.—Almost as densely punctured as elytra, punctures asperate; acrocostal sutures straight; without ground sculpture; pubescence fine, longitudinal throughout. Undersurface uniformly punctured and pubescent throughout.

Type locality.—Long Island, New York.

Male characters.—Anterior tarsus broadly dilated. Apical margin of 6th sternite with a shallow triangular emargination partly filled by membrane. Genitalia most similar to those of *Cafius sulcicollis* males; but aedeagus more pointed at apex, and paramere relatively shorter. Middle tumescence of aedeagus located very near to middle of paramere, rather than at about the basal ⅓ of the paramere as in *C. sulcicollis* males.

Female characters.—Anterior tarsus almost as broadly dilated as in male. Apical margin of 6th sternite entire.

Variation.—In some males, the head is slightly larger than in the females. Most west coast specimens have the tibiae a little darker than the femora and tarsi. The color of west coast specimens is otherwise fairly consistent except for an occasional specimen which is slightly darker.

Notes.—Adults of this species closely resemble those of *Cafius sulcicollis* and were reported as that species from the Salton Sea by Moore and Legner (1973) and from Sonora, Mexico, by Moore (1974). Western specimens differ from *C. sulcicollis* specimens in the shining surface with weak or absent reticulation of the central impunctate area of the pronotum; that area in *C. sulcicollis* adults is as strongly reticulate as the sides of the pronotum and the head. In all *C. bistriatus* specimens from western North America, there is always a prominent shiny impunctate area just lateral to the row of punctures which delimit the central impunctate area of the pronotum; such an area is rarely present in *C. sulcicollis* specimens, and when present it is dull due to strong reticulation. The punctures of the elytra in *C. bistriatus* adults are distinctly separated and not asperate, whereas in *C. sulcicollis* members they are asperate and tend to run together in weak lateral ridges so that the individual punctures are not easily seen. The color of western specimens of *C. bistriatus,* except for the black head, is usually bright reddish-brown, whereas *C. sulcicollis* members are usually dark brown.

The aedeagus of *Cafius bistriatus* is more pointed at the apex than that of *C. sulcicollis;* and the paramere is relatively shorter.

The larva was described by Moore (1975) as that of *C. sulcicollis.*

We have examined 480 specimens from western North America and 740 specimens from eastern North America.

Distribution.—This species was originally described from Long Island, New York, and has been recorded from various localities along the eastern seashore of the United States from Massachusetts to Florida, numerous localities in the West Indies and from

South America. We present here a first record from the west coast of North America. In that area, it is known from Desert Beach, Salton Sea, Riverside County, California, through almost the entire Gulf of California to Isla San José, Baja California Sur, near LaPaz, and from 63 kilometres north of Guerrero Negro, Baja California Norte on the Pacific coast of Baja California. We have seen the following specimens from western North America:

CALIFORNIA. Desert Beach, Salton Sea, Riverside County, 3 Mar. 68, K. Cooper (3; UCR).

MEXICO, SONORA. Punta Peñasco, 7 June 74, algae covered rock with small barnacles, V. Roth (1; ERIC); Punta Cirio, 29.50-112.40, wrack on sandy beach, V. Roth & W. Brown (99; UCR); near Punta Cirio, 28 Aug. 74, V. Roth & W. Brown (88; UCR); El Desemboque de Los Seris, 1 June 74, W. Brown (5; UCR); Tepoca, 29.18-112.20, wrack on sandy beach, V. Roth & W. Brown (2; UCR); Punta Chueca, 29.00-112.05, light trap on sandy beach, 18 Jan. 75, V. Roth (3; UCR); Punta Doble, 26 Feb. 74, P. DeBach & M. Rose (1; UCR); Huatabampo, D. Giuliani (1; UCR).

MEXICO, BAJA CALIFORNIA NORTE. 39 mi. n. Guerrero Negro on road to Miller's Landing, 8 Aug. 74, R. Haradon, V. Lee & E. Savary (6; UCR).

MEXICO, BAJA CALIFORNIA SUR. Santa Rosalia, 20 July 74, R.H. Haradon, V. Lee & E. Savary (1; UCR); Isla San José, 19 Apr. 72, rotting fish, L. Cheng (2; UCR).

10. *Cafius caribeanus* Bierig
Figs. 3B, 8E-F.

Cafius corallicola var. *caribeanus* Bierig, 1934, Revista Ent. 4:67, 68; Koch, 1936, Publ. Mus. Ent. Pietro Rossi 1:175, 176, 186.

Cafius caribeanus Bierig, Blackwelder, 1943, Bull. U.S. Nat. Mus. 182:436, 437.

Description of male.—From San Blas, Nayarit, Mexico.

Length.—5.0 mm.

Color.—Head and pronotum black, elytra piceus, abdomen dark reddish-brown, legs and trophi paler than abdomen, antenna gradually paler toward apex.

Head.—Quadrate, almost as wide as long, basal angles moderately broadly rounded; eyes as long as tempora; punctures of upper surface coarse, separated at sides by about their own diameters, with a small impunctate discal area, and a central linear longitudinal impression in apical half; surface sculpture of fine wavy, lines in a dactylographic pattern; undersurface with punctures and surface sculpture similar to that above; gula sculptured with fine wavy dactylographic lines; antenna as long as combined lengths of head and pronotum, 10th segment about as long as wide.

Pronotum.—Longer than wide, apex arcuate, widest near broadly rounded apical angles, thence narrowed and nearly straight to broadly rounded basal angles, base arcuate; surface with a broad longitudinal central impunctate area bounded on each side by a row of 16 or 17 large equidistant punctures, with a narrow, irregular, impunctate area next to same almost as long as the pronotum; sides somewhat evenly punctured to lateral margin; surface with a feeble dactylographic pattern of wavy lines.

Elytra.—With suture slightly shorter than pronotum; each elytron about ⅘ as wide as sutural length; surface very densely and roughly punctured.

Abdomen.—Almost as densely but somewhat more finely punctured than elytra; acrocostal suture straight; pubescence fine, longitudinal throughout. Undersurface finely, densely punctured.

Male characters.—First 4 segments of anterior tarsus dilated. Apical margin of 6th sternite with an oval emargination about as deep as wide. Aedeagus most similar to that of *C. luteipennis* male, but with apex of median lobe more blunt and somewhat bulbous.

Female characters.—Anterior tarsus almost as broadly dilated as in male. Apical margin of 6th sternite entire.

Notes.—Adults of this species are smaller and darker than western specimens of *Cafius bistriatus* (Erichson). They differ from members of all other North American

Cafius species in that the ground sculpture of the head and pronotum consists of fine wavy lines in a dactylographic pattern. This condition is most apparent on the gula. In adults of most other North American species the gula is so densely reticulate that it has a granular appearance.

We have seen 2 specimens from western North America and 21 specimens from eastern North America.

Distribution.—This species was originally described from the West Indies. We have seen 1 male and 1 female from San Blas, Nayarit, Mexico, September 17-20, 1953, B. Malkin collector in the collection of the California Academy of Sciences. This is the first record of this species from the west coast of North America.

THE SPECIES OF *CAFIUS* OF EASTERN NORTH AMERICA

We have not been able to treat the species of *Cafius* of eastern North America (including the West Indies) as exhaustively as those of western North America. Type specimens of most of them have not been studied. However, dissections have been made of the genitalia of what we believe to be authentically identified specimens.

On the basis of our studies, we have decided that the European species *Cafius sericeus* Holme has not yet been validly recorded from North America. The species which has gone under that name should be called *C. aguayoi* Bierig. *Cafius aguayoi* was synonymized with *C. sericeus* by Blackwelder, 1943. We believe *C. rufifrons* Bierig to be a valid species, not a synonym of *C. bistriatus* (Erichson) as suggested by Blackwelder, 1943. Other changes may be necessary, but we lack material on which to base these decisions. These possibilities are discussed under the notes on some of the following species.

Key for identification of *Cafius* of eastern North America

A. Head reddish-brown .... 1. *C. rufifrons* Bierig
AA. Head black or piceous.
B. Ground sculpture of gula granulose .... 2. *C. bistriatus* (Erichson)
BB. Ground sculpture of gula fine wavy lines.
C. Ground sculpture of head and pronotum fine wavy lines . . 3. *C. caribeanus* Bierig
CC. Ground sculpture of head and pronotum finely granulose.
D. Larger species (length of head, pronotum and elytra 2.2-2.8 mm) ....
Atlantic coast of the United States .... 4. *C. aguayoi* Bierig
DD. Smaller species (length of head, pronotum and elytra 1.8-2.2 mm) ....
West Indies .... 5. *C. subtilis* Cameron

1. *Cafius rufifrons* Bierig

Figs. 3C, 8G-H.

Cafius rufifrons Bierig, 1934, Revista Ent. 4:67-68; Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:176, 187; Blackwelder, 1943, Bull. U.S. Nat. Mus. 182:438.

This species was synonymized with *Cafius bistriatus* (Erichson) by Blackwelder, 1943; but we believe it to be distinct. Adults differ from those of other east coast *Cafius* species in its reddish-brown head. Although it is otherwise similar to *C. bistriatus,* the aedeagus is not as abruptly narrowed towards the apex as in males of that species.

A single specimen in the United States National Museum is labeled "Miami, VI-36, A. Bierig Coll., Fla./USA, Paratype No. 52746 USNM." This cannot be a paratype because the original description was in 1934, 2 years earlier than the specimen was collected.

We have examined 20 specimens.

2. *Cafius bistriatus* (Erichson)

Figs. 3A, 5E, 8C-D, 10.

This species is recorded in this paper for the first time from the west coast of North America. Full citations, descriptions and notes are given in that section of this paper.

Considerable variation exists in the ground sculpture in specimens from the extremes of range in eastern North America. However, only minor differencs have been found in the male genitalia and these appear to intergrade between the extremes of range. Long series of specimens from Long Island Sound and from Chesapeake Bay consistently have the head and pronotum with dense reticulate ground sculpture; whereas, in specimens from the West Indies and western North America, those parts are weakly reticulate with occasional smooth polished areas. Some specimens from the southeastern United States are intermediate. We lack extensive material from the intermediate region. For the present, it appears best to leave the synonymy as given. If the 2 forms are determined to be separate species, the name *C. bistriatus* (Erichson) will apply to specimens from northeastern United States and *C. bilineatus* (Erichson) to the southern and western form.

Most specimens from the West Indies and western North America were collected from open sandy beaches, whereas those from Long Island and Chesapeake Bay were found under sea lettuce (*Ulva*) on the shores of protected waters.

3. *Cafius caribeanus* Bierig

Figs. 3B, 8E-F.

This species is recorded in this paper for the first time from the west coast of Mexico. Full citations, description and notes are given in that section of this paper.

It has previously been known only from the West Indies. It is unusual in that the ground sculpture of the adult head and pronotum is in the form of fine wavy lines in a dactylographic pattern. In males of this species, the aedeagus is bulbous at the apex and the paramere is relatively longer than in males of other eastern species.

We have examined 21 specimens from the West Indies.

4. *Cafius aguayoi* Bierig

Figs. 3D, 9A-B.

Cafius sericeus (Holme), Horn, 1884, Trans. Amer. Ent. Soc. 11:235, 238 (not Holme, 1837).

Cafius aguayoi Bierig, 1934, Revista Ent. 4:66; Koch, 1936, Publ. Mus. Ent. Pietro Rossi 1:192.

This is a common species along the eastern seashore of the United States. It has been listed as *Cafius sericeus* Holme, a European species which is very similar in appearance. However, the male genitalia differ sufficiently for us to determine that they represent distinct species. The paramere is distinctly more slender than in males of the European *C. sericeus* Holme (Figs. 9E-F). Specimens of *C. aguayoi* Bierig appear not to differ from those of other east coast specimens, so we apply that name to this species. It is known only from the east coast of the United States.

We have seen 463 specimens.

5. *Cafius subtilis* Cameron

Figs. 4, 9C-D.

Cafius subtilis Cameron, 1922, Ann. Mag. Nat. Hist., Ser. 9, 9:121; Blackwelder, 1943, Bull. U.S. Nat. Mus. 182:436.

Cafius sericeus var. *subtilis* (Cameron), Koch, 1936, Publ. Mus. Ent. Pietro Rossi, 1:192.

The adults of this very small species are similar to those of *Cafius aguayoi* Bierig. There seems to be a slight difference in the male genitalia, the paramere of the *C. subtilis* males being relatively shorter than that of *C. aguayoi* males. Specimens seen are all from the West Indies. Blackwelder, 1943, treated this species as distinct from the species we call *C. aguayoi.* We feel that we have seen insufficient material to suggest any change. If the 2 species are ever synonymized, the name *C. subtilis* has precedence over *C. aguayoi.*

We have examined 23 specimens.

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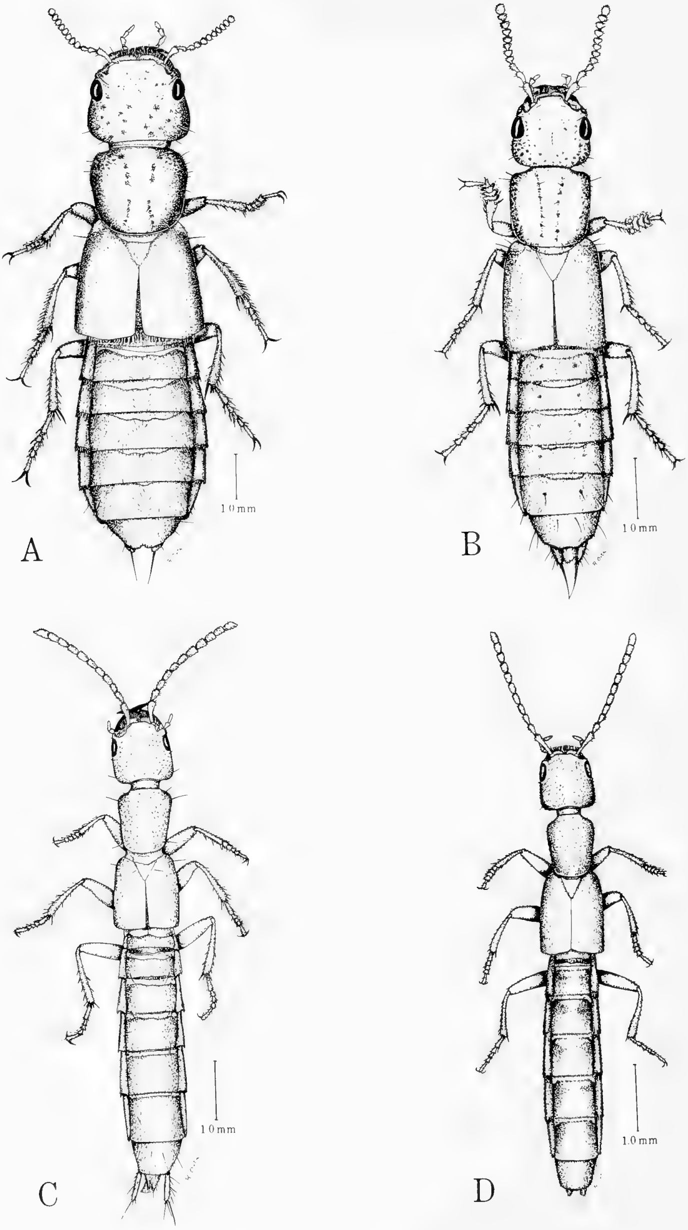

FIGURE 1. (A) *Cafius seminitens* Horn. USA, California, Santa Barbara County, Refugio State Beach, 22 April 1976, R. Orth; (B) *Cafius canescens* (Mäklin). USA, California, Santa Barbara County, Refugio State Beach, 22 April 1976, R. Orth; (C) *Cafius opacus* (LeConte). USA, California, Santa Barbara County, Refugio State Beach, 8 Nov. 1976, R. Orth; (D) *Cafius femoralis* (Mäklin). USA, California, Mendocino County, Needle Rock, 6 Oct. 1974, D. Giuliani.

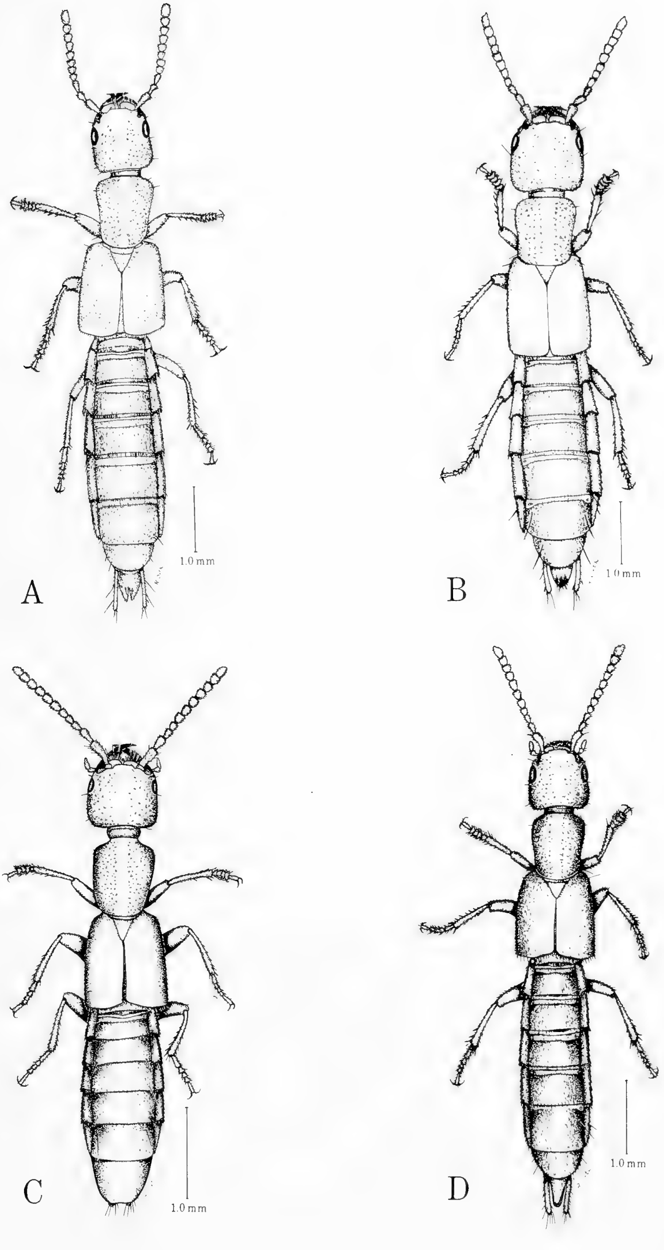

FIGURE 2. (A) *Cafius lithocharinus* (LeConte). USA, California, Santa Barbara County, Refugio State Beach, 18 May 1976, R. Orth; (B) *Cafius luteipennis* Horn. USA, California, Santa Barbara County, Refugio State Beach, 18 May 1976, R. Orth; (C) *Cafius decipiens* (LeConte). USA, California, San Diego, LeConte, Type 6290; (D) *Cafius sulcicollis* (LeConte). USA, California, Santa Barbara County, Refugio State Beach, 15 Sept. 1976, R. Orth.

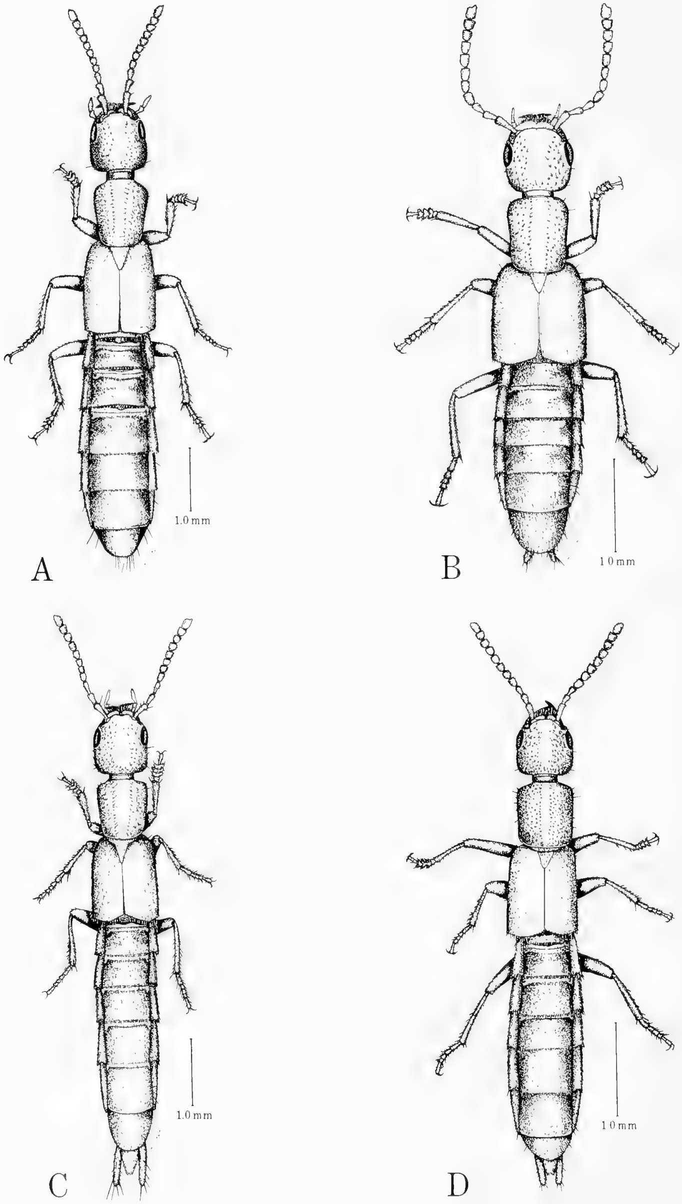

FIGURE 3. (A) *Cafius bistriatus* (Erichson). MEXICO, Sonora, El Desemboque, 23 May 1974, Brown and Speith; (B) *Cafius caribeanus* Bierig. MEXICO, Nayarit, San Blas, 17-21 Sept. 1953, B. Malkin; (C) *Cafius rufifrons* Bierig. USA, Florida, Miami, June 1936, A. Bierig; (D) *Cafius aguayoi* Bierig. USA, Connecticut, Fairfield County, Westport, Sherwood Island State Park, 20 Aug. 1978, R. Orth family.

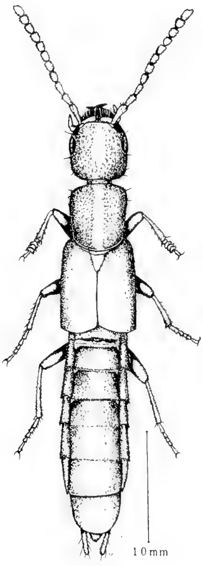

FIGURE 4. *Cafius subtilis* Cameron. CUBA, Provincia Habana, Playa Marianao, 1929, A. Bierig.

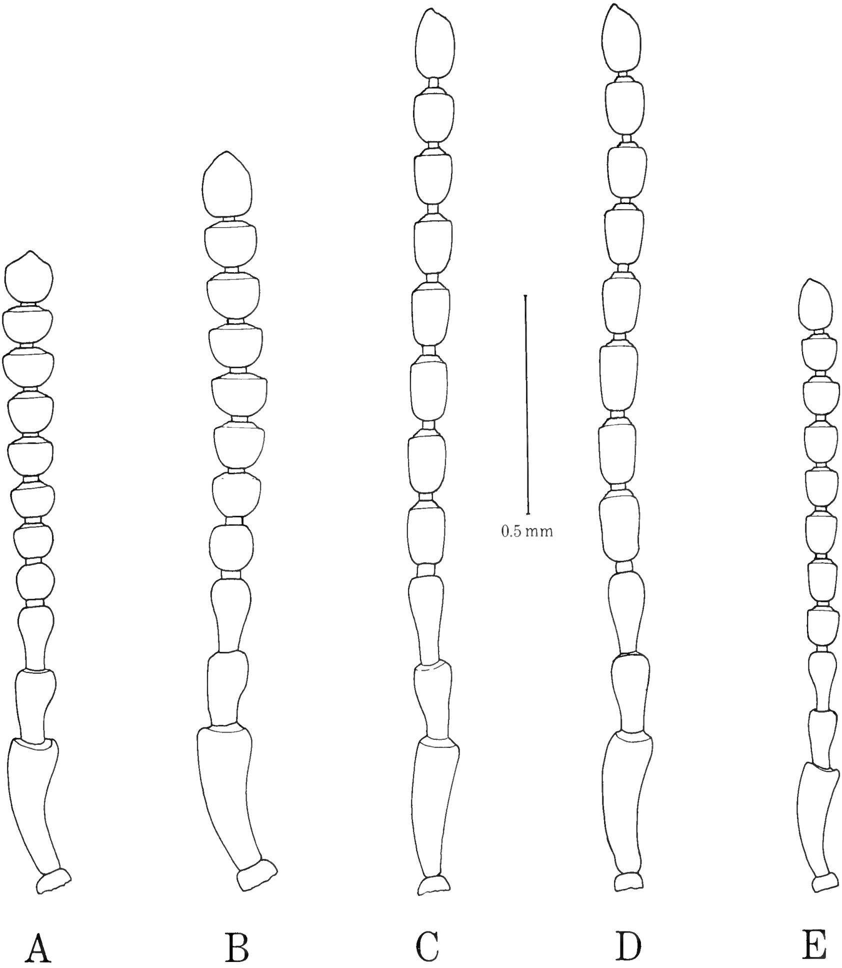

FIGURE 5. Antennae of *Cafius.* (A) *Cafius seminitens* Horn; (B) *Cafius canescens* (Mäklin); (C) *Cafius opacus* (LeConte); (D) *Cafius femoralis* (Mäklin); (E) *Cafius bistriatus* (Erichson).

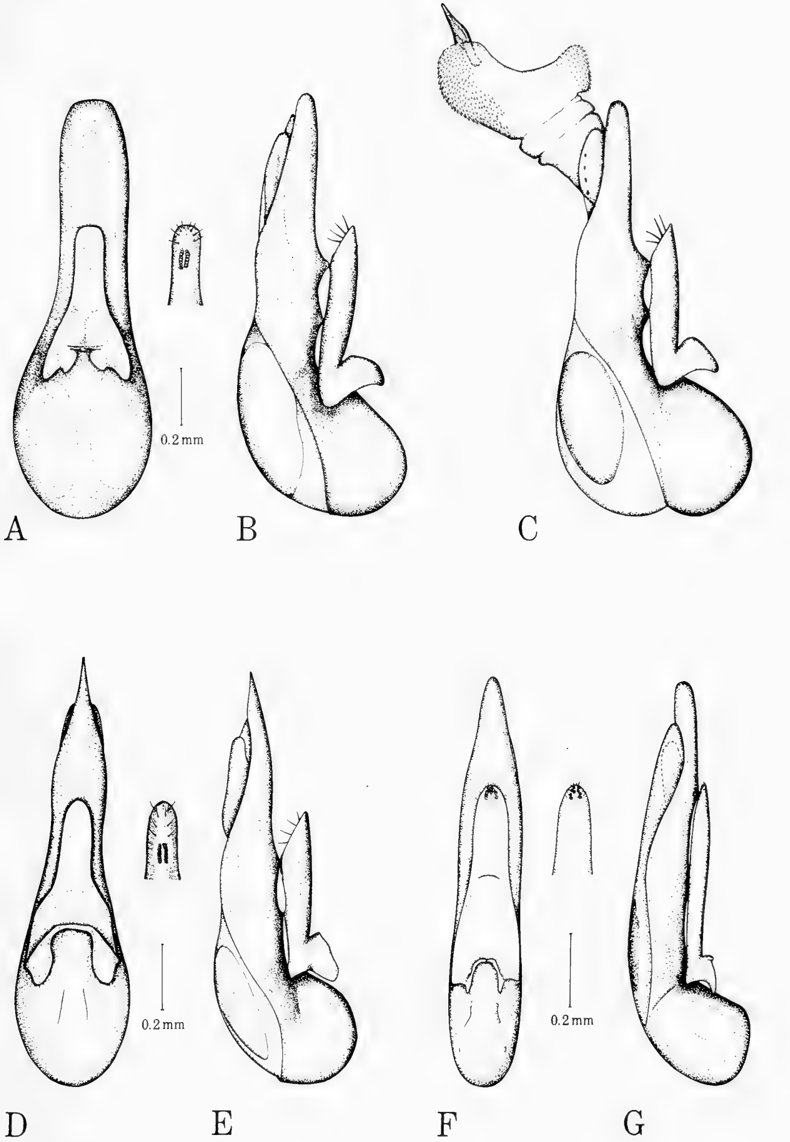

FIGURE 6. Aedeagi of *Cafius.* (A-C) *Cafius seminitens* Horn (USA, California, Santa Barbara County, Refugio State Beach, 22 April 1976, R. Orth); (A) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (B) lateral view of aedeagus; (C) lateral view of aedeagus with internal sac everted; (D, E) *Cafius canescens* (Mäklin) (USA, California, Santa Barbara County, Refugio State Beach, 19 July 1976, R. Orth); (D) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (E) lateral view of aedeagus; - (F, G) *Cafius opacus* (LeConte) (USA, California, Santa Barbara County, Refugio State Beach, 19 July 1976, R. Orth); (F) ventral view of aedaegus and apical part of underside of paramere with sensory tubercles; (G) lateral view of aedeagus.

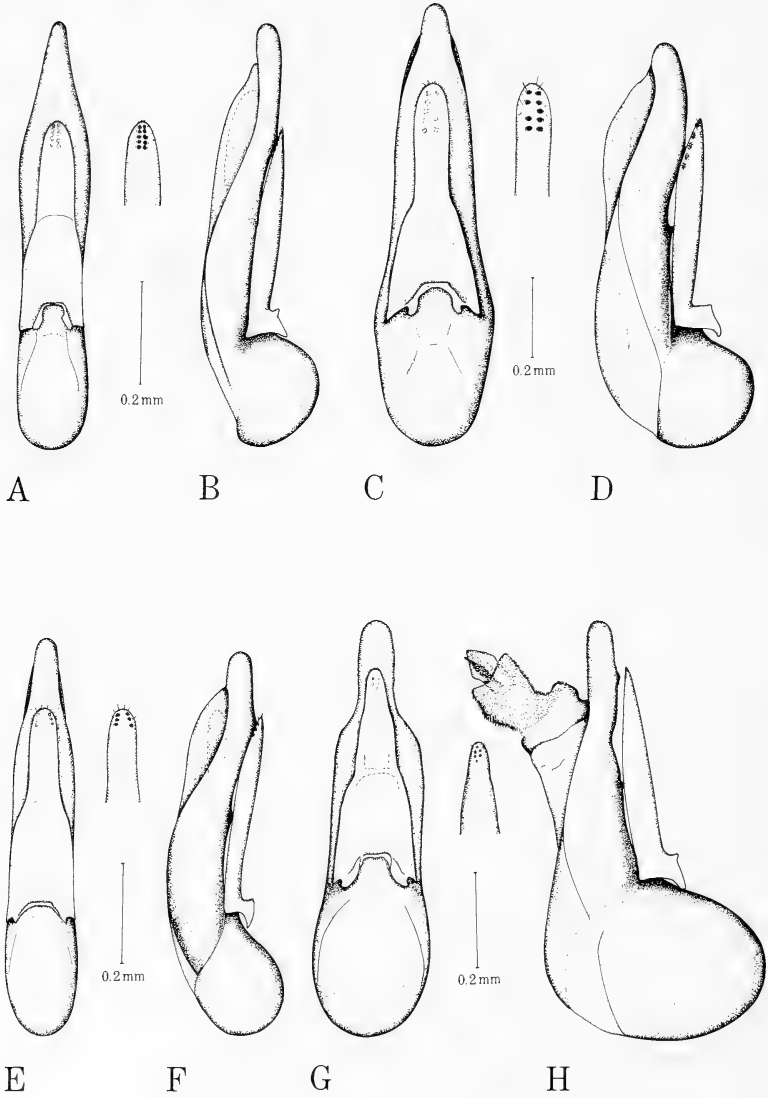

FIGURE 7. Aedeagi of *Cafius*. (A, B) *Cafius femoralis* (Mäklin) (USA, California, Mendocino County, Needle Rock, 6 Oct. 1974, D. Giuliani); (A) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (B) lateral view of aedeagus; - (C, D) *Cafius lithocharinus* (LeConte) (USA, California, Santa Barbara County, Refugio State Beach, 18 May 1976, R. Orth); (C) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (D) lateral view of aedeagus; - (E, F) *Cafius luteipennis* Horn (USA, California, Santa Barbara County, Refugio State Beach, 8 Sept. 1977, R. Orth); (E) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (F) lateral view of aedeagus; - (G, H) *Cafius decipiens* (LeConte) (USA, California, San Diego County, San Diego); (G) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (H) lateral view of aedeagus with internal sac everted.

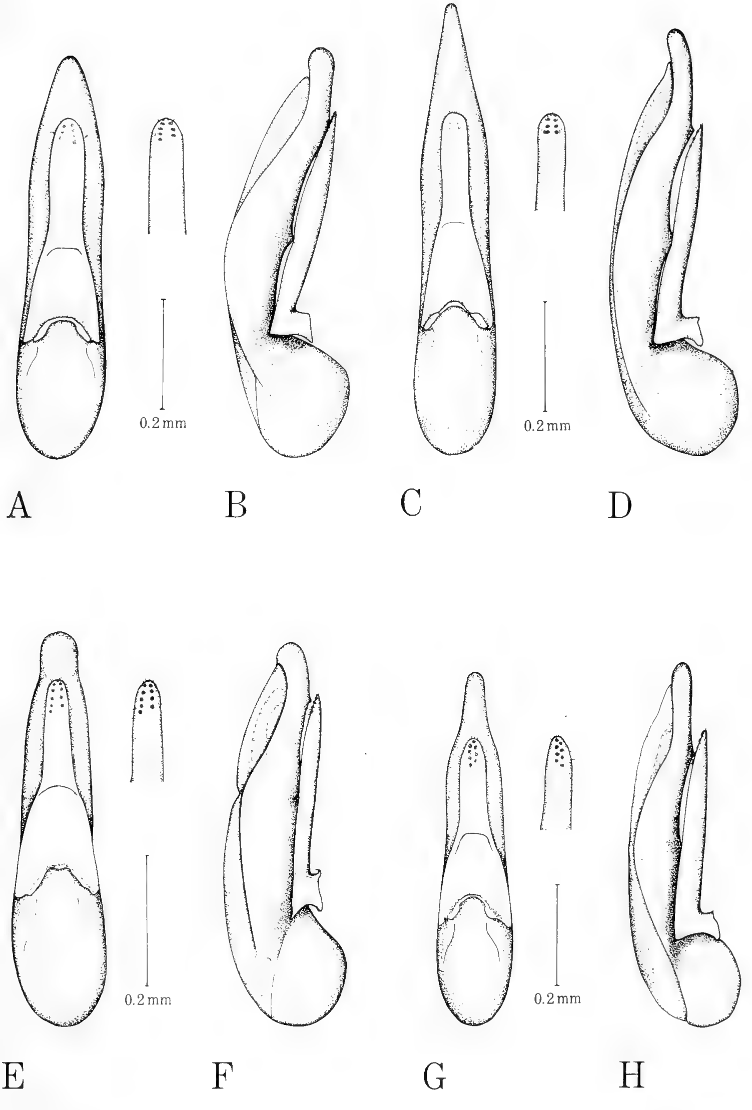

FIGURE 8. Aedeagi of *Cafius.* (A, B) *Cafius sulcicollis* (LeConte) (USA, California, Santa Barbara County, Refugio State Beach, 14 Mar. 1977, R. Orth); (A) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (B) lateral view of aedeagus; - (C, D) *Cafius bistriatus* (Erichson) (MEXICO, Sonora, El Desemboque, 23 May 1974, Brown and Speith); (C) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (D) lateral view of aedeagus; - (E, F) *Cafius caribeanus* Bierig (MEXICO, Nayarit, San Blas, 17-21 Sept. 1953, B. Malkin); (E) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (F) lateral view of aedeagus; - (G, H) *Cafius rufifrons* Bierig (CUBA, Playa Marianao, 8 Sept. 1929, A. Bierig); (G) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (H) lateral view of aedeagus.

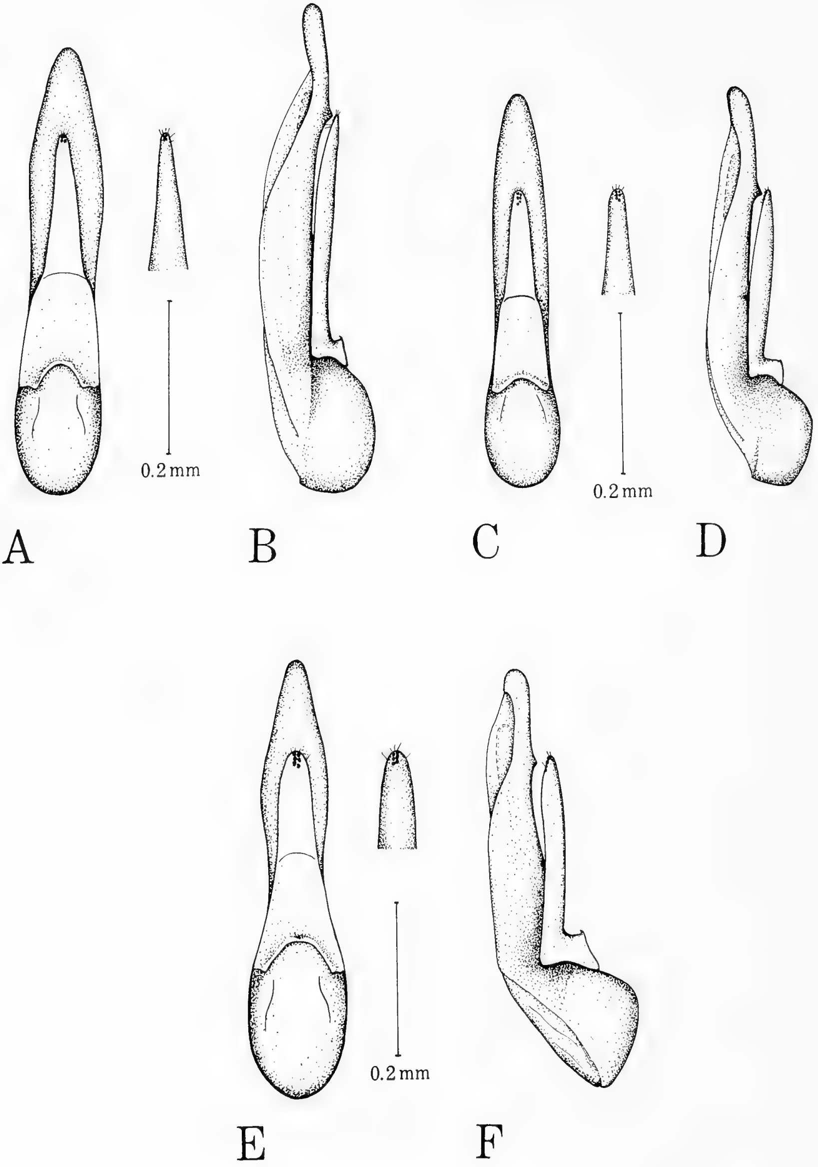

FIGURE 9. Aedeagi of *Cafius*. (A, B) *Cafius aguayoi* Bierig (USA, Connecticut, Fairfield County, Norwalk, Calf Pasture Beach, 9 Aug. 1978, R. Orth family); (A) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (B) lateral view of aedeagus; - (C, D) *Cafius subtilis* Cameron (PUERTO RICO, San Juan, 28 Sept. 1935, R. Blackwelder); (C) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (D) lateral view of aedeagus; - (E, F) *Cafius sericeus* Holme (Galliamer, Reitter, A. Fenyes collection); (E) ventral view of aedeagus and apical part of underside of paramere with sensory tubercles; (F) lateral view of aedeagus.

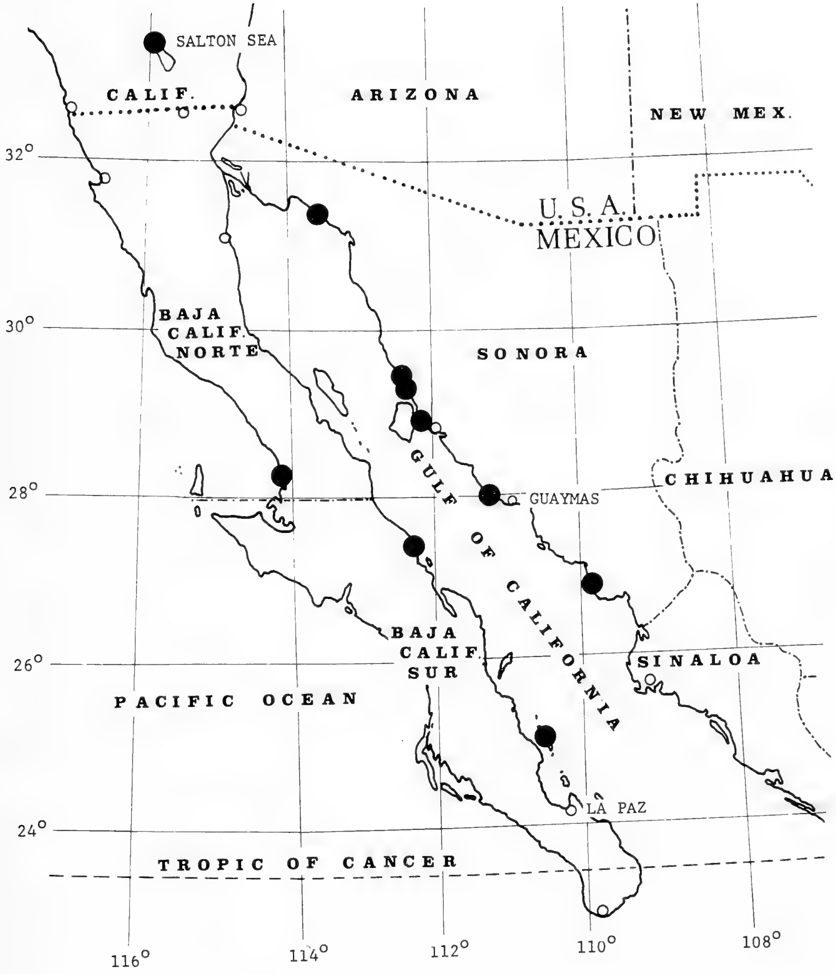

FIGURE 10. Map showing west coast distribution of *Cafius bistriatus* (Erichson).

TRANSACTIONS
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Dithyrocaris sp. (Phyllocarida) from the Allegheny Group of Ohio

Joan Matthews Schram

Abstract. Two phyllocarid carapaces and a phyllocarid tail collected from the Pennsylvanian Washingtonville Shale of Ohio are described and compared with known phyllocarid species. Not enough material was available to identify these specimens with a known species or to describe a new species, but the specimens are significant in documenting variation in the genus.

INTRODUCTION

Michael C. Hansen of the Ohio Division of Geological Survey called to my attention two *Dithyrocaris* carapaces collected by Lloyd J. Millhorn in the Washingtonville Shale and given to Myron Sturgeon of Ohio University, Athens, Ohio. A further search of the collections at Ohio University yielded a tail collected by Sturgeon at a different locality within the same unit. These 3 specimens from the Pennsylvanian Washingtonville Shale are not preserved well enough to identify satisfactorily with any known species or to describe as a new species. Although *Dithyrocaris* species are fairly common in Europe, there are so few in North America that any new material warrants description in the literature.

Dithyrocaris is fairly well known from the Devonian and Carboniferous of Europe. Jones and Woodward (1888–1899) wrote the definitive treatise incorporating all the European and North American specimens known at that time. Essentially no further work was done until Rolfe (1969) in the Treatise on Invertebrate Paleontology undertook a preliminary revision of the various phyllocarid taxa. The result was the incorporation of several former genera into one genus, *Dithyrocaris*. Rolfe stated a necessity for further revision, adding that features separating the genera of the Rhinocarididae may only be specific characters.

The known North American Carboniferous species include *Dithyrocaris carbonaria* Meek and Worthen, 1870, and *Rhacura? venosa* Scudder, 1878, placed in *Dithyrocaris* by Rolfe (1969). These species are based on specimens of tails, and neither is well known. Copeland (1967) described *Dithyrocaris quinni* from the Mississippian of Arkansas, based on carapaces and tails; and Schram and Horner (1978) described *Dithyrocaris rolfei*, an intact animal, from the Upper Mississippian of Montana.

Because the material from Ohio is fragmentary, and because the taxonomy of the group is confused, it seems better to designate these two carapaces and tail as *Dithyrocaris* sp. rather than erect new species which would only serve to further confound the situation. More and better material and/or a revision of the entire genus might permit a specific designation some day.

OSU 33450 (Fig. 1, upper and lower right) and OSU 33451, two carapaces, are from Ohio University locality CAr-2 (Hoare et al., 1979, p. 66) in Rose Township, Carroll County, Ohio, in the James Bros. Mining Company strip mine. The tail, OSU 33452 (Fig. 1, left), is from Ohio University locality Cc-7 (Sturgeon and Hoare, 1968, p. 80), Center Township, Columbiana County, Ohio. Both localities are in the marine horizon of the Washingtonville Shale, Allegheny Group, Pennsylvanian System. Stur-

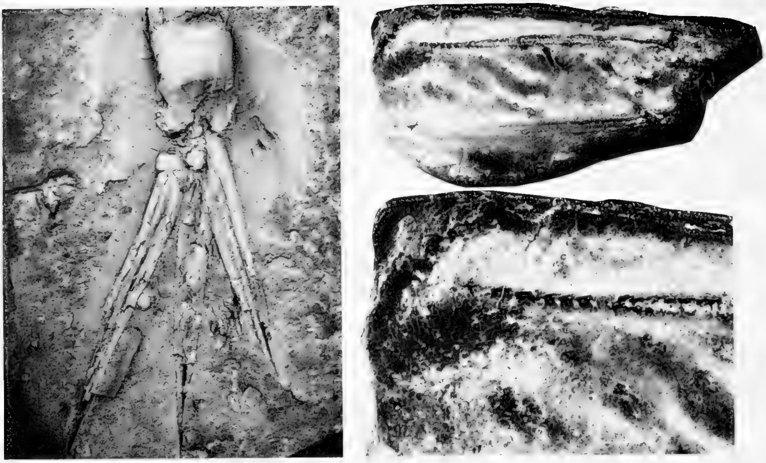

FIGURE 1. *Dithyrocaris* sp. Left. OSU 33452, the last abdominal segment showing the chevron line decoration, and telson and furca: Upper right. OSU 33450, carapace showing lateral carinae and part of the median dorsal plate: Lower right. Detail of posterodorsal corner of carapace OSU 33450, showing underlying segment with chevron line decoration, detail of juxtadorsal carina, and the "fish scale" pattern terrace lines of the carapace ornamentation.

geon and Hoare (1968) state that marine deposits of this age yield faunas often abundant in corals, bryozoans, fusilinids, arthropods, sponges, mollusks, and brachiopods. Although the Washingtonville Shale is heavily collected, Michael C. Hansen (*personal communication*) states that crustaceans of any sort are rare. These specimens are the only phyllocarids known to have been found.

The specimens are deposited in the Orton Museum of The Ohio State University, Columbus, Ohio with accession numbers OSU 33450, OSU 33451 and OSU 33452.

DISCUSSION

The tail OSU 33452 (Fig. 1, left) is similar to those of other *Dithyrocaris* species, with a telson about equal in length to the furca, and blade-shaped with a central median ridge. OSU 33452 resembles what is known of *D. venosa* (Scudder, 1878), though it is smaller than *D. venosa*. The tail (OSU 33452) does not seem to have many characters in common with *D. carbonaria, D. rolfei* or *D. quinni,* the other known American Carboniferous *Dithyrocaris* species with tails. Among the European *Dithyrocaris* species, *D. colei* and *D. testudinea* (Jones and Woodward, 1888–99) most resemble the tail and last segment of OSU 33452, including shape, the chevron decoration of the last segment, and a similar pattern of ridges on the telson and furca. The chevron lines on the last segment may relate the tail to the carapace OSU 33450, which appears to have the chevron lines on the segment underlying the carapace, but with the lack of further material, especially a whole specimen, relationship is uncertain.

The carapaces (OSU 33450, 33451) resemble the American Mississippian species, *D. quinni* (Copeland, 1967). However, they are not as strongly sclerotized in appearance, nor are the strong doublure edges preserved as in *D. quinni. Dithyrocaris quinni* has similar prominent lateral carinae. There is no close resemblance to *D. rolfei,* the other known Carboniferous American *Dithyrocaris* (Schram and Horner, 1978).

The unique "fish scale" terrace lines (Fig. 1, lower right) resemble in pattern that of the Devonian *D. neptuni* (Stumm and Chilman, 1969). Carapace decoration is a common *Dithyrocaris* characteristic.

Comparison of these specimens with European *Dithyrocaris* species shows a similarity to the median dorsal plates of *D. paradoxides* (Rolfe, 1969) and *D. testudinea* (Jones and Woodward, 1888–99). However, the carapace shape, the relative position of the lateral carinae and the decorative pattern seem to make these specimens unique and not directly comparable to any known American or European *Dithyrocaris* species. Other features used in analysis of *Dithyrocaris* species, such as a posterolateral spine, doublure or carapace edges, and most anterodorsal features, are missing in these two specimens.

SYSTEMATIC PALEONTOLOGY

Phyllocarida Packard, 1879
Archaeostraca Claus, 1888
Rhinocarina Clarke *in* Zittel, 1900
Rhinocarididae Hall and Clarke, 1888
Dithyrocaris Clarke *in* Hall and Clarke, 1888

Dithyrocaris sp.

Fig. 1

Material.—OSU 33450, OSU 33451, OSU 33452.

Remarks.—Specimen OSU 33452 (Fig. 1, left) is the last abdominal segment and a nearly complete telson with furca. The fossil is in black shale and consists of some calcite remains as well as partial impression in the shale. The fossil is presumably preserved ventrally with the furcal rami lying over the telson. The last segment is ≈5.1 mm in length while the telson is 11.4 mm. The furca measure ≈11.0 mm and 11.8 mm respectively. The measurements are approximate due to the crushed and somewhat distorted state of the fossil. The telson is judged to have been about equal to the furca in length. The telson is narrow and blade-shaped with a dorsal ridge down the center, viewed as a depression in the fossil. The telson has straight sides with no convexity and ends in a sharp point. No spines or spinules are present. The furcal rami are also long and narrow, with no convexity in their shape. There is a center ridge with two lateral, less distinct ridges to each side, which curve toward the center ridge at the head of the ramus and disappear toward the narrow tip. These may reflect depressions dorsally. There are no spines or spinules apparent on the furca. The last abdominal segment has the chevron decoration common in *Dithyrocaris* species. The chevrons point posteriorly.

Specimens OSU 33450 (Fig. 1, right upper and right lower) and OSU 33451 are incomplete carapaces in black shale and are partially replaced with calcite. Both are somewhat twisted, OSU 33451 more so, and are apparently flattened laterally. None of the carapace edges, posterior, anterior, or lateral, are complete. There is a possible remnant of doublure edging laterally on OSU 33451, but it seems broken and displaced. The dorsal length measured from the anterior tip of the carapace to the posterior edge is 25.2 mm on OSU 33450 and 24.5 mm on OSU 33451. OSU 33450 has remnants on one side anteriorly of a short cephalic carina running just above the anterior portion of the mesolateral carina and ending just below the juxtadorsal carina. Anteriorly it ends at the broken edge of the carapace. The mesolateral carina runs from anterior edge to posterior edge on both specimens. The mesolateral carina is a fold line and on both specimens there are remnants of blunt very short spinules pointing posteriorly on both specimens but they are for the most part missing and broken. There are apparently pitted areas running along both sides of the mesolateral carina, more apparent on OSU 33450 than on OSU 33451. The pits are tiny and perhaps had a sensory function. A strong juxtadorsal carina begins just above the end of the cephalic carina and ends just before the posterior edge of the carapace. This carina lies near the median dorsal plate dorsally. The carina is composed of raised knobs or blunt spinules joined at their base and directed in a latero-posterior direction, similar to the spinules present on the lateral carina mentioned above. The juxtadorsal spinules are more pronounced anteriorly than posteriorly along the carina. Both specimens have a median dorsal plate or the remains of one, which appears solid and separate from the carapace. The dorsal plate is in appearance composed of imbricating posteriorly pointed blunt chevrons. Where the dorsal plate appears to end on OSU 33450 near the anterior end of the carapace 2 rows of blunt spinules arise, point posterolaterally, and form 2 ridges which diverge slightly, run parallel to each other across the carapace and disappear at the broken anterior edge. The area between these ridges was probably the area of the rostral plate.

OSU 33450 and OSU 33451 are decorated with a "fish scale" or "terrace" pattern, which anterodorsally is composed of many fine wavy lines which become more like fish scales posterolaterally. These terraces end in an ordered fashion on either side of the juxtadorsal carina (OSU 33450, Fig. 1, lower right). OSU 33450 (Fig. 1, upper and lower right) is broken posterodorsally revealing an underlying segment with a pattern of straight lines aligned diagonally and posteriorly. This indicates that the segment underlying the carapace at this point had the chevron line decoration common in *Dithyrocaris* species and which I have seen in the pre-telson segment of the tail (OSU 33452). The "fish scale" pattern continues to the ventral broken edge of the carapace. Edges of the carapaces are not preserved. However, OSU 33451 has tiny fragmentary pieces of what may have been doublure but which is broken and displaced.

There does not appear to be a posteroventral spine, but as the posterior carapace edges are missing, absence or presence is uncertain. OSU 33450 has anteroventrally two large prominent protuberances which may be remains of large mandibles.

ACKNOWLEDGMENTS

Thanks must be extended to the following people: Michael C. Hansen for bringing these specimens to my attention, Thomas A. Deméré for taking the photographs, and Frederick R. Schram for criticism. Finally, special thanks to Martin D. Burkenroad for the grant which supported this work.

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A late Pleistocene molluscan fauna from San Dieguito Valley, San Diego County, California

Thomas A. Deméré

Abstract. A molluscan fauna, totaling 26 species of pelecypods and 21 species of gastropods, is described from a late Pleistocene deposit in San Dieguito Valley, San Diego County, California. The fauna lived ≈250 000 years B.P. along the north shore of a protected marine embayment, and contrasts with other much larger fossil assemblages from the San Diego Pleistocene in its preservation of a community death assemblage. Infaunal, suspension-feeding pelecypods requiring clean to muddy sand substrates represent the dominant trophic group in the fauna. Minor postmortem transport deposited these and other trophic groups (e.g., infaunal, deposit-feeding pelecypods, epifaunal deposit-feeding gastropods and epifaunal predaceous gastropods) as a shell lag which supported a trophic group of epifaunal, suspension-feeding pelecypods (oysters and jingle shells). Subsequent clastic deposition apparently preserved this shell lag habitat in situ. Five southern extralimital species suggest that water temperatures in this Pleistocene marine embayment were somewhat warmer than today. The presence of *Pinna* cf. *P. corteziana* Durham is a record for this genus and species in the late Pleistocene of southern California. In addition, 2 species, *Megapitaria squalida* (Sowerby) and *Tellina simulans* C. B. Adams, are new to the late Pleistocene of San Diego County.

INTRODUCTION

Upper Pleistocene marine deposits in coastal San Diego County are often richly fossiliferous and occur as patchy and thin basal veneers on elevated marine terraces and around the margins of sheltered embayment and drowned river mouths. Molluscan assemblages in these deposits have been described by numerous authors (*see references in* Kern, 1971, 1977).

One of the early pioneers in the Pleistocene paleontology of San Diego County was Frank Stephens who in 1929 published a paper entitled, "Notes on the marine Pleistocene deposits of San Diego County, California." This paper summarized all of the then known localities of Pleistocene deposits and provided a brief faunal listing from each. In recent years several of these localities have been re-examined (Emerson and Addicott, 1953; Valentine, 1960; Kern et al., 1971) and as a consequence their faunal and paleoenvironmental parameters are now more precisely known. As a continuation of this process of re-examination the present author has recollected and studied a rather unique locality in San Dieguito Valley near the city of Del Mar in San Diego County, California (Fig. 1).

Stephens (1929, p. 255) described SDSNH (San Diego Society of Natural History) locality 0069 as follows: "In its eastern part, the shells are weathered out and scattered over the hillside, with no stratum discernible. In the western part, in a small gulch, is a stratum of lime-cemented sandstone containing fossil shells . . . ." Stephens also included a small list of the more common molluscan species from this locality: "*Aletes squamigerus, Chione succincta, Chione undatella, Diplodonta sericata, Diplodonta subquadrata, Ostrea lurida, Phacoides nuttallii, Pecten aequisulcatus, Pinna* sp., *Tagelus californianus*."

In 1976, grading operations for a shopping center cut into the "western part" of SDSNH locality 0069, creating new exposures of unweathered Pleistocene sediments. Because Stephens' original locality was actually a composite of 2 localities (i.e., his

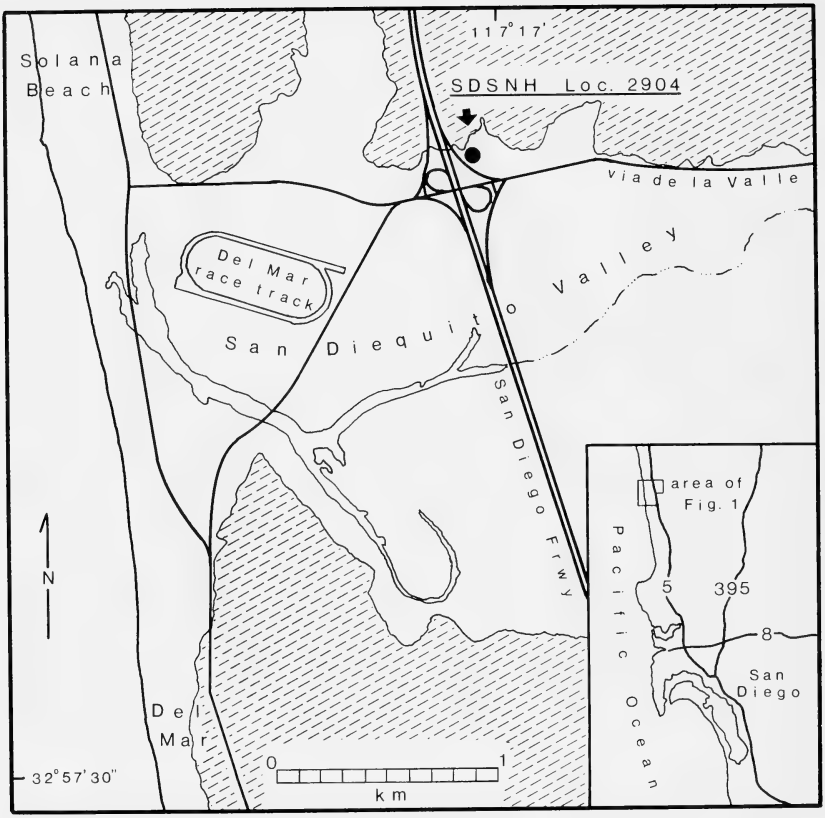

FIGURE 1. Map of the San Dieguito Valley area showing the location of SDSNH locality 2904. Inferred late Pleistocene land areas are indicated by diagonal lines.

"eastern" and "western" parts), this recent cut was assigned to a new locality (SDSNH locality 2904). The stratigraphic section exposed in this cut consists of ≈6 m of poorly consolidated marine sands that unconformably truncate siltstones and sandstones of the middle Eocene Delmar Formation (Fig. 2). The Pleistocene sediments are generally massive with the exception of a highly fossiliferous, 40-cm-thick bed that extends across the outcrop with a southerly dip of 5°. This bed is probably Stephens' "lime-cemented sandstone" as it is quite well indurated due to the high concentration of fossil shells. Lithologically this bed is composed of yellow-tan, poorly sorted, subangular, coarse- to fine-grained sand with occasional mudstone and "Poway"-type cobbles. Shells within the bed are randomly oriented except for large pen shells (*Pinna*) that lie with their long axes parallel to the bedding. Fossil preservation is excellent as all molluscan species retain their original shell material. The occurrence of fragile shells (*Bulla*, *Tagelus*, *Leptopecten* and *Pinna*) together with commonly paired valves of *Chione californiensis* (some with the ligament preserved) and *Felaniella sericata* suggests only a minor amount of postmortem shell transport.

Fossils were collected during April 1976 from a single 0.5 m^3 excavation. In all, ≈100 kg of fossils and matrix were removed and examined. The large pen shells were

FIGURE 2. SDSNH locality 2904 viewed from the east. The irregular dashed line represents the unconformable contact between the Pleistocene marine sands and the Eocene marine sediments. The vertical scale in the lower right corner represents 1 m.

removed from the outcrop individually whereas all remaining fossils were sorted from the bulk matrix.

In addition to the collection made from SDSNH locality 2904 several smaller collections obtained from near this locality by other workers were also examined. These are: SDSNH locality 0069; SDSU (San Diego State University) locality 636; and LACMIP (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section) locality 4585.

DISCUSSION

Age

Biostratigraphic dating of California marine Pleistocene deposits is inherently imprecise due to the modern aspect of the fossil faunas (e.g., 98% of the San Dieguito Valley fauna is represented by extant species). The variety of preserved facies in these deposits (e.g., exposed rocky shores, protected sand flats, offshore mud bottoms), each with its own associated fauna, also serves to limit biostratigraphic correlations.

Historically, the San Diego Pleistocene molluscan faunas have been assigned to the Bay Point Formation of Hertlein and Grant (1939, p. 71–72) which they and subsequent workers (Addicott and Emerson, 1959, p. 24) correlated with the regional type late Pleistocene Palos Verdes Sand of Woodring et al. (1946). However, recent work by Kern (1977), Masters and Bada (1977), Wehmiller et al. (1977), and Karrow and Bada (1980) has documented the existence of at least 3 temporarily distinct late Pleistocene marine terraces in the San Diego area. In terms of absolute ages they have distinguished terraces at 80–85 000 years B.P., 120–130 000 years B.P. and 250 000 (±50 000) years B.P. Preliminary work on *Chione* shells from San Dieguito Valley (SDSU locality 636) places this deposit within the 250 000 (±50 000) years B.P. range (J. P. Kern, *personal communication*).

Fauna

Forty-seven species of mollusks (26 pelecypods and 21 gastropods), one species of foraminifer, and unidentified Crustacea (Decopoda and Ostracoda) were recovered

Table 1. Checklist of fossils from SDSNH localities 2904 and 0069, SDSU locality 636, and LACMIP locality 4585. Counts were only made for fossils from loc. 2904 and are based on 2 hinges per pelecypod specimen and 1 aperture per gastropod specimen. *N* = number of specimens per species; % = percent abundance; x = presence (without counts).

	Localities				
	2904		0069	636	4585
Taxa	*N*	%			
Mollusca					
Pelecypoda					
Anomia peruviana Orbigny, 1846	53	3.0	x	x	x
Argopecten aequisulcatus (Carpenter, 1864)	26	1.4	x	x	
Chama pellucida Broderip, 1835					x
Chione californiensis (Broderip, 1835)	297	16.6		x	x
Corbula luteola Carpenter, 1864	2	.1	x	x	
Cryptomya californica (Conrad, 1837)	16	.9	x	x	
Diplodonta subquadrata (Carpenter, 1856)	18	1.0	x		
Donax californicus (Conrad, 1837)	1	.1			
Donax gouldii Dall, 1921	4	.2		x	
Felaniella sericata (Reeve, 1850)	379	21.1	x	x	
Laevicardium substriatum (Conrad, 1837)	32	1.8	x	x	
Leptopecten latiauratus (Conrad, 1837)	32	1.8	x		
Lucina approximata (Dall, 1901)	297	16.6	x	x	
Lucinisca nuttalli (Conrad, 1837)	75	4.2	x	x	
Macoma nasuta (Conrad, 1837)	5	.3			
Megapitaria squalida (Sowerby, 1835)	28	1.6	x		
Nemocardium centrifilosum (Carpenter, 1864)			x		
Ostrea lurida Carpenter, 1864	66	3.7	x	x	x
Pinna cf. *P. corteziana* Durham, 1950	12	.7	x	x	x
Pitar newcombianus (Gabb, 1865)	12	.7	x	x	
Protothaca staminea (Conrad, 1837)	2	.1			
Psammotreta viridotincta (Carpenter, 1856)	5	.3		x	
Raeta undulata (Gould, 1851)	1	.1			
Septifer bifurcatus (Conrad, 1837)	2	.1			
Tagelus californianus (Conrad, 1837)	41	2.3	x	x	
Tellina meropsis Dall, 1900	68	3.8	x	x	
Tellina simulans C. B. Adams, 1852	5	.3			
Trachycardium quadragenarium (Conrad, 1837)	1	.1			
Gastropoda					
Acteocina culcitella (Gould, 1853)	55	3.1		x	
Acteocina inculta (Gould, 1855)				x	
Alabina diegensis Bartsch, 1911	3	.2			
Alabina tenuisculpta Carpenter, 1864	12	.7		x	
Alabina tenuisculpta phalacra Bartsch, 1911	2	.1		x	
Anachis coronata (Sowerby, 1832)	85	4.7			
Astraea undosa (Wood, 1828)	6	.3		x	
Bulla gouldiana Pilsbry, 1893	7	.4			
Caecum crebricinatum (Carpenter, 1864)	3	.2		x	
Conus californicus Reeve, 1844	8	.4	x		
Crepidula onyx Sowerby, 1824	1	.1			
Crepipatella lingulata (Gould, 1846)	4	.2	x		
Hipponix antiquatus (Linnaeus, 1767)	1	.1			
Littorina scutulata Gould, 1849				x	
Melampus olivaceus Carpenter, 1857	1	.1		x	
Nassarius tegula (Reeve, 1853)	109	6.1	x	x	
Neverita reclusiana (Deshayes, 1839)	2	.1			
Notoacmea insessa (Hinds, 1842)	2	.1			
Odostomia cf. *O. fetella* Dall & Bartsch, 1909	2	.1			
Odostomia cf. *O. diegensis* Dall & Bartsch, 1903				x	
Pyramidella adamsi Carpenter, 1864	12	.7		x	
Rissoina californica Bartsch, 1915	1	.1			
Serpulorbis squamigerus (Carpenter, 1857)			x	x	
Triphora pedroana Bartsch, 1907	1	.1			
Tryonia cf. *T. imitator* (Pilsbry, 1899)	5	.3		x	

TABLE 1. Continued.

Taxa	Localities				
	2094		0069	636	4585
	N	%			
Foraminifera					
Ammonia beccarii (Linnaeus, 1758)	x				
Crustacea					
Ostracoda (sp. indeterminate)	x				
Decapoda (sp. indeterminate)	x				

from SDSNH locality 2904. In addition, examination of supplementary collections has added 6 species of mollusks (2 pelecypods and 4 gastropods) to this fauna. These are all listed in Table 1 along with abundance data.

Pelecypods dominate the fauna both in numbers of species and in numbers of individuals. The 3 most abundant species are *Felaniella sericata* (21% of specimens counted), *Chione californiensis* (16%), and *Lucina approximata* (16%).

The San Dieguito Valley fauna is small in terms of number of species when compared to other late Pleistocene molluscan assemblages from the San Diego area. For example, a collection from the old Spanish Bight locality on North Island (SDSNH locality 0056) contains more than 190 molluscan species. This high diversity is related to a mixing of faunal elements from several different marine habitats (i.e., a mixed death assemblage). The significance of the lower diversity, San Dieguito Valley fauna, lies in its apparent preservation of a more confined ecological unit (i.e., a community death assemblage).

Perhaps the most unusual taxonomic aspect of the fauna is the occurrence of the large pen shell, *Pinna* cf. *P. corteziana* Durham, 1950 (Fig. 3a, b). This extinct species was originally described from Pleistocene deposits on Isla Coronados in the Gulf of California. *Pinna corteziana* Durham differs from its closest living relative *Pinna rugosa* Sowerby, 1835, by its smaller apical angle and more nearly squared cross section (Durham, 1950, p. 57). In addition, the anterior muscle scar is much larger on *P. corteziana* than on *P. rugosa*. The San Dieguito Valley specimens possess the larger muscle scars and show a tendency towards squared cross sections, but the apical angles are greater than noted by Durham. His specimens measured 22°–23°, as opposed to a range of 22°–33° ($\bar{x} = 26°$) for the specimens from San Dieguito Valley. Because of the greater apical angle range, these specimens are only tentatively referred to *Pinna corteziana* Durham.

Stephens' (1929, p. 255) record of *Pinna* sp. from San Dieguito Valley (SDSNH locality 0069) was the only previous record of a fossil pinnid in the late Pleistocene of southern California. An examination of his original specimens shows them to be identical to those from SDSNH locality 2904. In addition, 2 other species, *Megapitaria squalida* and *Tellina simulans*, represent new records for the San Diego Pleistocene.

Paleoenvironment

Paleoenvironmental reconstruction of the San Dieguito Valley deposit is enhanced by the essentially modern aspect of the molluscan fauna, the preservation of the paleogeographic setting, the excellent preservation of the fossils, and the apparently low degree of postmortem shell transport.

The fauna is representative of protected conditions with such species as *Chione californiensis, Donax californicus, Tagelus californianus,* and *Nassarius tegula* restricted today to coastal marine embayments (i.e., either bays, lagoons or estuaries) (Ricketts and Calvin, 1968; Warme, 1971; Coan, 1971, 1973*b*, 1973*c*; McLean, 1978). Except for the occurrence of *Donax gouldii* there is a noticeable lack of exposed coast

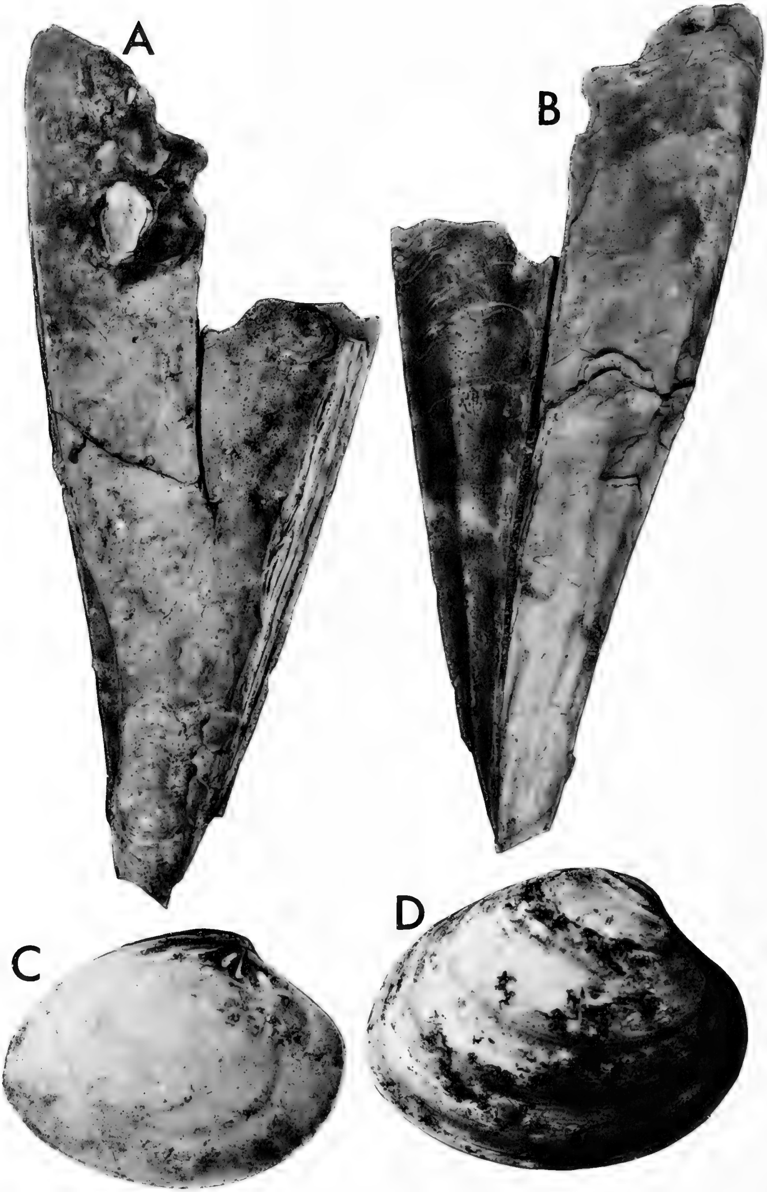

FIGURE 3. A, B. *Pinna* cf. *P. corteziana* Durham. SDSNH 04387. A, interior left valve, .4×; B, exterior same valve, .4×. C, D. *Megapitaria squalida* (Sowerby). SDSNH 04388. C, interior left valve, 2.3×; D, exterior right valve, 2×.

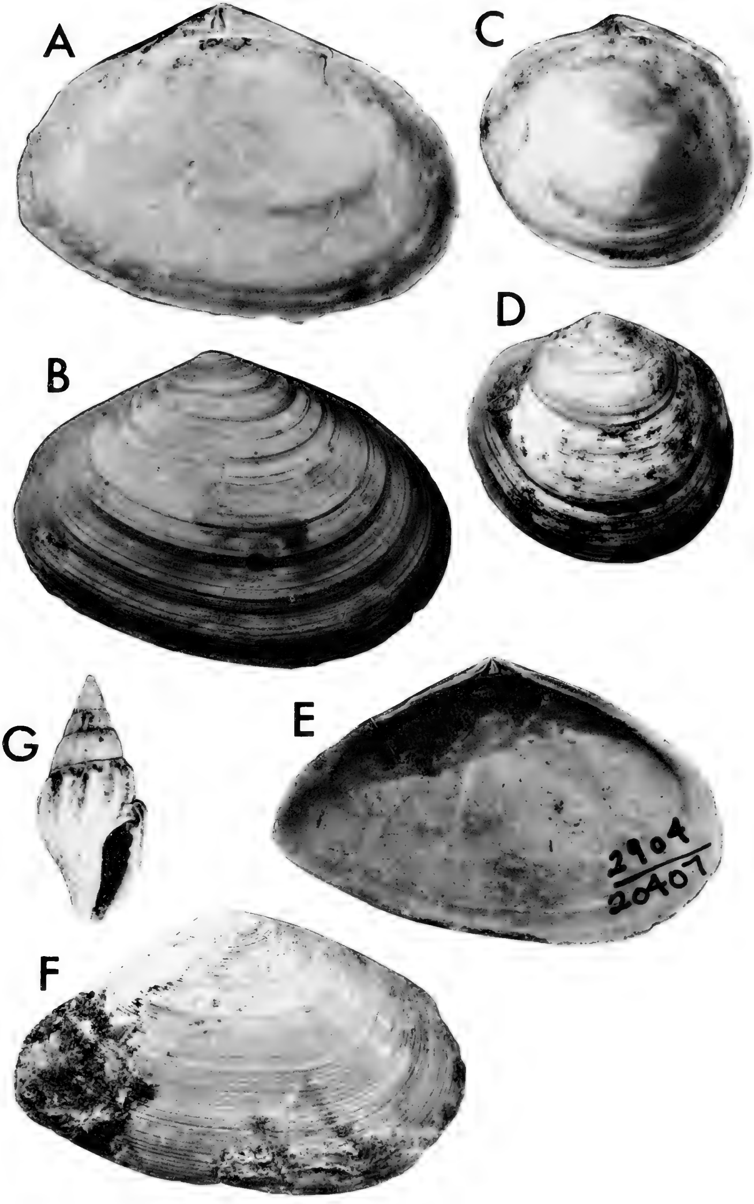

FIGURE 4. A, B. *Psammotreta viridotincta* (Carpenter). SDSNH 04389. A, interior left valve, 2×; B, exterior right valve, 2×. C, D. *Diplodonta subquadrata* (Carpenter). SDSNH 04390. C, interior right valve, 2×; D, exterior left valve, 2×. E, F. *Tellina simulans* C.B. Adams. SDSNH 04391. E, interior left valve, 2×; F, exterior right valve, 2×. G, *Anachis coronata* (Sowerby). SDSNH 04392. G, apertural view, 3×.

forms. Kern (1971, p. 815) pointed out that this species could easily be transported from the open coast into protected embayments. This agrees with the postulated paleogeographic setting in which an interglacial high sea stand flooded San Dieguito Valley creating a marine embayment. The inferred shoreline (Fig. 1) suggests that SDSNH locality 2904 on the northern shore of this embayment was exposed to >2 km of open water. Salinities within this portion of the embayment were probably normal marine as indicated by the majority of the faunal elements. Two species, *Tryonia* cf. *T. imitator* and *Melampus olivaceus,* however, require hyposaline conditions, but it is likely that these taxa are allochthonous elements of the fauna derived from a more inland region of the embayment. Kern (1971, p. 817–819) described a Pleistocene estuarine fauna from nearby Carmel Valley which was characterized by stunted molluscan individuals and abundant specimens of *Tryonia.* He concluded that his deposit accumulated under hyposaline conditions. There is no indication of this hyposaline-induced stunting in the San Dieguito Valley fauna, and it is probable that Kern's locality occupied a more back bay position within the late Pleistocene Carmel Valley embayment.

Bathymetric ranges suggest that the fauna inhabited lower intertidal to adlittoral depths (0 to 10 m), with the majority of the abundant species being derived from the shallower regions of this zone (e.g., *Nassarius tegula, Tagelus californianus* and *Chione californiensis*). *Pitar newcombianus* and *Raeta undulata* occur in deeper water today but are sometimes washed ashore (Abbott, 1974; McLean, 1978). Both species are rare at SDSNH locality 2904.

The presence of 6 southern extralimital species (i.e., those species that now range only south of their fossil occurrence) suggest that water temperatures were probably warmer during deposition of the San Dieguito Valley fauna than today. These species and their present northern range end points are: *Diplondonta subquadrata* (San Ignacio Lagoon, Baja California, Mexico); *Megapitaria squalida* (Scammons Lagoon, Baja California, Mexico); *Psammotreta viridotincta* (Gulf of California); *Tellina simulans* (Scammons Lagoon, Baja California, Mexico); and *Anachis coronata* (Baja California, Mexico) (see Figs. 3 and 4). *Pinna* cf. *P. corteziana,* an extinct species, is most closely related to *P. rugosa,* which in the Holocene does not occur north of southern Baja California, Mexico (Keen, 1971, p. 75). The remainder of the fauna has living representatives that include San Diego within their zoogeographic ranges. There are no northern extralimital species.

As regards substrate preference, the fauna is dominated by species that live today in clean to muddy sand (e.g., *Chione californiensis, Cryptomya californica, Felaniella sericata, Lucina approximata, Lucinisca nuttalli, Megapitaria squalida, Psammotreta viridotincta, Tagelus californianus* and *Tellina meropsis*). A minor element of a detritus-rich mud substrate is indicated by the presence of *Macoma nasuta. Notoacmea insessa* is species-specific in its association with the brown alga *Egregia* (Ricketts and Calvin, 1968, p. 130) implying the presence of this floral element. The common occurrence of *Anomia peruviana* and *Ostrea lurida* suggest the presence of firm substrates (i.e., rocks or shells). Interestingly several paired valves of these two species were observed still attached (life position) to slightly broken pen shells. This relationship together with the nearly coquina-like appearance of the deposit in outcrop suggests that the majority of the faunal elements accumulated as a shell lag which then served as a suitable substrate for the oysters and jingle shells. Subsequent clastic deposition essentially preserved this shell lag in situ.

Paleoecology

Autecological data obtained from numerous sources (Abbott, 1974; Coan, 1971, 1973*a*, 1973*b*, 1973*c*; Grant and Gale, 1931; Keen, 1971; McLean, 1978; Morris, 1966; Oldroyd, 1927; Ricketts and Calvin, 1968; Stanley, 1970; and Warme, 1971) allow some conclusions to be drawn concerning the paleoecology of the San Dieguito Valley fauna.

Infaunal, suspension-feeding pelecypods, characterized by *Chione californiensis,* *Megapitaria squalida* and *Tagelus californianus*, are the dominant trophic group in the fossil assemblage. Epifaunal, suspension-feeding pelecypods including byssally attached forms (*Anomia peruviana*) as well as cemented forms (*Ostrea lurida*) represent the next most dominant trophic group. An infaunal, deposit-feeding trophic group is represented by *Macoma nasuta*. Gastropods in the fossil fauna have herbivorous representatives such as the epifaunal, deposit feeders *Notoacmea insessa* and *Astrea undosa* but are dominated by first order, epifaunal predators (*Anachis coronata* and *Neverita reclusiana*). Also represented is a second order predator (*Conus californicus*) and several ectoparasites (*Odostomia* cf. *O. fetella* and *Pyramidella adamsi*). The most abundant gastropod, *Nassarius tegula*, is both a scavenger and passive predator.

This fossil assemblage with 75% of its individuals as infaunal detritus feeders (both suspension and deposit) and the remaining 25% divided among epifaunal deposit feeders, active predators, scavengers and ectoparasites possibly functioned as a biocoenosis. There are postmortem immigrants but their occurrence is rare. The various substrates indicated by the fauna appear to represent microhabitats (e.g., sand flats, mud flats, shell lag) within a lower intertidal to adlittoral, protected level bottom, marine embayment biotope.

As discussed earlier shell contributions from these various microhabitats were apparently deposited together to form a shell lag microhabitat which supported populations of *Anomia* and *Ostrea*.

Locality Description

SDSNH locality 2904.—Pleistocene. East-facing artificial cut on west end of Flower Hill Shopping Center near the northeast corner of the intersection of U.S. Interstate Highway 5 and Via de la Valle and east of the city of Del Mar, San Diego County, California. Lithology is a yellow-tan, poorly sorted, subangular, coarse- to fine-grained, moderately indurated, fossiliferous sand. Elevation ≈20 m above sea level. Latitude 32°58′57″ N; longitude 117°15′6″ W. NE ¼, SW ¼, Section 1, T14S, R4W (U.S. Geological Survey 7.5 minute Del Mar, California, quadrangle, 1967 edition). Collectors Toby and Tom Deméré, April 1976.

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The genera of the Nannoniscidae (Isopoda, Asellota)

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Abstract. Four new genera of the deep-sea asellote isopod family Nannoniscidae Hansen are described. Two new species of *Exiliniscus,* new genus, are described, *E. clipeatus* and *E. aculeatus. Nannoniscus hanseni* Just is transferred to *Exiliniscus. Nannoniscus crassipes* Hansen is transferred to *Rapaniscus,* new genus; *Rapaniscus dewdneyi,* new species, is described. *Nannoniscus tenellus* Birstein is transferred to *Panetela,* new genus; *Panetela wolffi,* new species, is described. *Nannoniscus armatus* Hansen is referred to *Regabellator,* new genus; *Regabellator profugus,* new species, is described. The bathymetric ranges of the new genera are: *Exiliniscus,* 80–5223 m; *Rapaniscus,* 220–2934 m; *Panetela,* 770–5495 m; *Regabellator,* 1964–4680 m. The other 6 nannoniscid genera are reviewed and illustrated. Two new species of *Nannoniscus* Sars are described, *N. intermedius* and *N. teres.* A key to the family and a list of species are given. These new descriptions are based on benthic samples taken at 74 stations in the North and South Atlantic Ocean, encompassing a depth range of 508–5223 m.

INTRODUCTION

The family Nannoniscidae (Isopoda, Asellota) encompasses a broad range of diverse morphologies. Recently, Siebenaller and Hessler (1977) have redefined the family to accommodate this diversity. The most useful features in distinguishing a nannoniscid are the bulbous fifth article of antenna I and the medial fusion dorsally of pereonites 6 and 7. However, these characters are not universally present in all of the species, and other characters must be employed: the single major dactylar claw on pereopods II–VII, the flat triangular molar process of the mandible, uropodal shape, and the presence of major anterolateral setae on the tergites of pereonites 2–4.

Within the genus *Nannoniscus* there is presently a striking diversity of morphologies. Many of the species in this genus differ markedly from the type species *N. oblongus* Sars, 1870. Perhaps because these unique forms have often been described from finds of single individuals or samples from a single locality, workers have been reluctant to erect additional genera. Extensive collections have become available from a number of deep-sea sampling programs. The present study is based primarily on materials from the deep-sea sampling program of the Woods Hole Oceanographic Institution (Sanders et al., 1965; Hessler and Sanders, 1967; Sanders and Hessler, 1969). The program has sampled transects throughout the Atlantic Ocean, running out from shallow coastal waters into the abyss. Such transects are located off the northeastern United States (Gay Head–Bermuda transect), Surinam, northern Brazil, Argentina, southwest Africa, Angola, Senegal, and Ireland. Additional samples have come from the Bay of Biscay (J. Allen, University of Newcastle upon Tyne), the Canary Islands (J. Allen), and the Weddell Sea (J. Rankin, University of Connecticut). A list of stations is given in Table 1.

It has become apparent from these additional materials that the morphologies of many of the described *Nannoniscus* species which appeared to be unique, specific characters in fact recur repeatedly in other species, and hence the establishment of new genera is both desirable and necessary. This study undertakes to establish these new genera as is warranted, and to delimit their geographic and bathymetric distribu-

Table 1. Station data.

	Station	Depth (m)	Latitude	Longitude
WHOI	Bermuda 1	1000	32°16.5′N	64°42.5′W
	Bermuda 2	1700	32°16.6′N	64°36.3′W
	Bermuda 4	1700	32°17.0′N	64°35′W
	Bermuda 5	2000	32°11.4′N	64°41.6′W
	Bermuda 6	1500	32°14.3′N	64°42′W
	Bermuda 7	2500	32°15′N	64°32.6′W
	Bermuda 8	1000	32°21.3′N	64°33′W
	HH 3	2900	38°47′N	70°08′W
	G 1	2000	39°42′N	70°39′W
	LL 1	4977	35°35′N	67°25′W
	JJ 3	4540	37°13.1′N	68°39.6′W
	OO 2	4667	33°0.67′N	65°2.2′W
	G 9	2021	39°44.7′N	70°38.3′W
	Chain 35, dredge 12	770–805	07°09′S	34°25.5′W
	61	2000	39°43.2′N	70°37.8′W
	62	2496	39°26′N	70°33′W
	65	2891	38°46.8′N	70°6.8′W
	66	2802	38°46.7′N	70°8.8′W
	70	4680	36°23′N	67°58′W
	73	1330–1470	39°46.5′N	70°43.3′W
	84	4749	36°24.4′N	67°56′W
	85	3834	37°59.2′N	69°26.2′W
	92	4694	36°20′N	67°56′W
	95	3753	38°33′N	68°32′W
	100	4743–4892	33°56.8′N	65°47′W
	109	4750	36°25′N	68°6.0′W
	118	1135–1153	32°19.4′N	64°34.9′W
			32°19.0′N	64°34.8′W
	119	2095–2223	32°15.8′N	64°31.6′W
			32°16.1′N	64°32.6′W
	120	5018–5023	34°43.0′N	66°32.8′W
			34°40.5′N	66°35.0′W
	121	4800	35°50.0′N	65°11.0′W
	122	4833	35°50.0′N	64°57.5′W
			35°52.0′N	64°58.0′W
	125	4825	37°24.0′N	65°54.0′W
			37°26.0′N	65°50.0′W
	126	3806	39°37.0′N	66°47.0′W
			39°37.5′N	66°44.0′W
	128	1254	39°46.5′N	70°45.2′W
	131	2178	36°28.9′N	67°58.2′W
	142	1624–1796	10°30.0′N	17°51.5′W
	145	2185	10°36.0′N	17°49.0′W
	149	3861	10°30.0′N	18°18.0′W
	155	3730–3783	00°03.0′S	27°48.0′W
	156	3459	00°46.0′S	29°28.0′W
			00°46.5′S	29°24.0′W
	159	834–939	07°58.0′S	34°22.0′W
	167	943–1007	07°58.0′S	34°17.0′W
			07°50.0′S	34°17.0′W
	169	587	08°03.0′S	34°23.0′W
			08°02.0′S	34°25.0′W
	175	4667–4693	36°36′N	68°29′W
			36°36′N	68°31′W
	195	3797	14°49′S	9°56′E
			14°40′S	9°54′E
	197	4595–4597	10°29′S	9°04′E
	199	3764–3779	9°47′S	10°29′E
			9°49′S	10°33′E
	200	2644–2754	9°41′S	10°55′E
			9°43.5′S	10°57′E
	201	1964–2031	9°29′S	11°34′E
			9°25′S	11°35′E

TABLE 1. Continued.

Station	Depth (m)	Latitude	Longitude
202	1427–1643	9°04′S	12°17′E
		8°56′S	12°15′E
209	1501–1693	39°47.6′N	70°49.9′W
		39°46′N	70°51.5′W
242	4382–4402	38°16.9′S	51°56.1′W
245	2707	36°55.7′S	53°01.4′W
247	5208–5223	43°33.0′S	48°58.1′W
256	3906–3917	37°40.9′S	52°19.3′W
259	3305–3317	37°13.3′S	52°45.0′W
287	4934–4980	13°16.0′N	54°52.2′W
		13°15.8′N	54°53.1′W
293	1456–1518	8°58.0′N	54°04.3′W
295	1000–1022	8°04.2′N	54°21.3′W
297	508–523	7°45.3′N	54°24.0′W
301	2487–2500	8°12.4′N	55°50.2′W
303	2842–2853	8°28.8′N	56°04.5′W
306	3392–3429	9°31.1′N	56°20.6′W
313	1491–1500	51°32.2′N	12°35.9′W
321	2868–2890	50°12.3′N	13°35.8′W
323	3338–3356	50°08.3′N	13°53.7′W
		50°08.3′N	13°50.9′W
326	3859	50°04.9′N	14°23.8′W
		50°05.3′N	14°24.8′W
328	4426–4435	50°04.7′N	15°44.8′W
330	4632	50°43.5′N	17°51.7′W
		50°43.4′N	17°52.9′W
Allen 33	1784	43°40.8′N	3°36′W
40	860	43°35.6′N	3°24.8′W
50	2379	43°46.7′N	3°38′W
65	1922	46°15′N	4°50′W
1969 Rankin 0022ES	3111	73°28.4′S	30°26.9′W

tions. Because of the great number of new species in the presently available materials, we will not attempt to describe all of the new species, but only to outline the composition of the genera. Occasional reference will be made to some of the undescribed species. Our intention is to reduce the unnatural heterogeneity of some of the present genera and to introduce a framework to permit future phylogenetic, biogeographic, and ecological studies. A key to the genera is given in Table 2. The described species of the family are compiled in Table 3.

Institutional abbreviations used in this study follow: WHOI, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA; USNM, United States Museum of Natural History, Washington, D.C., USA. Specimens without USNM numbers are presently in the working collection of R. R. Hessler.

SYSTEMATICS

Nannoniscidae Hansen, 1916 (Nannoniscini *auctoris*)

Exiliniscus, new genus

Diagnosis.—Pereonites 6 and 7 free. Body hemicylindrical, elongate and narrow; length greater than 5 times tergal width of pereonite 2. Cephalon with massive rostral crest, forming concave face. Antenna I compact, with bulbous distal segment. Antenna II short, tends to be compact and robust; length approximately one-quarter of total body length; some flagellar segments fused. Mandible lacks palp.

Additional descriptive notes.—Propodus of pereopod II with robust, medium-length setae distally, 1 dorsal and 1 ventral, setting off dactylus; both setae about

TABLE 2. A key to the genera of the Nannoniscidae.

		Nannoniscidae with pereonites 6 and 7 free	I
		Nannoniscidae with pereonites 6 and 7 fused medially	II
I.		Pereonite 7 fused with pleon	*Nannonisconus*
		Pereonite 7 not fused with pleon	1
	1.	Antenna I 5-segmented, with bulbous distal article	2
		Antenna I >5 segments	3
	2.	Protruding rostral crest, antenna I compact	*Exiliniscus*
		No rostral crest, antenna I not compact	*Panetela*
	3.	Body flattened and broad with expanded pleura and pleon	*Austroniscus*
		Body not exceptionally flattened or broadened	4
	4.	Female pleon with posterolateral spines; posterior pereopods not flattened for swimming; no opercular ventral medial spines; operculum indented distally	*Nannoniscoides*
		Female pleon generally without posterolateral spines; sexual dimorphism of pleon shape; posterior pereopods flattened for swimming; opercular ventral medial spines; operculum blunt distally	*Thaumastosoma*
II.		Pereopod I robust and thickened, much more so than other pereopods, which are slender in contrast	*Rapaniscus*
		Pereopod I normal, similar to other pereopods in thickness	5
	5.	Several major ventral medial spines	*Regabellator*
		One or no ventral medial spines	6
	6.	Antenna I >5 segments	*Nannoniscoides*
		Antenna I 5-segmented	7
	7.	Penultimate segment of antenna I without shelf-like process; pleon with posterolateral spines	*Hebefustis*
		Penultimate segment of antenna I with shelf-like process	*Nannoniscus*

equally well developed. Posterior pereopods often with natatory setae. Female operculum (pleopod II) length approximately equal to width; length approximately one-half length of pleon. Pleon spade-shaped in dorsal view, i.e., tapering anteriorly to posteriorly. Uropodal endopod long and narrow; exopod much reduced.

Type-species.—Exiliniscus clipeatus, new species.

Etymology.—Exiliniscus is taken from the Latin *exilis,* thin or slender. The gender of the name is masculine.

Remarks.—This genus is readily distinguished from most of the other Nannoniscidae by its narrow and elongate body and the lack of fusion of pereonites 6 and 7. *Exiliniscus* is distinct from the other nannoniscid genus *Panetela,* new genus (which has an elongate body and lacks fusion of pereonites 6 and 7), in its well-developed rostral crest (cf. Figs. 1B and 2B with Fig. 5B), the compactness of antennae I and II (cf. Figs. 1E and 2G with Fig. 5D), and the lack of a mandibular palp. *Exiliniscus* is the only nannoniscid known to lack a mandibular palp. *Nannoniscus hanseni* Just, 1970 is transferred to *Exiliniscus,* new genus. This species clearly possesses the diagnostic features of the genus. The presence or absence of a mandibular palp is not noted in Just's description. *Exiliniscus hanseni* is distinct from the other species of the genus in lacking notches in the cephalon for the insertion of antennae.

This genus contains the following species: *E. clipeatus,* new species; *E. hanseni* (Just, 1970); and *E. aculeatus,* new species.

Distribution.—Exiliniscus clipeatus: northwest Atlantic Ocean, 3834–5023 m; *E. hanseni:* Jørgen Brønlund Fjord, Greenland, 80–90 m (Just, 1970); *E. aculeatus:* southeast equatorial Atlantic Ocean, 1964–3797 m. This genus has a wide bathymetric distribution in the Atlantic Ocean, ranging from 80 to 5223 m. The stations at which the genus (including undescribed materials) has been taken are as follows: WHOI 65, 2891 m; WHOI 66, 2802 m; WHOI 84, 4749 m; WHOI 85, 3834 m; WHOI 95, 3753 m; WHOI 100, 4743–4892 m; WHOI 118, 1135–1153 m; WHOI 119, 2095–2223 m; WHOI 120, 5018–5023 m; WHOI 121, 4800 m; WHOI 122, 4833 m; WHOI 125, 4825 m; WHOI 142, 1624–1796 m; WHOI 145, 2185 m; WHOI 149, 3861 m; WHOI 159, 834–939 m; WHOI 167, 943–1007 m; WHOI 169, 587 m; WHOI 175, 4667–4693 m; WHOI 195,

TABLE 3. A compilation of the nannoniscid species (* indicates generic type-species).

Genus	Species
Nannoniscus	*acanthurus* Birstein, 1963; *aequiremis* Hansen, 1916; *affinis* Hansen, 1916; *analis* Hansen, 1916; *arcticus* Hansen, 1916; *australis* Vanhöffen, 1914; *bidens* Vanhöffen, 1914; *camayae* Menzies, 1962; *caspius* Sars, 1897; *coalescus* (Menzies and George, 1972); *detrimentus* Menzies and George, 1972; *inermis* Hansen, 1916; *intermedius*, new species; *laevis* Menzies, 1962; *laticeps* Hansen, 1916; *minutus* Hansen, 1916; *muscarius* Menzies and George, 1972; *oblongus** Sars, 1870 (figured 1899); *ovatus* Menzies and George, 1972; *perunis* Menzies and George, 1972; *plebejus* Hansen, 1916; *reticulatus* Hansen, 1916; *simplex* Hansen, 1916; *spinicornis* Hansen, 1916; *teres*, new species
Nannonisconus	*latipleonus** Schultz, 1966
Austroniscus	*acutus* Birstein, 1970; *groenlandicus* (Hansen, 1916); *karamani* Birstein, 1962; *ovalis** Vanhöffen, 1914; *rotundatus* Vanhöffen, 1914; *vinogradovi* (Gurjanova, 1950)
Nannoniscoides	*angulatus** Hansen, 1916; *biscutatus* Siebenaller and Hessler, 1977; *coronarius* Siebenaller and Hessler, 1977; *excavatifrons* (Birstein, 1970); *gigas* Siebenaller and Hessler, 1977; *latediffusus* Siebenaller and Hessler, 1977
Hebefustis	*alleni* Siebenaller and Hessler, 1977; *cornutus* Siebenaller and Hessler, 1977; *dispar* Siebenaller and Hessler, 1977; *hexadentium* Siebenaller and Hessler, 1977; *hirsutus* (Menzies, 1962); *mollicellus* Siebenaller and Hessler, 1977; *par* Siebenaller and Hessler, 1977; *primitivus* (Menzies, 1962); *robustus* (Birstein, 1963); *vafer** Siebenaller and Hessler, 1977
Thaumastosoma	*distinctum* (Birstein, 1963); *platycarpus** Hessler, 1970; *tenue* Hessler, 1970
Exiliniscus	*aculeatus*, new species; *clipeatus**, new species; *hanseni* (Just, 1970)
Rapaniscus	*crassipes* (Hansen, 1916); *dewdneyi**, new species
Panetela	*tenella* (Birstein 1963); *wolffi**, new species
Regabellator	*armatus* (Hansen, 1916); *profugus**, new species

3797 m; WHOI 197, 4595 m; WHOI 200, 2644–2754 m; WHOI 201, 1964–2031 m; WHOI 242, 4382–4402 m; WHOI 247, 5208–5223 m; WHOI 259, 3305–3317 m; WHOI 287, 4934–4980 m; WHOI 293, 1456–1518 m; WHOI 295, 1000–1022 m; WHOI 301, 2487–2500 m; WHOI 303, 2842–2853 m; WHOI 306, 3392–3429 m; WHOI 313, 1491–1500 m; WHOI 321, 2868–2890 m; WHOI 323, 3338–3356 m; WHOI 326, 3859 m; WHOI 328, 4426–4435 m; WHOI 330, 4632 m; WHOI HH 3, 2900 m; WHOI JJ 3, 4540 m; WHOI LL 1, 4977 m; WHOI OO 2, 4667 m; WHOI Bermuda 1, 1000 m; WHOI Bermuda 2, 1700 m; WHOI Bermuda 4, 1700 m; WHOI Bermuda 5, 2000 m; WHOI Bermuda 6, 1500 m; WHOI Bermuda 7, 2500 m; WHOI Bermuda 8, 1000 m; ALLEN 40, 860 m; ALLEN 50, 2379 m; ALLEN 65, 1922 m; 1969 RANKIN 0022ES, 3111 m.

Exiliniscus clipeatus, new species
Figure 1

Holotype.—WHOI 85, brooding ♀, 2.7 mm long, USNM 184182.

Other material.—WHOI 84, 1 individual; WHOI 120, 1 individual; WHOI 121, 2 individuals; WHOI 122, 5 individuals; WHOI 175, 1 individual.

Distribution.—Northwest Atlantic Ocean, 3834–5023 m.

Etymology.—Latin, armed with a shield.

Diagnosis.—Body length 6.6 times tergal width of pereonite 2. Pereonite 4 length to width ratio (l/w) 0.9. Pereonite 5 (l/w) 1.1. Pleon (l/w) 1.08; width 0.8 times width of pereonite 2. Rostral crest not protruding far forward, bluntly rounded. Antenna I with projection forming full shield over distal bulbous article. Antenna II robust; segment 5 (l/w) 1.38. Uropodal endopod (l/w) 3.13; exopod reduced, (l/w) 1.5; endopod length 8.33 times exopod length. Operculum (♀ pleopod II) rounded; distal margin straight.

Additional descriptive notes.—Pereopods I and II robust. Pereopod I carpus and

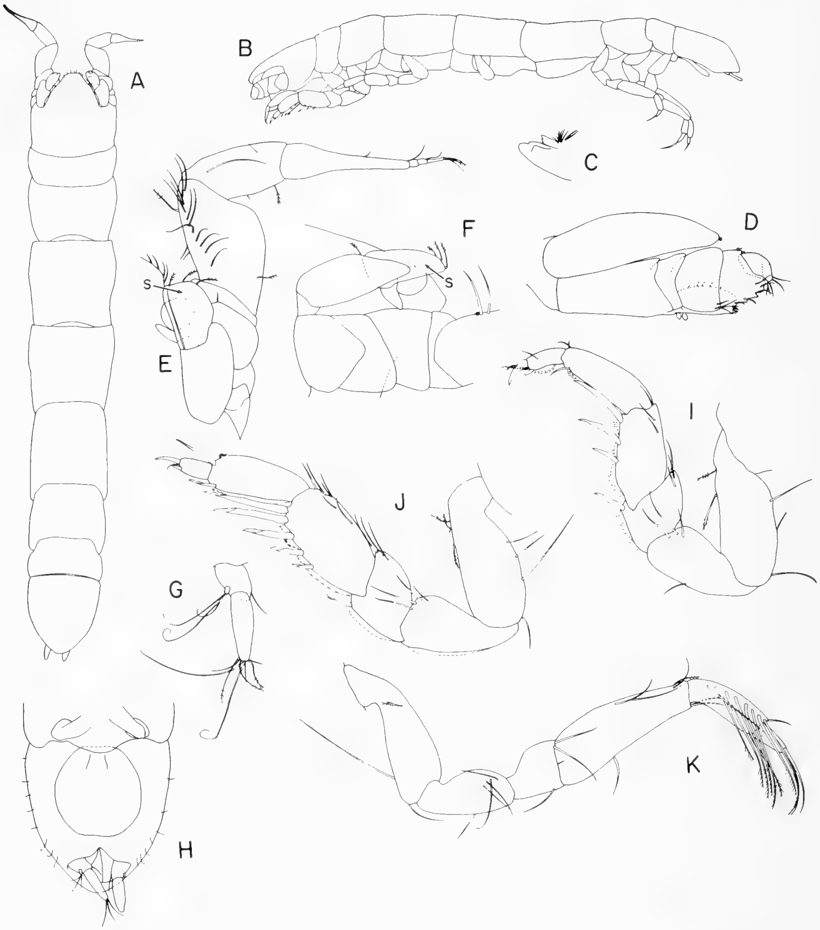

FIG. 1. *Exiliniscus clipeatus,* new species, WHOI 85. A. brooding ♀ (holotype), dorsal view; B. preparatory ♀, lateral view; C. juvenile ♀ left mandible; D. juvenile ♀, maxilliped; E. brooding ♀ (holotype) right antennae I and II (dorsal view), s: shield; F. brooding ♀ (holotype) antenna I and base of antenna II, lateral view, s: shield; G. brooding ♀ (holotype) right uropod; H. brooding ♀ (holotype) operculum (pleopod II); I. juvenile ♀ left pereopod I; J. juvenile ♀ left pereopod II; K. juvenile ♀ left pereopod VI.

propodus of approximately equal length; carpus with 3–4 robust setae on ventral surface; propodus with 1. Pereopod II carpus somewhat longer than propodus; carpus with 5 robust setae on ventral surface, propodus distal seta on dorsal surface somewhat longer than ventral seta. Pereopod VI propodus with natatory setae; limb slender, carpus much longer than propodus.

Remarks.—Exiliniscus clipeatus, new species, is readily distinguished from the other species of the genus by the well-developed shield, stemming from segment 2, which fully envelops the bulbous distal article of antenna I dorsally. Other distinctive features include the dimensions of pereonites 4 and 5, the length and shape of the uropodal rami, and the robustness of antennae II.

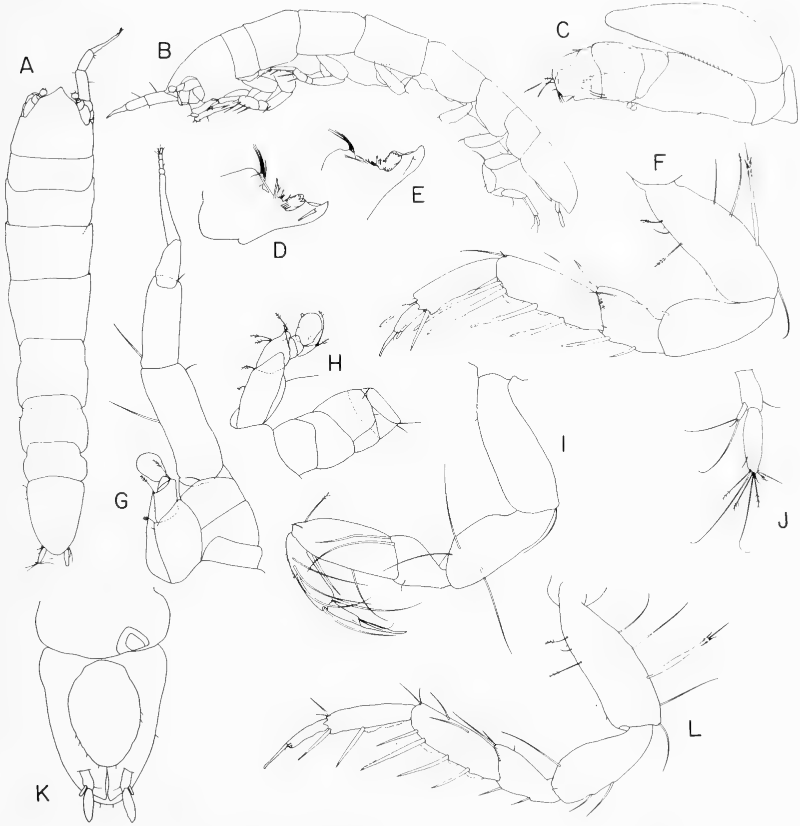

FIG. 2. *Exiliniscus aculeatus,* new species, WHOI 201. A. preparatory ♀ (holotype), dorsal view; B. preparatory ♀ (holotype), lateral view; C. brooding ♀ maxilliped; D. and E. brooding ♀ left mandible; F. brooding ♀ pereopod I; G. preparatory ♀ (holotype) antennae I and II; H. preparatory ♀ (holotype) antenna I and base of antenna II; I. brooding ♀ pereopod VI; J. preparatory ♀ (holotype) right uropod, *in situ*; K. preparatory ♀ (holotype) operculum (pleopod II), ventral view; L. brooding ♀ pereopod II.

***Exiliniscus aculeatus,* new species**
Figure 2

Holotype.—WHOI 201, preparatory ♀, 2.3 mm long, USNM 184183.

Other material.—WHOI 201, 11 specimens; WHOI 200, 3 specimens; WHOI 195, 4 individuals and 2 fragments.

Distribution.—Southeast equatorial Atlantic Ocean, 1964–3797 m.

Etymology.—Latin, sharp, pointed, stinging.

Diagnosis.—Body length 5.6 times tergal width of pereonite 2. Pereonites 3, 4, and 5 broader than long. Pereonite 3 length to width ratio (l/w) 0.6; peronite 4 (l/w) 0.75; peronite 5 (l/w) 0.8. Pleon somewhat elongate; (l/w) 1.38; width 0.67 times width of pereonite 2. Rostral crest drawn to a point. Antenna I bulbous distal segment exposed, not fully shielded by projection. Antenna II relatively thin; segment 5 (l/w) 2.65.

Uropodal endopod l/w 3.0; exopod l/w 4.5; endopod length 2.7 times exopod length. Female operculum elongate, oval-shaped, tapering distally.

Additional descriptive notes.—Pereopod I relatively slender; propodus with 2 robust setae distally; carpus with 4 robust setae ventrally. Pereopod II relatively slender; carpus with with 4 robust setae ventrally. Pereopod VI robust, carpus somewhat longer than propodus. Mandible with incisor processes sharply pointed; lacinia mobilis with well-developed and pointed teeth.

Remarks.—Exiliniscus aculeatus can be distinguished from the other species of the genus by its pointed rostral crest, the relatively slender anterior pereopods, and the shape of the ♀ operculum.

Rapaniscus, new genus

Diagnosis.—Pereonites 6 and 7 fused medially. Antenna I 5-segmented; distal segment bulbous; article 4 with well-developed, shelf-like process. Pereopod I massive, carpus broad, bearing long robust setae; carpus and propodus of approximately equal length. Pereopods II–VII slender. Body length approximately 3.4 times tergal width of pereonite 2. Females with large recurved ventral medial spine on operculum or venter of preopercular segments. Mandible with palp.

Additional descriptive notes.—Pleon length approximately equal to width. Where recurved ventral medial spine is present on ♀ operculum, ♂♂ lack the spine. Female operculum (pleopod II) oval, blunted distally.

Type-species.—Rapaniscus dewdneyi, new species.

Etymology.—Rapaniscus is from the Latin *rapax,* seizing, snatching, grasping. The name is masculine.

Remarks.—Rapaniscus is readily distinguished from the other nannoniscid genera which have a 5-segmented antenna I with a bulbous distal article and fusion of pereonites 6 and 7 by the massive development of pereopod I (*see* Fig. 4G), which is more heavily developed than the limb of other nannoniscid genera. *Nannoniscus crassipes* (Hansen, 1916), with a massive pereopod I and a recurved ventral medial spine stemming from the venter of pereonite 7, is transferred to *Rapaniscus.*

The genus contains the following species: *Rapaniscus dewdneyi,* new species, and *R. crassipes* (Hansen, 1916), and an undescribed species.

Distribution.—Rapaniscus dewdneyi: northwestern Atlantic Ocean, 1254–2223 m. *R. crassipes:* North and equatorial Atlantic Ocean, 220–2754 m. The stations at which the genus has been taken are as follows: *R. crassipes* (Hansen, 1916): Off Lofoten Islands, at Skraaven, 220–457 m (G. O. Sars, 1899, as new specimens of *Nannoniscus oblongus*); WHOI G1, 2000 m; WHOI 73, 1330–1470 m; WHOI 145, 2185 m; WHOI 200, 2644–2754 m; WHOI 209, 1501–1693 m; *R. dewdneyi,* new species: WHOI G9, 2021 m; WHOI 61, 2000 m; WHOI 119, 2095–2223 m; WHOI 128, 1254 m; *Rapaniscus* species: WHOI 95, 3753 m; WHOI 118, 1135–1153 m; WHOI 119, 2095–2223 m; WHOI 256, 3906–3917 m; WHOI 287, 4934–4980 m; WHOI 306, 3392–3429 m; WHOI 321, 2868–2890 m; WHOI 330, 4632 m.

Rapaniscus dewdneyi, new species
Figure 3

Holotype.—WHOI 209, preparatory ♀, 1.4 mm long, USNM 184184.

Paratype.—WHOI 209, male, 1.2 mm long, USNM 184185.

Other material.—WHOI G9, 1 specimen; WHOI 61, 4 specimens; WHOI 119, 1 specimen; WHOI 128, 4 specimens; WHOI 131, 2 specimens.

Distribution.—Northwestern Atlantic Ocean, 1253–2223 m.

Etymology.—For our colleague, Dewdney Somero, with whom we have closely worked, whose counsel we respect, and whose efforts in support of research continue through the Dewdney Endowment.

Diagnosis.—Body length 3.5 (♀), 3.6 (♂) times tergal width of pereonite 2. Pereonite 4 width 0.8 times tergal width of pereonite 2. Pereonite 5 0.6 (♀), 0.8 (♂) times

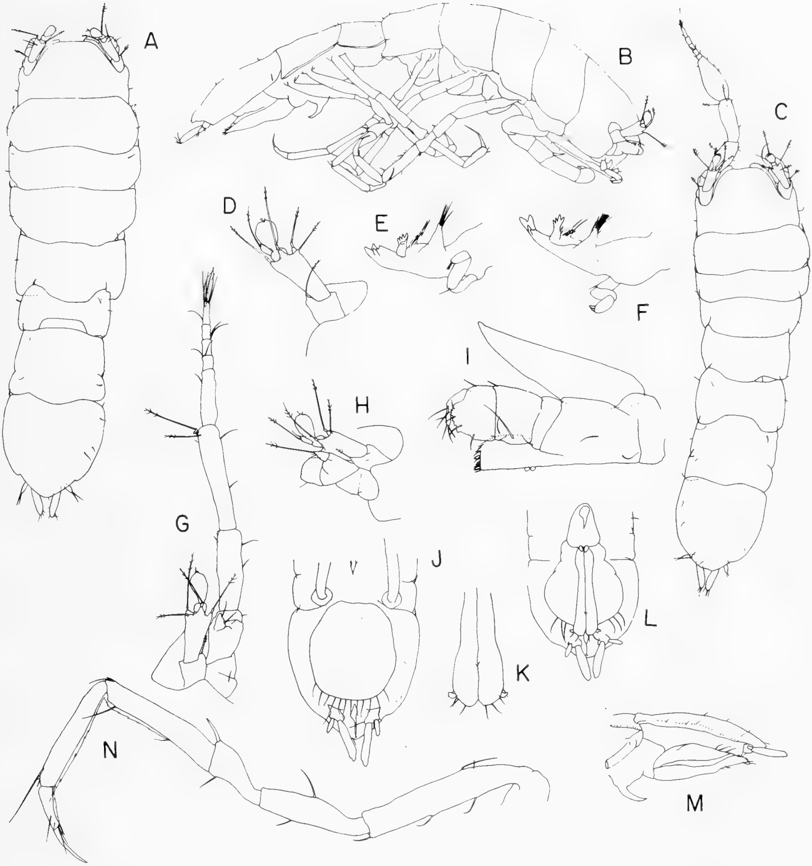

FIG. 3. *Rapaniscus dewdneyi*, new species, WHOI 209. A. preparatory ♀ (holotype), dorsal view; B. preparatory ♀ (holotype), lateral view; C. copulatory ♂ (paratype), dorsal view; D. preparatory ♀ (holotype) antenna I; E. and F. brooding ♀ left mandible; G. brooding ♀ antennae I and II; H. copulatory ♂ (paratype) antenna I; I. brooding ♀ maxilliped; J. brooding ♀ operculum (pleopod II); K. copulatory ♂ (paratype) pleopods I; L. copulatory ♂ (paratype), ventral view of pleon; M. copulatory ♂ (paratype) pleon, lateral view; N. brooding ♀ pereopod VI.

width of pereonite 2. Pleon length approximately equal to width; pleon tapers posteriorly. No sexual dimorphism of pleon shape. Pleon width 0.72 (♀), 0.76 (♂) times width of pereonite 2. Cephalic width 0.84 (♀), 0.91 (♂) times tergal width of pereonite 2. Uropod length 0.42 times length of pleon (measured in dorsal view). Endopod elongate and slender; length 5.6 (♀), 4.4 (♂) times width (l/w). Exopod short; (l/w) 3.4. Endopod length 2.6 times length of exopod. Male and ♀ with thin ventral medial spine on pereonite 7. Female operculum (pleopod II) relatively flat, not vaulted.

Remarks.—Rapaniscus dewdneyi was taken at the same station as *Rapaniscus crassipes* (WHOI 209). *Rapaniscus dewdneyi* can be differentiated from *R. crassipes* by the shape of the uropodal endopod, elongate in *R. dewdneyi,* much shorter in *R.*

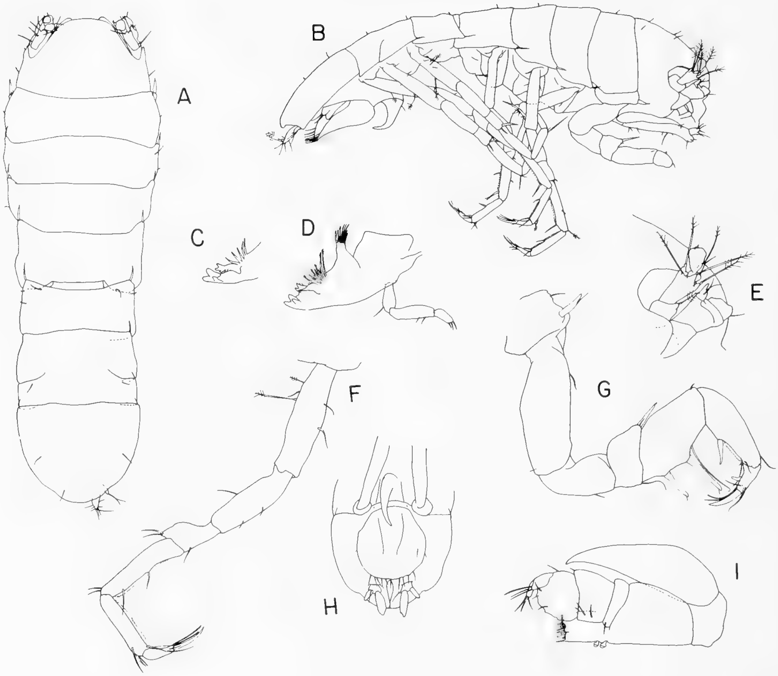

FIG. 4. *Rapaniscus crassipes* (Hansen, 1916), WHOI 209. A. preparatory ♀, dorsal view; B. preparatory ♀, lateral view; C. brooding ♀ left mandibular incisors; D. brooding ♀ left mandible; E. preparatory ♀ antenna I and base of antenna II; F. brooding ♀ pereopod VI; G. brooding ♀ pereopod I; H. brooding ♀ ventral view of pleon; I. brooding ♀ maxilliped.

crassipes (Figs. 3J, 4H). The body of *R. crassipes* is more robust, the pleon more blunt posteriorly, the ventral medial spine is elongate and robust, and the ♀ operculum is deeply vaulted (Figs. 3B, 4B). These two species may be distinguished from an undescribed species of *Rapaniscus* on the shape of the uropodal endopod, and the sexual dimorphism of the pleon, which is squared in the ♂ of the undescribed species, a condition unique among the species of the genus.

***Panetela*, new genus**

Type-species.—Panetela wolffi, new species.

Diagnosis.—Pereonites 6 and 7 free. Body cylindrical or hemicylindrical, narrow and elongate; length greater than approximately 5 times tergal width of pereonite 2. Cephalon lacks massive rostral crest. Antenna I 5-segmented, with bulbous distal article; segment 2 slender. Mandible with 3-segmented palp.

Additional descriptive notes.—Antenna II generally narrow and long relative to body length. Pereopods moderately robust; posterior pereopods may have natatory setae. Shape of uropods and ♀ operculum (pleopod II) may vary interspecifically. Some species possess a ventral medial spine, stemming from either the venter of pereonite 7 or from the operculum.

Etymology.—*Panetela* is taken from Spanish, referring to the slender, cigar-like body form. The gender is feminine.

Remarks.—*Nannoniscus tenellus* Birstein, 1963 is transferred to *Panetela* because it lacks fusion of pereonites 6 and 7, does not have a massive rostral crest, and has a 5-segmented antenna I with a bulbous distal article. Also of note is the slender and elongate antenna II which contrasts with the more robust antenna II in *Exiliniscus*. Wolff (1975, 1976) notes the occurrence of an unidentified ♀ nannoniscid taken from a *Thalassia* rhizome in the Cayman Trench at 6800 m at a station of the R/V Akademik Kurchatov (1242A) (*see* Fig. 2, part O of Wolff [1976]). This specimen is most probably a member of *Panetela*.

Panetela is readily distinguished from most of the other Nannoniscidae by its narrow and elongate body, and the lack of fusion of pereonites 6 and 7. In the overall slender appearance of the body it is very similar to *Exiliniscus*. However, *Panetela* may be easily distinguished by its lack of a protruding rostral crest, the less compact antenna I (Figs. 1E, 5E), the presence of a 3-segmented mandibular palp, and its more narrow and elongate antenna II (Figs. 1E, 2G, 5D).

The genus contains: *P. tenella* (Birstein, 1963) and *P. wolffi*, new species.

Distribution.—North and South Atlantic Ocean, northwest Pacific Ocean, 770–5495 m. The stations at which the genus has been taken are as follows: WHOI 62, 2496 m; WHOI 66, 2802 m; WHOI 84, 4749 m; WHOI 92, 4694 m; WHOI 95, 3753 m; WHOI 100, 4743–4892 m; WHOI 109, 4750 m; WHOI 118, 1135–1153 m; WHOI 119, 2095–2223 m; WHOI 120, 5018–5023 m; WHOI 121, 4800 m; WHOI 122, 4833 m; WHOI 125, 4825 m; WHOI 126, 3806 m; WHOI 128, 1254 m; WHOI 142, 1624–1796 m; WHOI 145, 2145 m; WHOI 156, 3459 m; WHOI 167, 943–1007 m; WHOI 199, 3764–3799 m; WHOI 200, 2644–2754 m; WHOI 201, 1964–2031 m; WHOI 202, 1427–1643 m; WHOI 242, 4382–4402 m; WHOI 245, 2707 m; WHOI 247, 5208–5223 m; WHOI 259, 3305–3317 m; WHOI 287, 4934–4980 m; WHOI 293, 1456–1518 m; WHOI 301, 2487–2500 m; WHOI 303, 2842–2853 m; WHOI 323, 3338–3356 m; WHOI 326, 3859 m; WHOI 330, 4632 m; WHOI Bermuda 7, 2500 m; WHOI Chain 35, Dredge 12, 770–805 m; ALLEN 33, 1784 m; Kurchatov Station 3575, 5461–5495 m (Birstein, 1963).

Panetela wolffi, new species

Figure 5

Holotype.—WHOI 201, preparatory ♀, 2.0 mm long, USNM 184186.

Paratype.—WHOI 202, copulatory ♂, 1.35 mm long, USNM 184187.

Other material.—WHOI 201, 19 individuals; WHOI 202, 4 individuals.

Distribution.—Equatorial southeastern Atlantic Ocean, 1427–2031 m.

Etymology.—After Torben Wolff.

Diagnosis.—Body length 8 (♀), 6.4 (♂) times tergal width of pereonite 2. Body appears very elongate, pereonites 4–7 0.46 times body length. Female pleon rounded distally; ♂ pleon somewhat squared distally. Uropodal endopod elongate; exopod very slender and short. Pereopods VI and VII with natatory setae. No ventral medial spines.

Remarks.—*Panetela wolffi* has a very elongate appearance due to the length of pereonites 3–7. This contrasts with the condition in *P. tenella* (Birstein, 1963) in which the body is more compact. Also, the operculum (♀ pleopod II) of *P. wolffi* is more pear-shaped and elongate than that of *P. tenella*. The sexual dimorphism of pleonar shape in *P. wolffi* should also be noted.

Regabellator, new genus

Diagnosis.—Pereonites 6 and 7 fused. Body length approximately 3.4 times tergal width of pereonite 2. Antenna I 5-segmented, with bulbous terminal article; segment 4 with long lateral projection. Two large medial spines on venters of pereonites 6 and 7. Posterior spine with broad basal region; anterior spine narrower, generally directed ventrally or slightly anteriorly. Short spine-like processes may be present on ventral medial surfaces of other pereonal segments. Pereopod I with anteriorly directed coxal plate bearing small robust seta. Propodus and carpus devoid of long robust setae dorsally and ventrally. (However, small robust terminal seta is present.) Pereopods II–IV

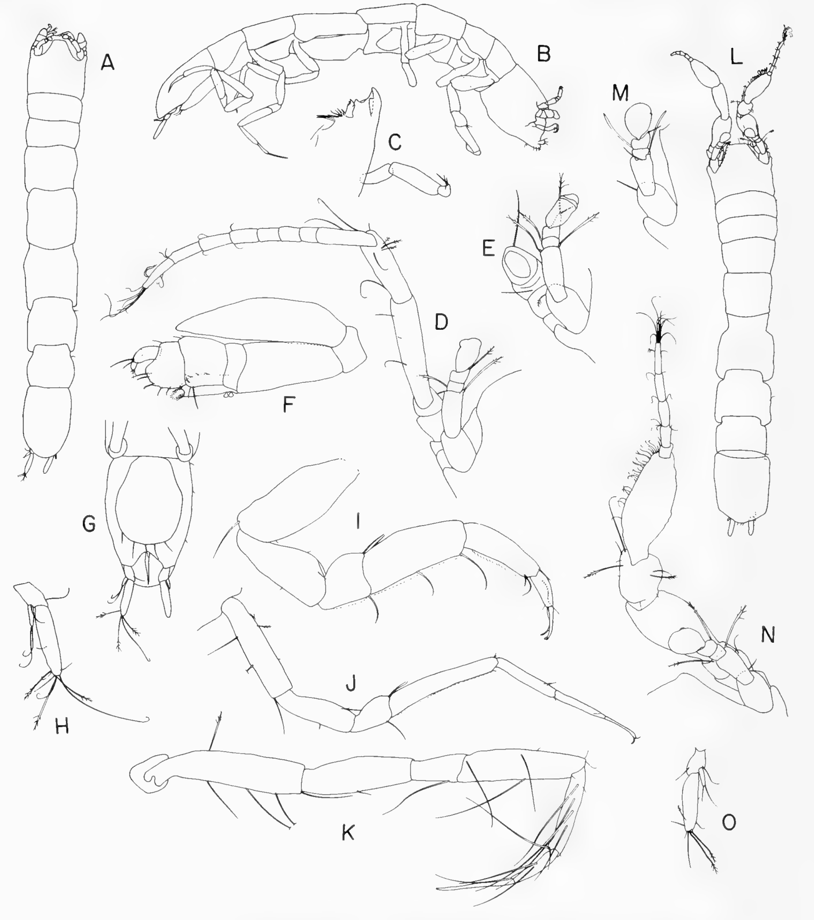

FIG. 5. *Panetela wolffi,* new species, WHOI 201. A. preparatory ♀ (holotype), dorsal view; B. preparatory ♀ (holotype), lateral view; C. brooding ♀ left mandible; D. preparatory ♀ (holotype) antennae I and II; E. preparatory ♀ (holotype) antenna I and base of antenna II; F. brooding ♀ maxilliped; G. brooding ♀ pleon, ventral view; H. brooding ♀ right uropod; I. juvenile ♀ right pereopod I; J. brooding ♀ right pereopod II; K. brooding ♀ left pereopod VI, WHOI 202, copulatory ♂ (paratype); L. dorsal view; M. antenna I; N. antennae I and II; O. left uropod.

with very long robust setae from ventral and dorsal surfaces of propodus and carpus. Pereopods V–VII not broadened, without well-developed natatory setae. Mandible with palp.

Additional descriptive notes.—Pereonites 4–7 distinctly narrower than anterior pereonites. Pleon tapers posteriorly, with ventral surface somewhat vaulted, deepening from lateral margins to branchial chamber. Posteriorly, lateral pleonar margins tuck under, setting off anal plates and uropods from rest of pleon. Uropods set close together and almost terminal. Uropods with small exopod; endopod variable in length.

Type-species.—Regabellator profugus, new species.

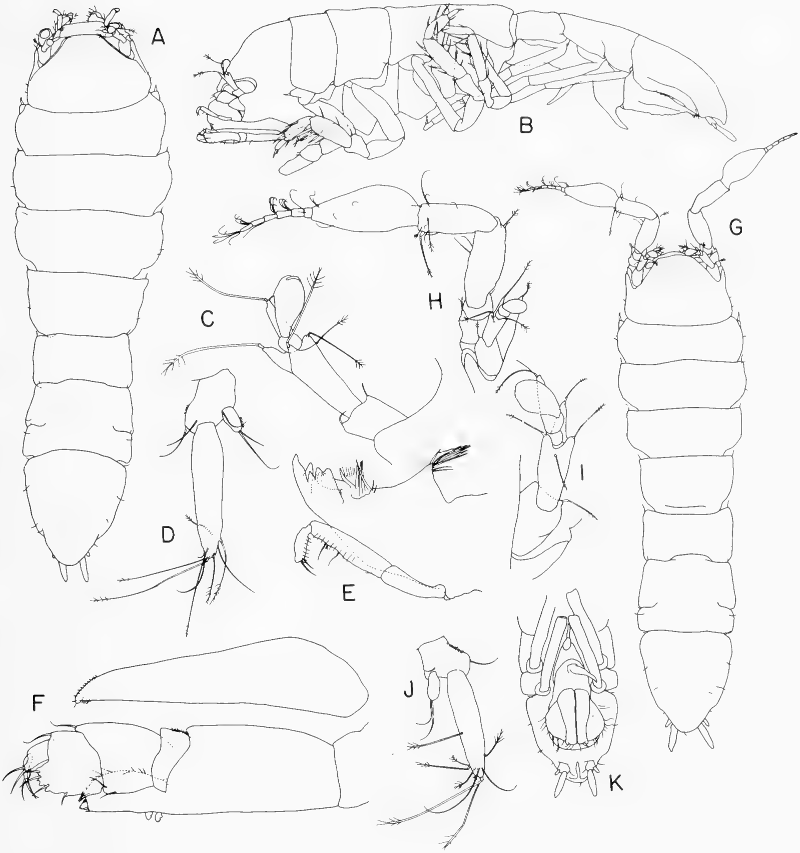

FIG. 6. *Regabellator profugus,* new species, WHOI 201. A. preparatory ♀ (holotype), dorsal view; B. preparatory ♀ (holotype), lateral view; C. preparatory ♀ (holotype) left antenna I; D. preparatory ♀ (holotype) left uropod; E. brooding ♀ left mandible; F. brooding ♀ maxilliped; G. ♂ (paratype), dorsal view; H. ♂ (paratype) antenna II; I. ♂ (paratype) antenna I; J. ♂ (paratype) right uropod; K. ♂ (paratype) pleopods I.

Etymology.—Regabellator is masculine, taken from the Latin *regalis* and *bellator,* regal warrior, referring to the presence of multiple ventral medial spines.

Remarks.—Nannoniscus armatus Hansen, 1916 is transferred to *Regabellator. Regabellator* is similar to described species of *Thaumastasoma* (*T. platycarpus* Hessler, 1970 and *T. tenue* Hessler, 1970) which also possess 2 major ventral medial spines (Fig. 11B). These 2 species also show similarities to *Regabellator* in the shape of the ♀ pleon and the close positioning of the uropods to the midline. *Thaumastasoma* has been removed from the Desmosomatidae to the Nannoniscidae by Siebenaller and Hessler (1977).

These two genera differ in the first antenna, which is 6-segmented and unmodified in *Thaumastasoma* (Fig. 11C), and 5-segmented with a bulbous distal article and a shelf-like process from the penultimate article in *Regabellator* (Fig. 6C). *Thaumas-*

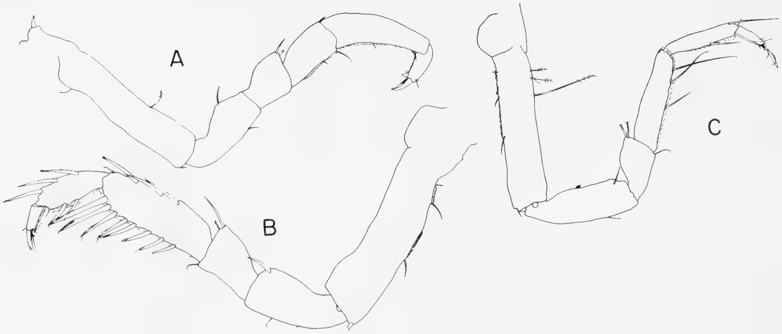

FIG. 7. *Regabellator profugus,* new species, WHOI 201, brooding ♀. A. right pereopod I; B. left pereopod II; C. left pereopod VI.

tasoma has long robust setae on the carpus and propodus of pereopod I; *Regabellator* lacks these. *Thaumastasoma* lacks fusion of pereonites 6 and 7. *Regabellator* does not display sexual dimorphism in the shape of the pleon; neither are the carpi of the posterior pereopods broadened (Figs. 7C, 11E). These features contrast with the condition in *Thaumastasoma.* The species of *Regabellator* and undescribed material in our collection do not have a spine on the ♀ operculum.

Regabellator is readily distinguished from the other nannoniscid genera which have an antenna I with a bulbous distal article and fusion of pereonites 6 and 7 by the presence of multiple ventral medial spines. Sexual dimorphism, aside from the differences in the pleopods, is most apparent in the much more robust antenna II of the ♂; the antenna I of the ♂ and ♀ are identical, the typical situation in the Nannoniscidae.

Regabellator contains the following species: *R. profugus,* new species, and *R. armatus* (Hansen, 1916).

Distribution.—Regabellator profugus, new species: southeast Atlantic Ocean, 1964–3797 m; *R. armatus:* North Atlantic Ocean, 2379–4435 m. The stations at which the genus (including undescribed material) has been taken are as follows: *R. armatus* (Hansen, 1916): Ingolf Station 38, 1870 fm [=3403 m] (Hansen, 1916); WHOI 85, 3834 m; WHOI 149, 3861 m; WHOI 328, 4426–4435 m; ALLEN 50, 2379 m; *R. profugus,* new species: WHOI 195, 3797 m; WHOI 200, 2644–2754 m; WHOI 201, 1964–2031 m; *Regabellator* species: WHOI 70, 4680 m; WHOI 256, 4563 m.

Regabellator profugus, new species
Figures 6, 7

Holotype.—WHOI 201, preparatory ♀, 3.1 mm long, USNM 184188.

Paratype.—WHOI 201, ♂, 2.5 mm long, USNM 184189.

Other material.—WHOI 195, 1 specimen; WHOI 200, 1 specimen.

Distribution.—Southeastern Atlantic Ocean, 1964–2754 m.

Etymology.—Latin, wandering, fleeing.

Diagnosis.—Body elongate; length 3.4 (♀), 3.8 (♂) times width of pereonite 2. Pereonite 4 length 0.5 (♀), 0.6 (♂) times width; width 0.77 (♀), 0.73 (♂) times width of pereonite 2. Pereonite 5 rectangular; length to width ratio (l/w) 0.4; width 0.63 (♀), 0.7 (♂) times width of pereonite 2. Pereonites 6 and 7 and pleon broaden slightly. Pleon width 0.64 (♀), 0.72 (♂) times width of pereonite 2; length 1.1 times width. Uropods 0.35 times length of pleon (latter measured in dorsal view). Endopod long; (l/w) 4.4 (♀), 4.6 (♂). Exopod short; (l/w) 4.4 (♀), 2.5 (♂). Endopod length 5.0 (♀), 3.9

(♂) times length of exopod. Pereopod II carpus with 3 long setae dorsally; 8 ventrally, increasing in length distally. Antenna I segment 2 with protuberances on distal edge, one of which is much more developed than others. Male pleopod I (l/w) 3.15; broadest proximally, squared distally. Lateral lobes developed as protuberances.

Remarks.—Characters which vary among *Regabellator* species are the length of the uropodal endopod, the relative proportions of the endopod and the exopod, and the large differences in the number of setae on the carpus of pereopod II. Note that the ♂ body width is much more uniform (i.e., relatively wider posteriorly) than the ♀ (Fig. 6A, 6G).

Nannoniscus Sars, 1870

Type-species.—*Nannoniscus oblongus* Sars, 1870 (figured 1899).

Diagnosis.—(Cf. Hansen, 1916.) Pereonites 6 and 7 fused medially. Body length generally less than 4 times tergal width of pereonite 2. Antenna I 5-segmented, with bulbous distal article. Pereopods I and II about equally robust. Mandible with 3-segmented palp. Uropods generally biramous.

Additional descriptive notes.—Species may have a ventral medial spine stemming from the venters of pereonites 6 or 7, or from the ♀ operculum. Antenna II generally long and slender, more robust in ♂♂. Body is generally depressed and generally less than 4 times the tergal width of pereonite 2; however, exceptions occur.

Remarks.—The genus consists of relatively unspecialized morphologies typical of the Nannoniscidae (i.e., have a 5-segmented antenna I with a bulbous distal article, and fusion medially of pereonites 6 and 7). More specialized forms are typified by the new genera *Exiliniscus, Panetela, Rapaniscus,* and *Regabellator. Exiliniscus* and *Panetela* both lack fusion of pereonites 6 and 7, which is generally a diagnostic feature of the family. However, both of the genera have 5-segmented antennae I with a bulbous distal article. *Rapaniscus* has a highly modified pereopod I; *Regabellator* has several ventral medial spines. Both of these genera also have the typical combination of nannoniscid features (i.e., a 5-segmented antenna I with a bulbous distal article and fusion medially of pereonites 6 and 7).

There still remain within the genus *Nannoniscus* several morphologies which may, at a later date, require elevation to generic rank (e.g., *Nannoniscus muscarius* and *N. ovatus*; *N. detrimentus*). Because of a possible intergradation of these forms with the more typical *Nannoniscus* form, we leave this question open.

Nannoniscus intermedius, new species, which is discussed below, possesses features which suggest that it should be assigned to the genus *Nannonisconus* Schultz. *Nannoniscus intermedius* is strikingly similar to general features of *Nannonisconus latipleonus* Schultz, but differs from Schultz's diagnosis of the genus *Nannonisconus* in that it lacks fusion of pereonite 7 with the pleon. Other than *Nannonisconus latipleonus,* no species with fusion of pereonite 7 with the pleon has been reported. Future investigations may reveal that the diagnostic characteristic of *Nannonisconus* is not the fusion of pereonite 7 with the pleon, but rather the characteristic proportions and shape of the pleon. However, we have refrained from redefining the genus *Nannonisconus.*

Table 3 lists the species of *Nannoniscus.* The following species have been transferred from *Nannoniscus* to other genera in this study: *N. armatus* Hansen, 1916 to *Regabellator,* new genus; *N. crassipes* Hansen, 1916 to *Rapaniscus,* new genus; *N. hanseni* Just, 1970 to *Exiliniscus,* new genus; and *N. tenellus* Birstein, 1963 to *Panetela,* new genus. For reassignments of other species of *Nannoniscus* see Siebenaller and Hessler (1977).

Nannoniscus intermedius, new species
Figure 8

Holotype.—WHOI 297, preparatory ♀, 2.7 mm long, USNM 184190.
Other material.—WHOI 297, 6 individuals.

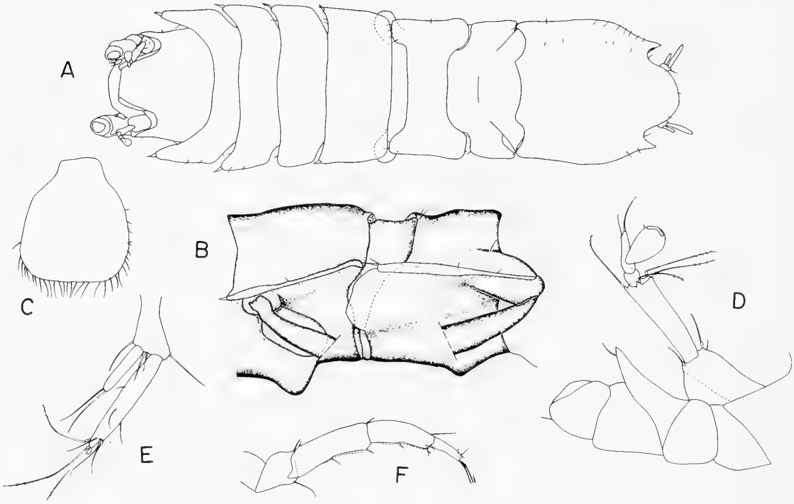

FIG. 8. *Nannoniscus intermedius,* new species, WHOI 297, preparatory ♀ (holotype). A. dorsal view; B. enlargement of the flap-like fold of pereonite 5; C. operculum (pleopod II); D. lateral view of left antenna I; E. right uropod, *in situ*; F. right pereopod I.

Distribution.—Equatorial west Atlantic Ocean, 508–523 m.

Etymology.—Latin, intermediate.

Diagnosis.—Body length 3.5 times tergal width of pereonite 2. Pleon broad, 0.9 times width of pereonite 2. Pleon with posterolateral spines. Cephalon narrow, 0.7 times tergal width of pereonite 2. Pereonite 1 lateral margins projecting strongly forward. Pereonite 5 anterolateral margins with ventrally projecting flaps. Uropodal endopod slender, length to width ratio (l/w) 6.4. Exopod slender and elongate; (l/w) 5.0. Endopod 2.2 times length of exopod. Female operculum (pleopod II) pear-shaped.

Remarks.—This species is very similar to *Nannonisconus latipleonus* Schultz, 1966 in the shape and width of the pleon (cf. Fig. 15). However, *Nannonisconus latipleonus* has pereonite 7 fused to the pleon. *Nannoniscus intermedius* can be readily distinguished from the other species of the genus *Nannoniscus* on the basis of the anterior margins of pereonite 5 and the protrusions anteriorly of the lateral margins of pereonite 1.

Nannoniscus teres, new species
Figure 9

Holotype.—WHOI 328, preparatory ♀, 4.2 mm long, USNM 184191.

Paratype.—WHOI 328, copulatory ♂, 4 mm long, USNM 184192.

Other material.—WHOI 328, 2 individuals.

Distribution.—Northeast Atlantic Ocean, 4426–4435 m.

Etymology.—Latin, refined, elegant.

Diagnosis.—Body length 3.1 (♀), 3.0 (♂) times tergal width of pereonite 2. Cephalon broad, 0.86 (♀), 0.77 (♂) times width of pereonite 2. Pereonite 1 with lateral margins projecting anteriorly. Pleon tapering to a point, triangular in shape; ♂ with stout spine projecting from apex. Female operculum (pleopod II) pear-shaped with medial spine stemming from proximal surface. Male pleopods I with well-developed

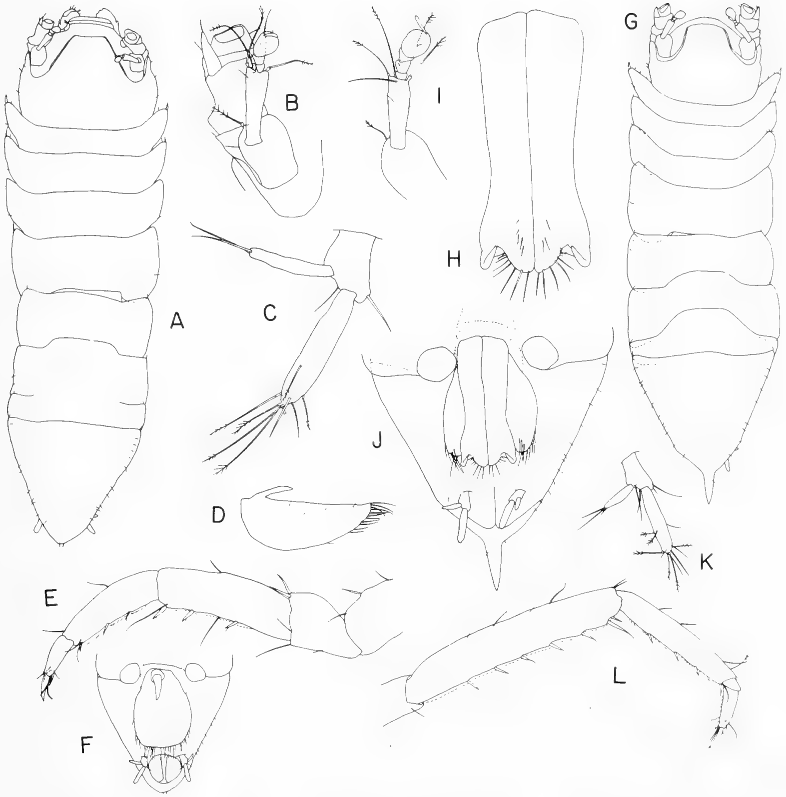

FIG. 9. *Nannoniscus teres,* new species, WHOI 328. A. preparatory ♀ (holotype), dorsal view; B, preparatory ♀ (holotype) left antenna I and base of antenna II; C. preparatory ♀ (holotype) right uropod; D. preparatory ♀ (holotype), lateral view of operculum (pleopod II); E. preparatory ♀ (holotype) left pereopod I; F. preparatory ♀ (holotype) operculum (pleopod II), ventral view; G. copulatory ♂ (paratype), dorsal view; H. copulatory ♂ (paratype) pleopods I; I. copulatory ♂ (paratype) left antenna I; J. copulatory ♂ (paratype) pleon, ventral view; K. copulatory ♂ (paratype) right uropod; L. copulatory ♂ (paratype) right pereopod II.

distolateral and distomedial lobes. Uropods small. Endopod 1.5 (♀), 2 (♂) times length of exopod. Endopod length to width ratio (l/w) 4.6 (♀), 4.8 (♂). Exopod (l/w) 5.5 (♀), 3.8 (♂).

Remarks.—Although this species is not unique in possessing a triangular-shaped pleon (cf. *N. acanthurus* Birstein, 1963), it is singular in that the ♂ has a spine stemming from the apex. The two species are very similar overall, but differ inter alia in the shape of the uropods and the distal margins of the ♂ pleopods I.

Austroniscus Vanhöffen, 1914
Figure 10

Synonymy.—*Nannoniscella* Hansen, 1916 (Birstein, 1962).

Diagnosis.—Body flattened; pereon and pleon expanded laterally into flat marginal flanges; on anterior pereonites, expansions extending anteriorly. Pleon without pos-

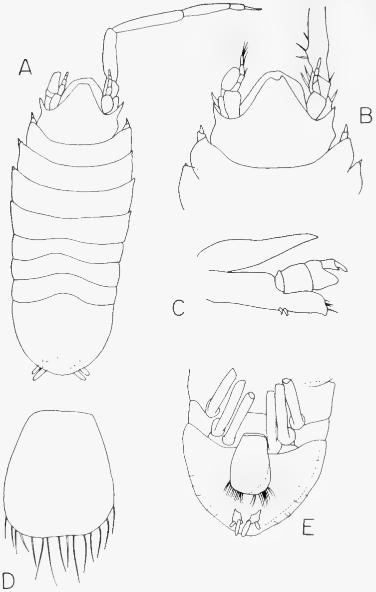

FIG. 10. *Austroniscus vinogradovi* (Gurjanova, 1950). A. dorsal view; B. cephalon; C. maxilliped; D. ♀ operculum (*redrawn from* Gurjanova, 1950). *Austroniscus* No. 6 (undescribed species, WHOI Station 195), preparatory ♀. E. pleon, ventral view.

terolateral spines; no ventral spines on body or operculum. Branchial chamber relatively small. Antenna I 6-segmented, with unspecialized distal articles. Pereopod I with conspicuous, anteriorly projecting epimere; where known, pereopod I of similar size to pereopod II and III. Pereopods V–VII not especially expanded for swimming, with only a few scattered swimming setae.

Additional descriptive notes.—A rostrum may or may not be well developed; where present, it may be slender or broad. On one undescribed species from WHOI 247, antenna I on mature ♂ has 9 articles with numerous aesthetascs, as opposed to the single aesthetasc of the other species. On another undescribed species from WHOI 155, WHOI 195, and WHOI 245, pereonite 7 is not developed laterally. This is the only known case where pereonites 6 and 7 are fused in the midline region. On many species, lateral expansion of pereonites 5–7 is so great that the base of the pereopods is only halfway from the midline; this trend is emphasized going from 5 to 7. On mature ♂♂, pleopod I exhibits a range of morphologies. For *A. rotundatus* and *A. ovalis* Vanhöffen, 1914, its medial lobe is rounded and extends only a short distance beyond the small, hook-like lateral lobes. On *A. karamani* Birstein, 1962, the medial lobe is long and pointed, and the lateral lobes are large but not hooked. An undescribed species from WHOI 195 is intermediate, having long but rounded medial lobes.

Type-species.—Austroniscus ovalis Vanhöffen, 1914 designated by Birstein (1962:34).

Remarks.—Vanhöffen's diagnosis contained a single character, the unspecialized flagellum of antenna I. The addition of other species has demonstrated the presence of other features, the most notable of which is the flat marginal expansions of the pereon and pleon. Menzies and Pettit (1956) correctly removed *A. ectiformis* Vanhöf-

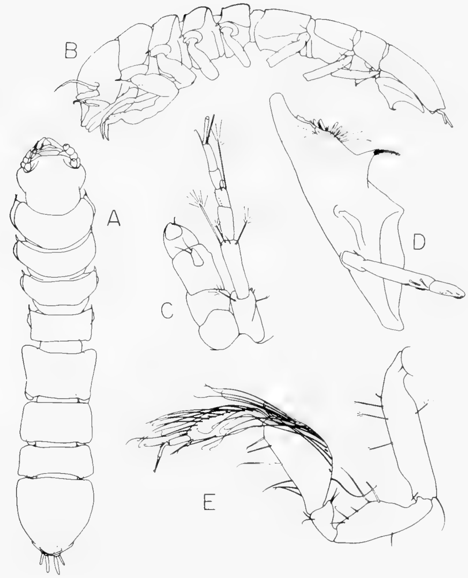

FIG. 11. *Thaumastosoma platycarpus* Hessler, 1970. A. preparatory ♀, dorsal view; B. preparatory ♀, lateral view; C. brooding ♀ antenna I and base of antenna II; D. brooding ♀ left mandible; E. brooding ♀ pereopod V (*from* Hessler, 1970).

fen, 1914 and placed it in *Caecianiropsis*. Birstein (1970) gives a key to the six currently described species. Our collection contains several undescribed species.

Distribution.—*Austroniscus ovalis:* Antarctic Indian Ocean, 70–385 m. *A. rotundatus:* Antarctic Indian Ocean, 70–385 m. *A. groenlandicus:* W. Greenland, 10–132 m. *A. karamani:* E. of Japan, 5000–5450 m. *A. acutus:* E. of Japan, 5005–6135 m. *A. vinogradovi:* Kamchatka Sea (Avachin Bay), 125 m. Undescribed material: northern, equatorial, and southwestern Atlantic Ocean, 1000–5600 m; east equatorial Pacific Ocean, 4800–5100 m.

Thaūmastosoma Hessler, 1970
Figure 11

Synonymy.—*Desmosoma* (part) Birstein, 1963.

Diagnosis.—Body slender, not depressed. Cephalon without rostrum. Pereonites 5–7 and pleon with small lateral flanges; pereonites 6 and 7 not fused; pereonite 7 venter and ♀ pleopod II with medial, posteriorly directed spine; pleon with posterolateral spines on mature ♂; presence of small spines variable on ♀. Antenna I 6-segmented, with unspecialized distal articles. Mouthparts produced conspicuously, accompanied by many modifications of specific appendages (*see* Additional descriptive notes, below). Mandible with well-developed palp. Pereopod I stouter than pereopod II.

Additional descriptive notes.—Mandible elongate; incisor process bent forward; lacinia mobilis membranous. Maxilliped with unusually elongate coupling hooks; palp segments 2–4 produced forward medially such that on article 3 the medial setae are distributed in an arc on the ventral surface of the article, rather than from the disto-

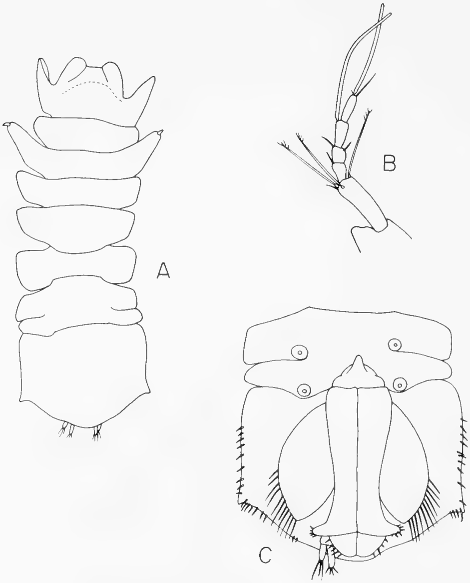

FIG. 12. *Nannoniscoides angulatus* Hansen, 1916. A. ♂, dorsal view; B. ♂ antenna I; C. ♂, ventral view of pleon and pereonites 6 and 7 (*from* Just, 1970).

medial margin; joint between articles 2 and 3 angles distomedially. Basal endite of maxilliped II less than half the length of the other lobes.

Type-species.—*Thaumastosoma platycarpus* Hessler, 1970.

Remarks.—This genus was first regarded as being part of the Desmosomatidae (Hessler, 1970; Birstein, 1963). At that time, the distinction between that family and the closely related Nannoniscidae was still unresolved. When their differences were finally clarified, it became obvious that *Thaumastosoma* must be a nannoniscid (Siebenaller and Hessler, 1977).

Distribution.—*Thaumastosoma platycarpus:* northwestern Atlantic Ocean, 2886 m. *T. tenue:* northwestern Atlantic Ocean, 2886–3753 m. *T. distinctum:* northwestern Pacific Ocean, 5680–5690 m. Undescribed material: northern, equatorial, and southwestern Atlantic Ocean, 1000–5600 m; eastern equatorial Pacific Ocean, 4800–5100 m.

Nannoniscoides Hansen, 1916
Figures 12, 13

Diagnosis.—Antenna I unspecialized, 6 (or rarely 7) segmented. Pleon with posterolateral spines. Operculum (♀ pleopod II) elongate, with concavity and calcareous fringe at midline of distal edge. Pereopod I of medium robustness; ventral surface of carpus and propodus with thin setae except for distal robust seta on carpus. Cephalon with pointed lateral lappets. Pereonites 6 and 7 free or fused. Pereonite 2 with robust seta on anterolateral corners. Medial lobes of ♂ pleopods I taper distally. Body depressed; length roughly 3 times tergal width of pereonite 2.

Type-species.—*Nannoniscoides angulatus* Hansen, 1916.

Remarks.—Mature or nearly mature ♂♂ may have a more massively developed cephalon than ♀♀ (cf. ♂ and ♀ of *N. latediffusus* [Siebenaller and Hessler, 1977]), and more strongly produced lateral lobes of pereonite 2. There is also some indication

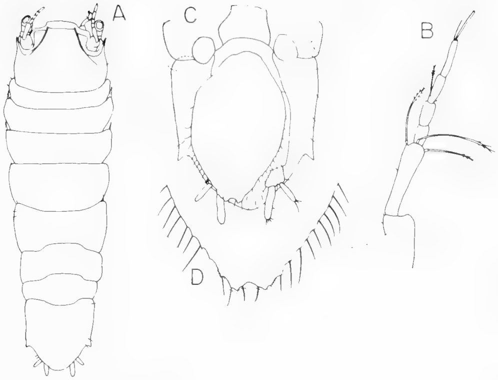

FIG. 13. *Nannoniscoides biscutatus* Siebenaller and Hessler, 1977. A. brooding ♀, dorsal view; B. brooding ♀ right antenna I; C. brooding ♀ operculum (pleopod II); D. posterior margin of operculum (*from* Siebenaller and Hessler, 1977).

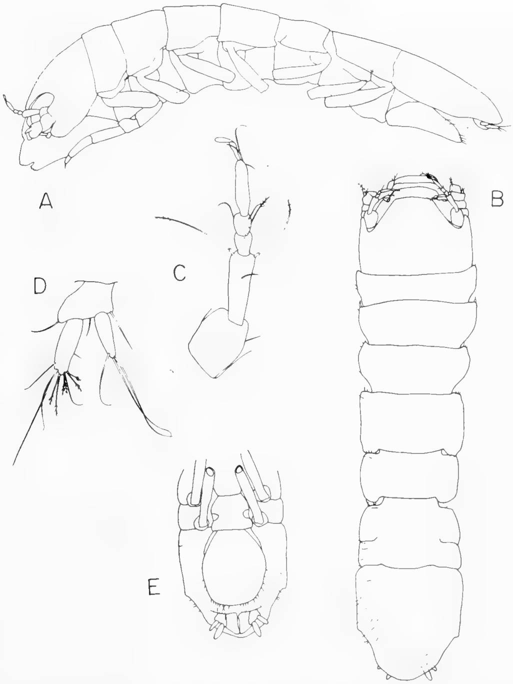

FIG. 14. *Hebefustis vafer* Siebenaller and Hessler, 1977, preparatory ♀. A. lateral view; B. dorsal view; C. right antenna I, dorsal view; D. uropods; E. pleon, ventral view (*from* Siebenaller and Hessler, 1977).

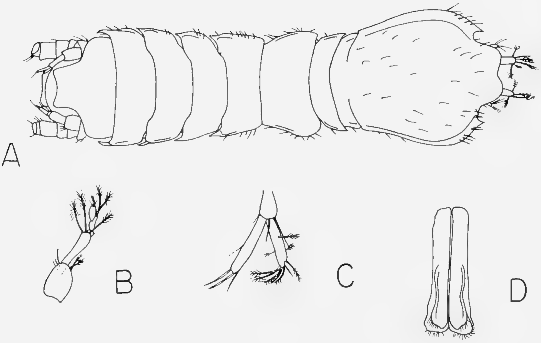

FIG. 15. *Nannonisconus latipleonus* Schultz, 1966. A. ♂, dorsal view; B. ♂ right antenna I; C. ♂ uropods; D. ♂ pleopods I (*from* Schultz, 1966).

of sexual dimorphism of the first antenna, unique in the Nannoniscidae. There may be differences in the number of aesthetascs and relative lengths of segments 5 and 6 (cf. *N. biscutatus* [Siebenaller and Hessler, 1977]).

Distribution.—Nannoniscoides angulatus: North Atlantic Ocean, north of the Faroes, 1284 m (Hansen, 1916); northernmost part of the Kara Sea, 698 m (Gurbunov, 1946); Jørgen Brønlund Fjord, Greenland, 160–180 m (Just, 1970). *Nannoniscoides excavatifrons:* northwest Pacific Ocean, in the Kurile-Kamchatka area, 1440–1540 m (Birstein, 1970). *Nannoniscoides latediffusus:* northwest Atlantic Ocean, equatorial southwest Atlantic Ocean, 587–4833 m (Siebenaller and Hessler, 1977). *Nannoniscoides biscutatus:* equatorial southwest Atlantic Ocean, 3459–3783 m (Siebenaller and Hessler, 1977). *Nannoniscoides coronarius:* equatorial southwest Atlantic Ocean, 1493 m (Siebenaller and Hessler, 1977). *Nannoniscoides gigas:* South Atlantic Ocean, Argentine Basin, 3909–3917 m (Siebenaller and Hessler, 1977). Undescribed material: South Atlantic Ocean, Argentine Basin, 2707 m.

Hebefustis Siebenaller and Hessler, 1977
Figure 14

Synonymy.—Nannoniscus (part), *Nannoniscoides* (part) (Siebenaller and Hessler, 1977).

Diagnosis.—First antenna 5-segmented, distal segment elongate and somewhat inflated; segment 4 lacks a lateral projection. Pleon with posterolateral spines. Operculum (♀ pleopod II) ovoid to pear-shaped; distal margin straight, without calcareous fringing margin. Pereopod I of medium robustness; ventral surface of carpus and propodus with robust setae. Cephalon with rounded lappets. Male pleopods I widest proximally; sides convex proximally, concave to straight distally. Pereonites 6 and 7 fused medially. Body depressed; length about 3.8 tergal width of pereonite 2.

Type-species.—Hebefustis vafer Siebenaller and Hessler, 1977.

Remarks.—Siebenaller and Hessler (1977) list the species and distinguishing specific characteristics of this genus.

Distribution.—Hebefustis alleni: Bay of Biscay and northeast Atlantic Ocean, 1623–1796 m (Siebenaller and Hessler, 1977). *Hebefustis cornutus:* northwest Atlantic Ocean, 3753–3806 m (Siebenaller and Hessler, 1977). *Hebefustis hexadentium:* Argentine Basin, South Atlantic Ocean, 5208–5223 m (Siebenaller and Hessler, 1977). *Hebefustis dispar:* southeast Atlantic Ocean, 1427–1643 m (Siebenaller and Hessler, 1977). *Hebefustis hirsutus:* South Atlantic Ocean, 5024 m (Menzies, 1962). *Hebefustis mol-*

licellus: equatorial South Atlantic Ocean, 943–1007 m (Siebenaller and Hessler, 1977). *Hebefustis par:* northeast, equatorial, and South Atlantic Ocean, 3459–4435 m (Siebenaller and Hessler, 1977). *Hebefustis primitivus:* Caribbean Sea, North Atlantic Ocean, 2868–2875 m (Menzies, 1962). *Hebefustis robustus:* northwest Pacific Ocean, 5461–5690 m (Birstein, 1963). *Hebefustis vafer:* equatorial southwest Atlantic Ocean, 587 m.

Nannonisconus Schultz, 1966
Figure 15

Diagnosis.—Pereonite 7 fused medially with pleon. Pleon at widest point wider than cephalon or pereon. Lateral outline of body concave. First antenna 5-segmented, with bulbous distal article.

Type-species.—*Nannonisconus latipleonus* Schultz, 1966.

Remarks.—Only 1 species of this genus has been reported in the literature. (However, *see Nannoniscus intermedius,* new species.)

Distribution.—Southern California Continental Borderland (Redondo Canyon), 465 m.

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The Higher Taxonomy and Evolution of Decapoda (Crustacea)

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Abstract. The decapods are herein divided into four suborders: Dendrobranchiata, Euzygida, Eukyphida, and Reptantia. Evidence for monophyly of these taxa is supplied by the adult morphology of characters of gill arrangement, modes of pleopodal incubation, patterns of overlap of abdominal pleura, pleural lock and hinge arrangements, chelation of legs, presence of appendix interna, and form of spermatozoa; the fossil record; and ontogeny. Some possible lines of investigation are outlined which might yield a more natural classification within the Eukyphida and Reptantia.

INTRODUCTION

The difficulty in devising a satisfactory general classification for the Decapoda arises from doubts concerning the higher relationships of the numerous well defined and more or less isolated groups relatively low in the taxonomic hierarchy. For example, Peneidea, Stenopodidea, and Caridea are regarded by Holthuis (1955) as members of a supersection Natantia of the suborder Macrura, which he distinguished from two other suborders Anomura and Brachyura. This classification was derived from Bouvier (1917) and Milne-Edwards (1837). The same three "natant" groups (Peneidea, Stenopodidea, and Eucyphidea) are regarded by Balss (1957) as forming the suborder Natantia, while the remaining decapods are grouped together as Reptantia (more or less after Borradaile, 1907; Ortmann, 1892*a*, 1892*b*, 1892*c*; and Boas, 1880). Glaessner (1960), a paleontologist, divides the same three "natant" groups between two different suborders. The Penaeidea and Stenopodidea together with reptant Nephropsidea form a suborder Trichelida, while the Caridea together with the reptant Thalassinidea and Paguridea form an infraorder Anomocarida of the suborder Heterochelida (the other infraorders being Palinura, Anomura, Brachyura, and the Glypheocarida). This is a modification of an earlier scheme proposed by Beurlen and Glaessner (1930). Gurney (1942) also restricted Natantia, placing the Euphausiacea among the Decapoda and the Stenopodidea among the Reptantia. Burkenroad (1963*a*) divided the natant groups still differently. Peneids and sergestids were placed in the suborder Dendrobranchiata while the Caridea and Stenopodida were placed with the other decapod groups in the suborder Pleocyemata, an arrangement essentially followed by Glaessner (1969).

The view of this paper is that the Decapoda are monophyletic and distinct from the Euphausiacea, but that most previous subordinal arrangements of the decapods are polyphyletic. It is suggested that the three traditional "natant" groups are not at all closely related to each other and must be regarded as three independent suborders comparable to the fourth homogeneous suborder, Reptantia. It is further suggested that the Reptantia are naturally divisible into several major groups, with the brachyuran forms distinct from all the rest. Within the non-brachyuran Reptantia, thalassinideans seem to be quite distinct from the anomuran, astacuran, and palinuran reptants and are treated in this paper as an independent supersection equal in status to the other three macruran and anomuran supersections.

The presence of chelate legs in the early Triassic reptant *Clytiopsis* seems to imply that differentiation within the Reptantia by the development of chelae was already then advanced. Evidence from the structure and development of the living decapods suggests a "hump-backed" common ancestor of stenopodids and eukyphids. Eukyphids must have separated from an achelate stem having pleopodal incubation before the development of the definitive branchial characteristics of the Reptantia, in time before the subdivision of the Reptantia was established in early Triassic. Consequently, it seems that at least three main lines of decapods must have been distinct in the Permian. The many striking differences between the living stenopodids and eukyphids suggests that the divergence of these two lines from their common ancestor also may have occurred in the Paleozoic, soon after separation of their stem from the line which then gave rise to the reptants.

The formal classification here proposed is as follows:

- Order Decapoda Latreille, 1803
  - Suborder Dendrobranchiata Bate, 1888
    - Superfamily Peneoidea Rafinesque, 1815
    - Superfamily Sergestoidea Dana, 1852
  - Suborder Euzygida nov.
    - Family Stenopodidae Huxley, 1879
  - Suborder Eukyphida Boas, 1880
    - Several superfamilies with about 20 living families
  - Suborder Reptantia Boas, 1880
    - Supersection Thalassinida Boas, 1880
    - Supersection Astacina H. Milne-Edwards, 1839
    - Supersection Palinura Borradaile, 1907
    - Supersection Anomala de Haan, 1841
    - Supersection Brachyura Boas, 1880

SYSTEMATICS

Order Decapoda Latreille, 1803

Diagnosis.—Antennular peduncle with statocyst; maxilla with a large exite which draws respiratory water through the gill chambers; the first three thoracic appendages reduced and modified as mouth parts and the last five specialized as raptorial and walking legs; the exopodites when present taper throughout without an enlarged stalk; gills in three series, of which the distalmost (podobranch) forms part of a coxal exite and is lacking from the fifth thoracic leg (which often bears a pleurobranch); genital apertures coxal. (Exceptions to the above are secondary: statocyst, exopodites, gills and some legs may be lost; and genital aperture may migrate to sternum.)

Suborder Dendrobranchiata Bate, 1888

Diagnosis.—Eggs freely broadcast (or briefly hung from pereiopods as in *Lucifer*); hatched as nauplii (or protozoeas); pleurobranchs appear later during ontogeny than do the pairs of arthrobranchs, and are lost before the latter, when, during phylogeny, the branchial formula becomes impoverished; gill stems bear a double series of primary rami equipped with secondary filaments or plates; first three pairs of legs chelate, none much enlarged (except the first pair in adult males of *Heteropeneus*); pleopods without appendix interna (unless such is represented by hooks on endopod of male first pleopod, or by the unarmed blade on the male second pleopod of Aristeidae); first pair of pleopods in males with endopod much modified as a copulatory organ (reduced or absent in females); pleura of first pleonic somites overlap those of the second; pleonic somites locked to each other by mid-lateral hinges, which are usually exposed at the two anterior and the two posterior somite articulations but always hidden under the posterior margin of the third somite at the middle articulation (in Recent forms).

Etymology and remarks.—The name of the suborder refers to the compound branching of gills, unique among decapods. It is derived from Bate's "Macrura Dendrobranchiata'' (1888), although present use applies only to Bate's ''Dendrobranchiata Normalia'' (his ''Aberantia'' comprised the mysids and euphausiids).

It has been traditional to use descriptive names rather than generic derivatives for the higher categories of Decapoda (e.g., Macrura and Brachyura of Latreille; Macrura, Anomura, and Brachyura of H. Milne-Edwards; Brachygnatha, Oxystomata, Anomala, and Carides [although Astacina from *Astacus*] of de Haan; Natantia and Reptantia of Boas; Trichobranchiata and Phyllobranchiata of Huxley; Trichelida and Heterochelida of Beurlen and Glaessner). In the case of Dendrobranchiata, desirability of a neutral name at the subordinal level is increased by the likelihood that a new section will have to be created for some of the fossils, Dana's section name Peneidea being best reserved for the living forms.

The superfamily names are simple promotions of two of Dana's three families of Peneidea (excluding *Stenopus* from his Peneidae and transferring *Lucifer* from his Mysidae to his Sergestidae). The spelling Peneoidea is here used in the view that since *Penaeus* has been placed on the Official List of Generic Names in Zoology by illegal means (so that the orthographic question remains an open one) *Peneus* is preferable for both etymological and practical reasons (Burkenroad, 1963*b*).

Suborder Euzygida nov.

Diagnosis.—Eggs hung from pleopodal setae; hatched as zoeas (or later); pleurobranchs appear before arthrobranchs during individual development, present on five somites when one of the two arthrobranchs per somite is missing in those few adults with an impoverished branchial formula; gill stems bear numerous simple filaments, not arranged in regular rows; three anterior pairs of legs chelate, the third being enlarged; pleopods entirely without appendix interna, first pair uniramous in both sexes; pleura of anterior pleonic somites usually not expanded, but when they are, enlarged enough so the first overlap the second; only the three posterior pleonic somites are hinged together by definite locking points.

Etymology and remarks.—This subordinal name comes from *eu*-, truly, and *zygios,* yoked (from *Zygia,* Juno as the goddess of marriage), which refers to the well-known tendency of members of the group to live in couples even when not imprisoned in sponges (Limbaugh et al., 1961). It also refers to the presumptive Paleozoic conjunction of the group with the yoke-shaped (kyphonid) Eukyphida, from which time it retains a tendency to the bent posture (discussed below). The reasons for a descriptive name rather than using Stenopodida for the suborder are similar to those given above for Dendrobranchiata. It may be added that according to Holthuis (1947, 1955), *Stenopus* might fall prey to Rafinesque's prior use of the name *Byzenus.*

Suborder Eukyphida Boas, 1880

Diagnosis.—Eggs hung from pleopodal setae; hatched as zoeas (or later); pleurobranchs appear earlier than arthrobranchs during individual development; no more than one arthrobranch ever present on a somite and all may be absent even when pleurobranchs are still retained on all the legs; gill stems bear double series of platelike rami without secondary branches; one or both of the two anterior pairs of legs chelate (except in *Procaris*), of which one or both of either pair may be enlarged; pleopods usually with appendix interna, the first pair with an endopod (usually reduced; typically not elaborately modified in males); pleura of the second pleonic somite overlap those of the first; the two anterior and two posterior pleonic somites are hinged together, but the middle articulation lacks a hinge; the pleon is often carried bent between the third and fourth somites (the first maxillipede usually with a setose expansion on the outer side of the base of the exopod, not found in the other suborders).

Etymology and remarks.—This name comes from Ortmann's modification (1890) of Boas's (1880) name Eukyphotes, employed by Balss (1927) in Kükenthal and Krumbach's Handbuch and (1957) in Bronn's Tierreich. Boas derives the name from *kuphos,* crooked (which seems to be cognate with *kuphon*, a yoke). This usage is preceded in classical antiquity by Aristotle's, ". . . ton men karidon ai te kuphai . . ." in the *Historia Animalium* (*see* Thompson, 1910).

Boas made a new name for this group of his suborder Natantia because he felt that to follow Dana in restricting Latreille's "Carides" would result in confusion as to what was meant (because of persistent use of Latreille's name in its original polyphyletic sense). An analogous reason for now sustaining Boas's name is that "Caridea" in Dana's sense has of recent years been used chiefly by those who do not recognize the fundamental nature of Boas's revision and who continue to group long-tailed decapods together whether they are reptants or not. A desirable difference in nomenclature, corresponding to the difference in systems of classification, thus results from the present rejection of "Caridea" as a name for the suborder.

The broad use of *karis* (which was general, except for Dana, from Aristotle until 1907 when Borradaile revived "Carides" in Dana's restricted definition) is appropriately preserved in Calman's Eucarida, and in the term "caridoid facies of the Malacostraca" (which does not mean "eukyphid facies" [H. Milne-Edwards, 1837]).

The hump and flexure of the third and fourth pleonic somites, so characteristic of many eukyphids, seems to be the relic of an ancient conjunction of this suborder with the euzygids; and the latter name has accordingly been coined in reference to the former (the roots of both names having apparently originated in the terminology of the cattle yoke).

The Eukyphida contains some twenty more or less distinct living families, the relationships of which are in the main still so debatable that no generally accepted groupings between the subordinal and family levels have yet been proposed. Compare Holthuis (1955) with Balss (1957, who gives a good summary of the distribution of characteristics within the group) and note the remark by the former, p. 10: "I fully realize that the arrangement of the families given here is by no means a natural one . . . ."

The mentioned arrangement by Holthuis, including two new superfamilies and several more or less novel regroupings, is only sparsely characterized, discussed, or documented. It does not distinguish between arbitrary groupings by Holthuis, for which there seems nothing favorable to be said, and valid groupings developed by prior authors, e.g., p. 12, ". . . OPLOPHOROIDA . . . Three families are left in this superfamily"; but no reasons are given for retention of Nematocarcinidae when other families traditionally grouped with Hoplophoridae are removed. Of another sort is Holthuis' statement on p. 82, "In my opinion the Processidae are so closely related to the Hippolytidae . . . that they cannot be placed in a different superfamily. Both Borradaile and Balss assigned the Processidae to the superfamily Crangonoida, but this is certainly incorrect"; which is a conclusion evidently taken from Lebour (1936), who is not cited. Again, p. 117, ". . . Pandaloida . . . consists of the three families Pandalidae, Thalassocaridae, and Physetocaridae," but reasons for making *Thalassocaris* a family are not given, and the somewhat intricate reasons (Burkenroad, 1942) for regarding *Physetocaris* as a pandaloid are not cited. Holthuis states on p. 36, "The Bresiliidae generally were believed to belong to the Pasiphaeoida, the Eugonatonotidae and the Disciadidae were placed in the Oplophoroida, while the Rhynchocinetidae formed part of the Palaemonoida . . . . The Rhynchocinetidae and the Eugonatonotidae certainly are closely related . . . . The Disciadidae in several respects are intermediate between the Bresiliidae and the other two subfamilies . . . "; but compare this to Gurney (1939, 1941), Burkenroad (1939), or Lebour (1941), none of which are cited.

In effect, Holthuis seems to have employed only those selected results of others which are compatible with a simplified, artificial arrangement based almost entirely on the structure of the chelate legs (structures actually often intergradient, and apparently highly subject to convergence). His system thus seems unlikely to stand the test of monophyly.

Suborder Reptantia Boas, 1880

Diagnosis.—Eggs hung from pleopodal setae; hatched as zoeas (or later); arthrobranchs and pleurobranchs generally appear simultaneously in development, but pleurobranchs never occur anterior to the second leg (pleurobranchs seem to appear later than arthrobranchs in ontogeny of thalassinids that have any pleurobranchs, while arthrobranchs appear later than pleurobranchs or are absent on second to fourth legs of Brachyura); gill branches range from multiple filaments (trichobranchs like those in Euzygida) through quadruple or double rows of filaments or flattened, narrow plates, to fully developed phyllobranchs (like those in Eukyphida), but are never secondarily branched as in Dendrobranchiata; number of chelate legs ranges from none to all five pairs (and second and third maxillipedes are also occasionally chelate); first pair of legs enlarged; pleopods with, but more commonly without, appendix interna, first pair uniramous in both sexes and usually reduced, modified, or absent; pleura of second pleonic somite overlap those of first when pleura are sufficiently well developed; all five articulations between pleonic somites locked by mid-lateral hinge points when the pleon is large and strong, but pleon often reduced (the first somite always so) and the pleura often small even when pleon is well developed.

There are characteristics which distinguish most Reptantia from the other decapods and are appended here to the standard list above because the wide range among reptants in structure of gill rami, number of chelate legs, form of pleopods, etc., permits only a single completely diagnostic distinction from the other two incubatory suborders (lack of a pleurobranch on the first legs). Body never laterally compressed, too heavy for really effective pleopodal swimming; rostrum never laterally compressed as a serrate blade; antennule usually without a stylocerite; antennal exopodite never expanded disto-medially into a foliaceous blade (at least in living forms); basis and ischium of first legs usually immovably joined (as frequently in the other legs also); legs usually stout, with a breaking plane in the basis; propodus usually movable in only one plane; exopods usually entirely absent from the pereiopods (and never more than rudimentary in the adult); podobranchs often present on the third maxillipedes and the anterior four pairs of legs.

Beurlen and Glaessner's "infraorder" Glypheocarida does not appear to be comparable with the above five supersections, since distinctions between their Glypheidea and Thalassinidea seem rather obscure, while their Pemphicidea seem to be primitive Palinura (cf. Balss, 1957).

The names and authors here given for higher groups beyond the governance of the Rules are intended as the earliest corresponding to the present definitions. The name Anomala was coined by Latreille but unlike de Haan he excluded the lithodids. Astacini of Latreille was a melange, restricted in Milne-Edwards's "Famille des Astaciens." Eryonids and loricates were first united by Borradaile although Boas recognized their close relationship. Brachyura seems not to have been used in exactly the present sense from Latreille on until Boas; similarly, the "Famille des Thalassiens" of Milne-Edwards and the Thalassinidea of Dana included the pagurid *Glaucothoë*. The name Anomura, introduced by Milne-Edwards for those decapods which establish "le passage entre les Brachyures et les Macroures . . . ," has always included the thalassinids or dromiids etc., and it is not equivalent to de Haan's and Boas's Anomala either in composition or in connotation. It seems best dropped, along with the comparable grade-name Macrura Latreille.

DISCUSSION

In this section is given in some detail the reasoning behind the above proposed subdivision of the Decapoda, as based on a consideration of a broad range of decapod biological features.

Evidence from Morphology

Various features which heretofore have been regarded as characteristic of the Reptantia are either not so universal among them or not so limited to them as had been thought. First, a stylocerite is quite as well developed in the Stenopodidae as in the Anomala. Second, a two-hinged articulation of propodus and carpus which is usual in the pereiopods of Reptantia is lacking in the chelipeds of at least some Eryonidea (the chelae in that group being mobile in many directions, as is usual in dendrobranchiates and eukyphidans). Third, the basis and ischium are not fused in any pereiopods in at least some of the axiid Thalassinidea, whereas they are fused in alpheid eukyphidans as an exception to the natant rule. Fourth, the coxal position of the male genital apertures usual in Reptantia (sternal in the higher Brachyura) is matched by stenopodids as well as by the eukyphidan *Pandalus* (Boas, 1880). Fifth, the first pleonic somite is as much reduced in some stenopodids as in some Reptantia. Sixth, the pleopods of some thalassinid Reptantia are almost as well developed and used as much for swimming as are those of stenopodids.

Branchial pattern.—Reptantia do possess at least one characteristic unique among decapods which seems to demonstrate the homogeneity of the group and to emphasize its distinctness from the Euzygida, Eukyphida, and Dendrobranchiata. This character is that, in the Reptantia, pleurobranchs never occur on the first pereional somite, even when one occurs on all of the following pereional somites; whereas, in the other three groups, when a pleurobranch is present on the somite of the second leg it is preceded by a homologous gill on the first leg. It is difficult to avoid the conclusion that loss of the first pereional pleurobranch was a basic difference between the ancestral reptant and the ancestral decapod. Table 1 expands on this and compares the various decapod groups. It supplies strong evidence of a monophyletic origin of the Reptantia later in date than the separation of the eukyphid-euzygid line as discussed below.

The extreme formulae given in Table 1 are synthetic and do not necessarily represent any one species. If any gill is known to be present in any member of a given group, it has been entered in the "rich" or maximal formula; similarly, if any gill is known to be absent in any species which retains any gills, it has been omitted in the "impoverished" formula. For example, a dorsal arthrobranch of the second maxillipede is present in laomediid thalassinids, which lack pleurobranchs; whereas, in the axiid thalassinids, some of which have pleurobranchs, the dorsal arthrobranch of the second maxillipede is absent. In the maximal formula given here for thalassinids both the dorsal arthrobranch of the second maxillipede and the pleurobranchs are shown. Intermediate formulae are selected actual ones. However, it should be noted that relatively few branchial formulae have been determined; therefore, all statements concerning them should be understood as qualified by the phrase "as far as known."

The specific branchial formulae from which the present table has been prepared are given in compilations by Calman (1909), Gurney (1942) and Balss (1957), in part corrected or confirmed by my own published and unpublished observations. The principles employed in identifying those gills which are present on somites where the full complement is lacking are as follows: the *podobranchs* spring from (or at the base of) a stem, the epipodite, which has a coxal insertion, and which is often present without bearing branchial filaments; the *arthrobranchs,* primitively in pairs from narrowly separated insertions, spring from the body wall above the coxa and sometimes originate in larval development by the splitting of an unpaired rudiment (Burkenroad, 1945), with the posterior one of the pair usually quite appreciably dorsal to the ventral one and near the posterior margin of the somite; the *pleurobranchs* are never paired, and insert on the body wall above the arthrobranchs, near the anterior margin of the somite. When there are only two body gills on a somite, the homology of the dorsal-most has to be judged chiefly by its position anterior or posterior to the ventral one. Although the lack of three body gills on any somite of Eukyphida prevents complete certainty that the dorsal one is a pleurobranch, it seems likely from the euzygid pattern that the rule of position is applicable also to eukyphids.

Table 1. Maximal, intermediate and impoverished branchial formulae among the living decapod Crustacea. (r) rudimentary, (0) absence, (e) epipodite, (p) podobranch, (a) arthrobranch, (pl) pleurobranch.

	Thoracic somite	1		2			3			4			5			6			7			8	Total of branchial exites	
		Maxillipede								Pereiopod														
	Limb	1		2			3			1			2			3			4			5		
	Branchial class	e + p	a?	e + p	a	pl	e + p	a	pl	e + p	a	pl	e + p	a	pl	e + p	a	pl	e + p	a	pl	pl	e	p, a, pl
	Dendrobranchiata	1 + 0	r	1 + 1	1	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 0	2	1	1	7	24
		1 + 0	0	1 + 1	1	1	0 + 0	2	1	1 + 0	2	1	1 + 0	2	1	0 + 0	2	1	0 + 0	1 + r	0	0	4	17
		1 + 0	0	1 + 0	0	0	0 + 0	1	0	0 + 0	1	0	0 + 0	1	0	0 + 0	0	0	0 + 0	0	0	0	2	3
	Euzygida	1 + 0	1	1 + 1	1	0	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1	7	19
		1 + 0	r	1 + r	r	0	1 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0	3	13
		1 + 0	0	1 + r	0	0	1 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	r	1	0	3	11
	Eukyphida	1 + 0	0	1 + 1	0	0	1 + 0	1	1	1 + 0	1	1	1 + 0	1	1	1 + 0	1	1	1 + 0	1	1	1	7	12
		1 + 0	0	1 + 0	0	0	1 + r	0	r	0 + 0	r	1	0 + 0	r	1	0 + 0	r	1	0 + 0	r	1	1	3	11
		0	0	0 + 0	0	0	0 + 0	0	0	0 + 0	0	1	0 + 0	0	1	0 + 0	0	1	0 + 0	0	1	r	0	5
Reptantia	Homarida	1 + r	r	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	23
		1 + 0	0	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	r	1 + 1	2	r	1 + 1	2	r	0	7	20
		r + 0	0	1 + 0	r	0	1 + 1	1	0	1 + 1	1 + r	0	1 + 1	1 + r	0	1 + 1	1 + r	0	1 + 1	1 + r	0	0	7	15
	Palinura	1 + 0	0	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	21
		1 + 0	0	1 + 0	0	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	19
		1 + 0	0	0 + 0	0	0	r + 0	1	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	6	17
	Thalassinida	1 + 0	1	1 + 1	2	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	r	7	23
		1 + 0	0	1 + r	r	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	0	0 + 0	2	0	0 + 0	2	0	0	5	15
		0 + 0	0	1 + 0	0	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0	1	10
	Anomala	1 + 0	0	r + 0	0	0	1 + 0	2	0	1 + 0	2	0	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1	7	14
		1 + 0	0	0 + 0	0	0	1 + 0	2	0	1 + 0	2	0	1 + 0	2	1	1 + 0	2	1	0 + 0	2	1	1	5	13
		1 + 0	0	0 + 0	0	0	0 + 0	1	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	1	1	10
	Brachyura	1 + 0	0	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	21
		1 + 0	0	1 + 1	0	0	1 + 0	2	0	0 + 0	2	0	0 + 0	0	1	0 + 0	0	1	0 + 0	0	1	0	3	8
		1 + 0	0	0 + 0	0	0	r + 0	1	0	0 + 0	2	0	0 + 0	0	0	0 + 0	0	0	0 + 0	0	0	0	2	3
	Hypothetical Stem-decapod	1 + 1	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	27

When there is only one body gill (as always on the first maxillipede and fifth leg) its homology is uncertain. Since the gill of the fifth leg appears after the arthrobranchs of preceding somites in Dendrobranchiata (like the pleurobranchs in this group), and before the arthrobranchs in the Euzygida and Eukyphida (like the pleurobranchs in these groups), I have called it a pleurobranch throughout the Decapoda. There is no reason to think that the body gill of the first maxillipede is not homologous in all decapods, but to call it an arthrobranch is a convention. It should be noted that this gill is a lamella fringed with filaments in Dendrobranchiata (the filaments tend to be separated into two groups in Solenocerinae, but this probably does not mean that they represent two distinct gills as thought by Kubo [1949] whose observations on branchiae seem erratic). In contrast, in the euzygidan *Stenopus* cf. *S. scutellatus* the gill of the first maxillipede is an ordinary one of large size (as well developed as that of the second maxillipede); and the gill of the first maxillipede is also normal in form, though minute, in the laomediid reptant *Axianassa* sp.

There are two body gills on the second maxillipede in many Dendrobranchiata and in reptant laomediid Thalassinida, but none elsewhere in the order. Holthuis (1947) has mistaken the gill of the first maxillipede of Euzygida for a second one on the second maxillipede, except in *Spongicoloides profundus* for which he evidently copied the correct formula from Hansen. There may be a real difference between Dendrobranchiata and Reptantia in homology of the dorsal of these two gills. The dorsal gill in Dendrobranchiata is clearly anterior to the ventral one, which inserts on the posterior margin of the somite. In *Axianassa* sp., the dorsal gill is directly above the ventral one, which is in the middle of the somewhat roomier lower part of the narrow somite. The dorsal gill appears to be the one missing in Euzygida, according to the low and medial emplacement of the one which is present.

The dorsal of the two body gills of the third maxillipede of Eukyphida has been termed an arthrobranch by some observers, a pleurobranch by others. Its position seems to be anterior to the ventral gill in all, so it is here considered a pleurobranch since in Burkenroad (1939) "somite VIII" is a *lapsus calami* for somite IX.

Gills absent in the adult seem never to be present in the larvae, although it is important to note that gills relatively weak in the earlier larva sometimes outgrow their previously larger neighbors (Burkenroad, 1945). In general, gills absent in adults with impoverished formulae are relatively delayed in the larval development of related forms with rich adult formulae (Burkenroad, 1934, 1939, and 1945).

It is most important to note the following. Inasmuch as any body gill on a somite can presumably serve the function of another, the differences among decapods in patterns of loss of gills from the primitive, maximal formula seem likely to be controlled chiefly by genetic accident in ancestral forms and not to be much subject to adaptive convergence. There are several significant features to be derived from Table 1. First, there is the tendency of dendrobranchiates to lose pleurobranchs in contrast to the preferential loss of arthrobranchs in euzygids and eukyphids. Second, there is the persistence of a podobranch on the first maxillipede and the fourth leg in some Reptantia (Calman, 1909, p. 278). Third, there is the total lack of pleurobranchs anterior to the second leg in any reptant (although pleurobranchs are present on the second and following legs in some members of all reptant supersections). Fourth, there is a total lack of podobranchs in all Anomala. Fifth, there is the total loss of arthrobranchs posterior to the first legs in all but the most primitive Brachyura despite the retention of pleurobranchs on posterior somites in most of the higher Brachyura. Any natural evolutionary system of decapod classification must give serious consideration to these features.

One conclusion that can be reached is that the gills of living Dendrobranchiata and Reptantia cannot be derived one from the other but only from a common ancestor with a richer formula than in any living form. That is, no dendrobranchiate has a podobranch on the first maxillipede or the fourth leg, and no reptant has a pleurobranch on the maxillipedes or the first pereiopods. Similarly, the branchial pattern in Brachyura cannot be derived from one like that in any living Anomala, since a podobranch is present on at least one of the pairs of maxillipedes of some member of every brachyuran group. Therefore, it seems doubtful whether the podobranch-bearing ancestor of the Brachyura could be defined as an anomalan.

Pleopodal incubation.—The basic reason against accepting Boas's "Natantia" as a natural group is that it would require that pleopodal incubation of the eggs arose independently in at least two different decapod lines. The condition in the Dendrobranchiata, where the eggs are broadcast (or by exception briefly incubated under the thorax), must be regarded as a primitive characteristic correlated with eclosion in the naupliar (or by exception, the protozoeal) state, and almost certainly retained from the ancestral decapod. Therefore, if the dendrobranchiates, euzygids, and eukyphids had a common "natant" ancestor distinct from that of Reptantia, the euzygids and eukyphids must have invented pleopodal incubation and abbreviated development independently of the reptants—which is possible but seems improbable.

As shown by Burkenroad (1947), incubation in decapods is made possible by the temporary self-fusibility of the outermost of the three membranes secreted by the ovum. Essentially, the eggs can become attached to any structure around which their outer shells can meet to fuse. Although an enzymatic intensifier from pleopodal glands seems usually involved in the process, incubation appears to be more an invention in behavior—retention of the eggs in contact around suitable projections until the outer membranes have fused and hardened, together with an inhibition of subsequent cleaning behavior—than in structure.

Attachment of the eggs of the sergestoid dendrobranchiate *Lucifer* to spinules on the coxa of the third leg shows that the independent development of incubatory behavior can occur. It would, however, be surprising if the euzygids, eukyphids, and reptants had each independently developed not only behavior leading to egg attachment, but also egg attachment exclusively to special pleopodal setae. It is therefore probable that euzygids, eukyphids, and reptants had a common ancestor which diverged from the dendrobranchiates by developing pleopodal incubation. Pleopodal incubation made abbreviation of development possible by reducing larval mortality, thus permitting fewer and larger eggs. Abbreviated development facilitates change in the form and order of appearance of various structures since the embryonic structures no longer have to be functional as they were with naupliar eclosion, which characterized the decapod stem form and the Dendrobranchiata. Therefore, the development of pleopodal incubation may have been the crucial step that freed decapod evolution from the limitations of the caridoid facies.

Overlap direction of abdominal pleura.—Euzygida resemble Dendrobranchiata in having the first pleonic pleura overlapping the second. Eukyphida resemble Reptantia in that, when any overlap is detectable, the second pleuron overlaps the first (compare *Crangon* with the undoubtedly convergent *Naushonia*). It seems likely that the decapod stem form had unexpanded pleura with no decided overlap, as in many living Reptantia. However, the fact that the pleural overlap in reptants (when detectable) seems always to be of the second pleuron over the first suggests that the pleura of living Reptantia may have been reduced from an ancestral state of greater expansion and decided overlap. It is my view that the direction of overlap must have been variable in the common ancestor of the euzygids and eukyphids. The resemblance in pleural overlap of euzygids to dendrobranchiates and of eukyphids to reptants is, then, the result of independent development. If the directions of overlap were not independently derived, this would imply independent development of the peculiar euzygid-eukyphid branchial pattern and a multiple origin of pleopodal incubation (among other features), which seems unlikely.

Pleural lock and hinge arrangements.—In addition to the direction of overlap of the pleura, their contacts supply another distinctive set of patterns among the decapods. Euzygids are unique in having the anterior three pleonic segments more or less loosely and flexibly bound together, with a locking point present only between the fourth and fifth, and fifth and sixth somites. Reptants with well-developed pleura have, in contrast, all of the segments locked together by mid-lateral hinge points.

These reptant hinge points are exposed and strong in eryonids, scyllarids, and some homarids. They are present in *Cambarus,* but hidden under the pleura except between the fifth and sixth somites. They are present but hidden except between the first and second somites in *Upogebia.* They are exposed on all segments in *Munidopsis* but weak between the fifth and sixth somites. In raninids they grow stronger from front to rear.

Eukyphids have a still different pattern. In those I have examined there is no well-defined hinge point between the third and fourth somites. These somites are quite flexibly coupled although bound rather firmly in, e.g., *Spirontocaris.* The other pleonic somites are locked to each other, with all four pairs of hinges usually externally visible. The one between the second and third somites is sometimes weak and hidden under the pleura (e.g., in *Spirontocaris*).

Finally, the dendrobranchiates resemble the eukyphids in having well-developed hinges at the anterior two and posterior two pleonic joints. These hinges are externally visible except the anterior two in *Sicyonia* which are hidden under the pleura. No hinge is externally visible between the third and fourth somites. The dendrobranchiates differ from the eukyphids in having the third and fourth somites quite inflexibly coupled by a rather ill-defined hinge point hidden under the pleura.

It seems possible that the decapod stem form may have had all pleonic somites obviously hinged and that a tendency towards loss of pleonic hinges was a special characteristic of the hypothetical euzygid-eukyphid line. At any rate, it seems significant that the euzygids, although resembling the dendrobranchiates in direction of pleonic overlap, are far different in pleonic hinge pattern.

Pleonic hinge patterns can be observed in fossils. In *Aeger,* an available specimen of *A. tipularius* from Solenhofen shows the dendrobranchiate pattern including the covered locking-point in the joint between the third and fourth somites. It is also noted that the figures of *Acanthochirus* and *Dusa* by Balss (1922) suggest an exposed hinge in this position such as now occurs only in Reptantia.

Branchial development.—A fundamental feature in which the euzygids resemble the eukyphids, and the reptants resemble the dendrobranchiates, has been described by Burkenroad (1939). In the course of euzygid and eukyphid ontogeny pleurobranchs appear before arthrobranchs. When the gill formula of their thoracic somites three to seven (second maxillipede to fourth leg) is impoverished in an adult, it is one or both of the pair of arthrobranchs which is missing rather than the pleurobranchs, e.g., some species of the euzygids (*Spongicoloides* [Holthuis, 1947]) and in all Eukyphida. In contrast, in peneids and axiid reptants the pleurobranchs appear later in development than the arthrobranchs (Gurney, 1942). In adult peneids and reptants, pleurobranchs may be absent on thoracic segments three to seven even though paired arthrobranchs are present on all of them. The higher Brachyura, with greatly impoverished branchial formulae, differ from other reptants in that pleurobranchs may occur on the somites of the second and third legs although arthrobranchs are completely lacking there. It seems possible that the euzygids and the eukyphids had a remote common ancestor distinguished from the stem leading to the reptants by the precocious appearance of larval pleurobranchs.

Chelate legs and appendix interna.—The euzygids share with the dendrobranchiate and the astacuran reptants the characteristic of having chelae on the three anterior pairs of thoracic limbs, and with the dendrobranchiates the lack of the appendix interna. These similarities are probably not phylogenetically significant since the similarity to reptants in these same features has almost certainly not been the result of retention from a common ancestor. Likewise, certain thalassinids resemble eukyphids in possessing two pairs of chelate legs and sometimes the appendix interna, and this also seems unlikely to signify any special relationship.

The appendix interna is assuredly a primitive character, independently lost in a variety of groups (note its retention on the second male pleopod of aristeid peneoids and the astacine genus *Enoplometopus* [Barnard, 1950]).

The unknown ancestor of the decapods may have had no chelae at all, as in males of the living scyllarid Palinura. However, unless the decapod stem form had the posterior maxillipede and all five pairs of legs chelate, so that the differing patterns in various groups all represent reduction of the ancestral number, there must have been some independent development of chelae among decapods.

Spermatozoan construction.—Similarity of spermatozoa among "Natantia" has been cited as evidence of the unity of such a group by Balss (1957, p. 1515; "Die Natantia z. B. stimmen in Bau der Spermien überein . . . ."). This supposed uniformity does not in fact exist. There is as great a variation in gross form and structure among Dendrobranchiata as among Reptantia—from superficially simple ellipsoids in the sergestid *Lucifer faxoni* (comparable with the reptant *Callianassa seilacheri*) to subdivided cells with a seta-like, obliquely directed appendage in the peneoid *Trachypeneus birdi* (apparently comparable in complexity with the structure in such reptants as *Pagurus longicarpus*). In some dendrobranchiates (e.g., *Parapeneus longirostris, Hymenopeneus robustus*) the spermatozoa do show a resemblance in general form to those of some eukyphids, a more or less flattened head and a tapering central spike like a tack. However, there is no reason to think that these cells are any more like each other cytologically than they are like reptant spermatozoa. The tack-like form is not universal in eukyphids (there are exceptions such as *Xiphocaris elongata* and *Atya scabra*). Finally, the euzygids have still another type of spermatozoan according to my examination of unstained material from the jelly-column in the vas deferens of a formalin-fixed, alcohol-preserved male of *Stenopus* cf. *S. scutellus* (apparently the first spermatozoan from this group to be described). This cell is superficially like the diagram of a "*Squilla*" spermatozoan given by Nichols (1909). It is a slightly flattened spheroid, apparently lacking appendages, with a small refractile body in the middle of one side of the disc.

Before the various types of decapod spermatozoa can be interpreted in terms of relationship at the subordinal level, it will be necessary to have electron microscope studies of a variety of them, like those of Moses (1961*a*, 1961*b*) on *Procambarus clarki*. It would also be helpful to understand the functional significance of the differences in structure (*see* Burkenroad [1947] on the mechanism of fertilization in decapods). Despite the difficulty of interpretation of gross structure, the decapod spermatozoa might be of considerable use in distinguishing taxa. Burkenroad (1934, 1936) made routine descriptions intended as notes toward possible future use in setting generic limits.

Evidence from the Fossil Record

Not having examined much fossil material, I am not in a position to discuss with authority the compatibility of the fossil record with the foregoing hypotheses, but will venture a few remarks. Triassic dendrobranchiates include a form quite indistinguishable from the living *Peneus—Antrimpos,* known back to the lower Triassic (Burkenroad, 1936; Balss, 1922, 1957). There is also an extinct type perhaps representing the common ancestor of Peneoidea and Sergestoidea—*Aeger* (Burkenroad, 1936, 1945; Balss, 1957), which has a petasma which would ensure that it is not a euzygid.

Reptantia of the groups Astacina and Palinura Eryonidae, already with chelae like those of living members of these groups, were also present in the Triassic (Glaessner, 1969). Also known from the Triassic are the Glypheidae, without chelae and somewhat suggesting thalassinids, and the Pemphicidae, which suggest scyllarid Palinura but with rostrum, diaeresis, and rudimentary chelae on the second and third legs. The Glypheidae seem to have survived into the Recent without developing chelae. Thalassinida, Anomala, and Brachyura have not yet been found before the Jurassic. The Jurassic Anomala, however, included both pagurid and galatheid forms, implying that this supersection must have separated long before from the others. The earliest decapod, *Palaeopalaemon newberryi* from the Late Devonian, cannot be assigned with confidence to "any of the recognized infraorders" (Schram et al., 1978).

Eukyphida also have not yet been found before the Jurassic. *Adorella* is of special interest as apparently lacking chelae, all of the legs being subchelate with the dactyls folded against the body of the propodus (Balss, 1957).

Euzygidan fossils have not so far been recognized. However, the supposed dendrobranchiate *Acanthochirana* (Jurassic) evidently had the first pleonic somite rather reduced, the pleura narrow and spiny and the uropodal exopod lacking a diaeresis (Balss, 1922); thus it might be a euzygid.

Glaessner (1960) believes that Glypheidae gave rise to the Pemphicidae and to all of the extant reptant groups except the Astacina. He derives the Astacina separately with the dendrobranchiates and euzygids. However, he does not discuss the surprising similarity of the carapace of his stem astacine, *Lissocardia*, to that of the glypheids. In my judgement, a glypheid-like stem form, lightly built and without hypertrophied first legs, gave rise to all the reptant supersections. This would seem to imply that, despite its great age, *Palaeopalaemon* may be well advanced along the reptant line. It will have differentiated before the Late Devonian from a similarly achelate euzygid-eukyphid stem-form with large first pleonic somite, both of these being distinct from a dendrobranchiate stem-form already with chelae. Although the lack of fossils of higher Brachyura before the Cretaceous seems highly significant, the lack of early specimens of the lightly constructed and probably rather scarce eukyphids and euzygids need not be surprising. Fossils now being laid down in warm seas are probably also mostly heavily armored reptants, though in the modern fauna these may be fewer than the dendrobranchiates (the eukyphids and especially euzygids being sparser still).

Evidence from Ontogeny

Gurney's valuable but rather disappointing summary (1942) of knowledge of the larvae of the Eucarida does not attempt "to define the larval characters of the major groups." However, it does offer a brief estimate of certain relationships on p. 11–12, some further remarks and a table of characteristics helpful "in placing a larva" on p. 177–179, and a summary of the characteristics of caridean larvae on p. 192–193. Gurney indicates that "the primitive larval history which characterizes all Penaeidea distinguishes the group sharply from all others" among the decapods; that the larvae of Stenopodidea "are very peculiar, but suggest some relationship to the Anomura and Thalassinidea"; that the Eukyphida show a peculiar resemblance to the protozoea of dendrobranchiates in having only 6 pairs of spines on the embryonic telson; and that larval Reptantia are peculiar in having the antennal scale unsegmented, as well as in never having an exopod on the maxillule (indicated as present in all Dendrobranchiata and in a few Eukyphida and Euzygida). Gurney's chief reason for relating the Euzygida to the Reptantia is the hair-like form of the second spine of their telson, but on p. 239 he notes that "the possession of so primitive a maxillule in one species is difficult to reconcile with such a view." On p. 146–147 he seems to doubt the significance of the peculiar difference of euzygids and eukyphids from dendrobranchiates in order of development of the gills, and suggests that instead "the dorsal gills of Caridea may actually be arthrobranchs of the dorsal series." However, it must be noted that, whatever the homology of the dorsal gill of eukyphids, there is a real resemblance to euzygid development, and a real difference from dendrobranchiates (Burkenroad, 1945).

Gurney's (1942) pessimistic feeling that, "It must be confessed that the evidence from development so far accumulated has not produced any very serious contribution to the systematics of the group," seems to me simply a result of the natural reluctance of systematists to attempt to organize the mass of specialized information, difficult to check or extend, which has become available about the larvae; I should like to acknowledge here that the present revision of the Decapoda stems from an early collision with that stimulating work of Gurney, and to note again that the revision is directly dependent on the lead supplied by the peculiarities of branchial ontogenesis.

A larval pattern, the possible large scale significance of which has not been previously considered, is provided by the order of development of the pleopods. The first pleonic somite of the reptant larvae never has pleopods until long after those of posterior somites are well developed and biramous (indeed, never until after metamorphosis, if then, except in eryonids). In euzygids the first pleopod "seems generally if not always to be delayed in appearance till the end of larval life" (Gurney, 1942). In eukyphids, all five pleopods usually appear together, but according to Gurney's account (1941) of *Rhynchocinetes* the first pleopod in it seems to be somewhat delayed after those of 2–5; and the first pleopod does not appear until post-larval stages in *Leptochela* (Gurney, 1938). In dendrobranchiates, the pleopods usually appear all together, but (in contrast to the incubatory groups) when the appearance is serial it is the anterior most pleopod which first develops (*Gennadas*) or is the best developed (*Acetes*). In this tendency to precociousness of the first pleopod, the dendrobranchiates seem to make some approach to the serial development found in euphausiids; and it seems possible that in the evolution of the incubatory decapods there was a more or less progressive tendency to increased delay of the first pair of pleopods.

Another larval feature, the possible phylogenetic significance of which has not been previously noticed, is the tendency for the pleon to be "bent at the third segment at almost a right angle" in the late larvae of euzygids (Lebour, 1941). This posture resembles that of eukyphid larvae and seems correlatable with the lack of a hinge between third and fourth somites in adults of both groups, since it does not seem to be found in other decapod larvae. It seems likely to have characterized the larvae if not the adults of the common ancestor of Euzygida and Eukyphida.

The hair-like second telson spine in larvae of Euzygida, Thalassinida, Anomala, and Dromiacea (and probably some Astacina: note that Gurney's remark in 1942, p. 227, that the telson is "normal for this stage" in his possible *Nephrops* from the Great Barrier Reef is quite different from his remark in 1938, p. 296, "The telson, indeed, is exactly the same as that of *Callianassa* . . .") seems to be a character of considerable significance, as Gurney thought. Rather than a mark of special relationship between euzygids and thalassinids, or dromiids and Anomala, however, it seems more likely to be a relic from the stem-form of the three incubatory suborders, never present in dendrobranchiates, and effaced in eukyphids, most Astacina, Palinura and the higher Brachyura.

A more thorough review of decapod development from a phylogenetic outlook might be fruitful.

Taxonomic Issues

In both the Eukyphida and the Reptantia there is a large number of more or less clearly distinguished living groups, the interrelationships of which are still poorly understood. I am not fully prepared to attempt a definitive arrangement of either of these two suborders, but will offer scattered remarks based on new but incomplete observations.

A) Among Eukyphida, the male genital aperture is in the articular membranes and definitely proximal to the coxa in a number of Palaemonidae (including Pontoniinae) and Alpheidae which I have examined. It is coxal in all others so far checked (several Hippolytidae, Atyidae, Hoplophoridae, Pandalidae, and Crangonidae). This coxal position is rather different from the coxal aperture in *Stenopus* and various Reptantia, being low on the segment instead of in the distal part. I believe the articular apertures probably indicate a close relationship (as concluded by Gurney from embryological evidence). This evidence would suggest that Holthuis's (1955) superfamilies overemphasize the relative dimensions of the chelate legs.

B) Like other authors after Borradaile (1907), Balss (1957) has stated, that in the Reptantia "der Stylocerit fehlt immer . . . ." However, later in that same work Balss says of the Eryonidea Palinura, "Antennula . . . manchmal mit Stylocerit." The basal joint of the antennule of *Polycheles typhlops* bears a pair of spines which may or may not be homologous with the stylocerite of dendrobranchiates, eukyphids, and euzygids. These resemble those of the galatheoid *Munidopsis* and pagurids in form and relation to the statocyst. The galatheoid *Petrolisthes* has the statocyst expanded into a lateral projection of the base of the antennule which seems likely to be a homologue of the "natant" stylocerite. The hippid *Lepidopa* is comparable. The eryonids, then, probably do retain a stylocerite lost in the scyllarids.

The eryonids seem to differ from the scyllarids (Loricata) in a number of other features which seem of importance (as far as can be judged from my comparison of *Polycheles typhlops* with *Panulirus argus*). The eryonids have a less completely fused basis and ischium of the legs (Barnard, 1950; Balss, 1957). They lack a double hinge between carpus and propodus of the legs. They have chelae on the anterior four legs (Balss), and the base of the antenna is not fused to the carapace and epistome but is free. The fusion of carapace and epistome is concealed under the frons and visible only inside the branchial chamber as in homarids. Borradaile (1907) and subsequent authors are thus in error in distinguishing the eryonids as well as the scyllarids from the Astacina by "carapace fused at sides with epistome." The scyllarids are intermediate between eryonids and Astacina in grade of loss of appendix interna, which is present on the male second pleopod of *Enoplometopus,* which appears to be an astacine (Barnard, 1950). The living eryonids resemble the scyllarids and differ from the astacines in lacking a diaeresis on the uropodal exopod, but some fossil eryonids had a diaeresis (Balss, 1957). The loss must have occurred independently in the chelate and the achelate lines, unless the latter branched off from the eryonids and lost the chelae (which seems less likely than that the scyllarids stemmed from achelate pemphicids). In fact, it is not easy to define Borradaile's "Palinura" with precision except by their possession of a peculiar button fastening the carapace to the side of the last thoracic somite (presumably it necessitates special arrangements at the molt and therefore seems of considerable phylogenetic interest). The eryonids and scyllarids may not have had a common ancestor since the early Triassic (if the pemphicids were, as seems possible, ancestral to the scyllarid stem rather than to that of all Palinura).

C) The "Anomura" are said by Borradaile (1907) and subsequent authors to have "Carapace not fused with epistome." However, this is quite untrue of *Callianassa* and *Upogebia,* where the frons above the linea thalassinica is openly fused with an extension of the sternite behind the antenna. A similar fusion in some axiids at least seems to be indicated by Bouvier's remark (1925) that in *Calocaris aberrans* "Le bord anterieur de la carapace . . . au dessous des antennes . . . est fusionné avec l'epistome"; and this is probably also true of the laomediid *Naushonia,* according to Chace's figure (1939) of it.

The frons in other "Anomura" (the Anomala) is somewhat different, the fusion of carapace and epistome being shallowly concealed (Chace, 1939, Fig. 6a, b, c, d); and this, together with the presence of a stylocerite would seem to distinguish the Anomala as a unit from the Thalassinida. Gurney (1942) believes that the thalassinids are not homogeneous but include two groups, one (Axiidae and Callianassidae) shown by its development to be homarid in relationship and the other (Laomediidae and Upogebiidae) related to the Anomala. However, Gurney ultimately found the larval distinctions to be less absolute than he at first believed, and it is difficult to believe that the peculiar frons of *Callianassa* and *Upogebia* was independently invented (although it then seems surprising that in thalassinid larvae the frons is produced to conceal the point of fusion). It would be of great interest to know whether an exposed fusion of carapace with epistome might be combined with presence of a stylocerite in the glypheids.

D) The loss of arthrobranchs from pleurobranch-bearing thoracic somites posterior to the fourth is highly distinctive of Brachyura with a reduced gill complement. It therefore seems likely that there was a brachyuran stem form with a more or less complete branchial formula and coxal genital apertures which was distinguished from other reptant lines by delayed appearance of posterior arthrobranchs (relative to posterior pleurobranchs) during individual development. Although it is not completely certain that the dromiids qualify as true Brachyura by delayed development of the posterior arthrobranchs, this seems probable from Gurney's account (1924) of the gills

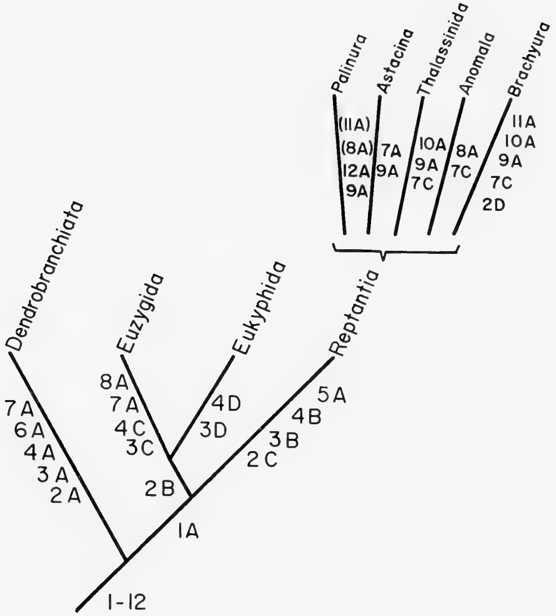

FIG. 1. Cladogram of relationships of decapod suborders postulated in this paper. Reptant groups not arranged phylogenetically. Numbers and letters keyed to text. Parentheses indicate lack of the particular advanced character in important members of that group.

of what Lebour (1934) agrees must be a *Dromia*. Gurney describes the third zoea as having the paired arthrobranchs already present on thoracic somites 3 and 4, while unpaired rudiments occur on "each of the following limbs." In the fourth zoea, there are pleurobranchs on each of the legs 2–5, and an unpaired arthrobranch has appeared on legs 2–4. In Lebour's fifth zoea, the adult complement has been completed by the addition of a second arthrobranch on legs 2 and 3. It thus seems that the gills on legs 2–5 in Gurney's third zoea were pleurobranchs, and that *Dromia* possesses the developmental pattern to be expected of the brachyuran stem form. The combination in *Dromia* of unique larval characteristics and brachyuran features with others found in thalassinids and in Anomala (which Lebour thinks make it necessary to "remove the Dromiacea from the Brachyura" to "a separate group") seems likely to result from the retention of larval characteristics from the common reptant stem in this surviving representative of the primitive Brachyura.

E) The possibility that the linea "thalassinica," "anomurica," "dromidica," and "homolica" are homologous and retained from a common ancestor rather than, as suggested by Glaessner (1960), acquired independently in different lineages, is of considerable interest (Burkenroad, 1963*a*). This is especially so since the Late Devonian *Palaeopalaemon* seems to possess a linea.

CONCLUSIONS

A diagram showing the presumptive order of appearance of the characteristics of the suborders of Decapoda, up to the differentiation of the supersections of Reptantia in the Triassic, is presented in Figure 1. Changes from a hypothetical ancestor are shown at each branching of the lines by code numbers which are explained in the chart below, primitive characteristics being retained except as indicated. (In some of the ultimate branches, characteristics different from those shown in their hypothetical stems have since appeared.)

Decapod Characteristics (see Fig. 1)

Primitive	Advanced
1. Eggs set free; eclosion naupliar.	1A. Pleopodal incubation; development abbreviated.
2. Thoracic somites 3–7 each with a podobranch-bearing epipodite, two arthrobranchs and a pleurobranch, which appear more or less simultaneously during individual development.	2A. Pleurobranchs delayed. 2B. Arthrobranchs delayed. 2C. Anterior pleurobranchs omitted. 2D. Posterior arthrobranchs delayed.
3. First pleonic somite large; first and second pleura not expanded enough to overlap; all pleonic somites hinged together by an exposed diarthrosis.	3A. First pleura expanded and overlapping the second; hinge between third and fourth pleomeres covered. 3B. First somite reduced; second pleura slightly expanded to overlap the first. 3C. First somite somewhat reduced; its pleura somewhat expanded and overlapping the second; hinge between third and fourth pleomeres lost. 3D. Second pleura expanded to overlap the first; hinge between third and fourth pleomeres lost.
4. All pleopods large, biramous and with an appendix interna which couples each pair together.	4A. Appendix interna lost except traces in male first and second pleopod. 4B. First pleopods reduced and uniramous; appendix interna on the rest. 4C. First pleopods more or less reduced: uniramous; no appendix interna. 4D. First pleopod with endopod usually reduced, appendix interna on all pleopods usually.
5. Legs with propodus movable in more than one plane; all seven joints free.	5A. Carpal-propodal joint with two hinges, restricting propodus to movement in a single plane.
6. Trichobranchiae.	6A. Dendrobranchiae.
7. Legs not chelate.	7A. First three pairs chelate. 7B. First four pairs chelate. 7C. First pair chelate.
8. Diaeresis on uropodal exopod.	8A. No diaeresis.
9. Antennular stylocerite present.	9A. No stylocerite.
10. Attachment of carapace to anterior sternite (epistome) hidden under the produced frontal margin.	10A. Fusion of carapace to epistome exposed.
11. Pleon large and extended.	11A. Pleon reduced.
12. Carapace not fastened down posteroventrally (unless by overlap of anterior margin of first pleonic pleuron).	12A. Posteroventral sides of carapace held in place by a projection of the last thoracic pleura which engages inner side of carapace.

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Biomere boundaries in the Phanerozoic time scale

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Abstract. Abrupt nonevolutionary changes in the fossil record of trilobites during the Cambrian, without associated evidence of lithologic changes or discontinuities, are known as biomere boundaries. We suggest that biomere boundaries are more widespread in the Phanerozoic time scale than previously reported. Accordingly we have expanded the original biomere concept to include nonevolutionary biotic changes, involving one or more phyla, that are the results of major environmental changes of local or worldwide extent. The effects of these changes on benthic taxa are nearly synchronous on the craton and diachronous in shelf and slope environments. The Ordovician-Silurian boundary may provide an example of this type of biomere boundary as indicated by changes in biota. The existence of a biomere boundary rather than a synchronous time boundary at the traditional Ordovician-Silurian systemic boundary, would indicate that there is a significant amount of time equivalency between the Ashgillian and Llandoverian.

INTRODUCTION

A major focus of the earth sciences since the time of William Smith has been the development and continued refinement of the geologic time scale. Numerous difficulties have been encountered, but evidence of considerable progress and standardization recently has been published (Hedberg, 1976; Cohee et al., 1978). Major chronostratigraphic units (system, series, etc.) and corresponding geochronologic units (period, epoch, etc.) of this time scale have been established on a global scope; by definition, these units have isochronous boundaries. The boundaries of chronostratigraphic units are best defined by well-documented changes in the fossil record. Ideally, these changes are recognized by lineage biozones, based on first occurrences of fossil taxa established at a stratotype section for each boundary (Committee on the Silurian-Devonian Boundary and Stratigraphy, 1972; Murphy, 1977). In practice, most boundaries and especially system boundaries are poorly defined and difficult to correlate on a global scale. We propose herein that a major obstacle to regional and global correlation of some system boundaries (e.g., Cambrian-Ordovician, Ordovician-Silurian, Permian-Triassic, Cretaceous-Paleogene, etc.) is that they are not isochronous as traditionally assumed, but rather represent intervals of time manifested by biomere boundaries and therefore are diachronous. Consequently they do not meet the requirements of synchronous time-stratigraphic boundaries. Biozones previously recognized as representing the upper part of one system (e.g., Ordovician) and those representing the lower part of the overlying system (e.g., Silurian) may be partly or completely time equivalent where they are transected by a biomere boundary. We believe the interval of time for the total duration of a biomere boundary is considerably greater than the interval of time necessary for simple faunal migrations—an interval traditionally considered insignificant by stratigraphers (*see* sections on Biomere Boundaries and Ordovician-Silurian Boundary).

The purpose of this paper is to expand the concepts of biomere and biomere boundaries as originally defined by Palmer (1965*a*) and to apply the expanded concepts to systemic boundaries. We do not intend to prove that the Ordovician-Silurian boundary is a biomere boundary; rather we point out an alternative explanation for the existing data and indicate how this interpretation would affect attempts at regional correlation. The concepts presented here are not restricted to the Ordovician-Silurian boundary but also may apply to other time-stratigraphic boundaries in the Phanerozoic.

BIOMERE BOUNDARIES

Biomeres were first defined on the basis of the stratigraphic distribution of Late Cambrian trilobites in the Great Basin (Palmer, 1965*a*, 1965*b*). They represent ". . . a regional biostratigraphic unit bounded by abrupt nonevolutionary changes in the dominant elements of a single phylum. These changes are not necessarily related to physical discontinuities in the sedimentary record and they are, or may be, diachronous." Subsequent work on the recognition of biomeres and biomere boundaries has been sparse, but they have been recognized in collections of Late Cambrian trilobites from Texas and Oklahoma (Longacre, 1970; Stitt, 1971*a*, 1971*b*). Changes in Late Cambrian conodonts and inarticulate brachiopods closely correspond with the changes in trilobites reported from the Great Basin (Rowell and Brady, 1976). More recent evidence in support of the biomere concept was provided by the changes in trilobites from a very detailed measured section in the Great Basin (Palmer, 1979).

The changes in trilobites between biomere boundaries were classified into four stages (not chronostratigraphic) by Stitt (1971*a*, 1971*b*); Palmer (1979) has recently modified Stitt's faunal stages. As most recently described by Palmer (1979), stage one of a biomere follows immediately after a major crisis eliminates most of the existing benthic trilobite taxa, and it is characterized by very low diversity and high abundance of generalist species. Stage two represents an initial evolutionary radiation of remaining stocks and contains relatively short ranging taxa. Stage three is represented by a decrease in diversity and establishment of new major taxonomic groups. In stage four, trilobites again increase in diversity to fill most or all habitats; this climax in diversity is followed by another crisis. Taylor (1977) and Palmer (*personal communication*) suggested that Cambrian biomeres were produced by the rising of the thermocline and consequent rapid extinction of warm-water, shelf trilobites; new stocks of colder, deeper-water trilobites subsequently migrated into the depauperate habitats on shelf areas and then underwent adaptive radiations. Of interest is the fact that no biomeres have yet been formally proposed in rocks younger than Cambrian (500 m.y.) in age.

A significant new stratigraphic concept is available if the original concept of biomere is expanded as follows: 1) biotic changes at biomere boundaries are due to major environmental changes of local or worldwide extent; 2) biotic changes may affect one or more phyla; 3) in cratonic seas these changes may appear to be essentially synchronous (Palmer, 1978), whereas in offshore (shelf or slope) environments the changes may be diachronous; and 4) the diachroneity of a biomere boundary may span millions of years (discussed below). This expanded concept of a biomere may provide a more accurate explanation for many erathemic or systemic boundaries previously considered synchronous, unconformable, or paraconformable.

We believe that the diachroneity of a biomere boundary may span millions of years (point 4 of above). Our belief is based on faunal patterns of the Ordovician-Silurian boundary (*see* following section on the Ordovician-Silurian boundary) and the nature of the invading stock. The invading stock originates from genetically conservative, deeper-water faunas. The genetically conservative nature of the group is suggested by 1) the morphological similarity between invading stocks of different biomeres (Palmer, 1965*a*), suggesting a common basic stock for the invading trilobites which were evolving much slower than the contemporaneous shallow-water taxa; 2) the less dense populations in modern deep-sea environments (Ingle, 1975; Wigle and Emery, 1967) because it is harder to find a mate; 3) the reduction in egg numbers, K-mode reproduction, in modern deep-sea faunas (Allen, 1979; Sanders, 1979; Rex, 1979); and 4) the extreme lengths of time between generations due to the "late" sexual maturity of modern deep-water faunas (Allen, 1979; Sanders, 1979; Rex, 1979).

For a genetically conservative invading stock to migrate from the stable, colder,

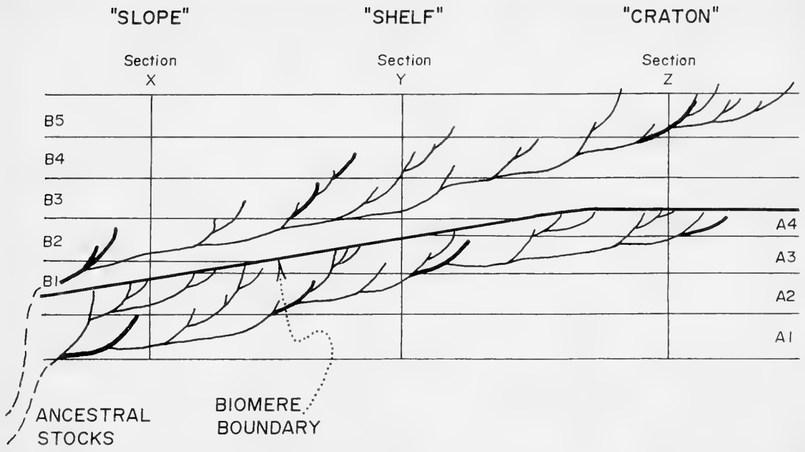

FIGURE 1. Generalized concept of a biomere boundary. A1 through A4 and B1 through B3 represent lineage biozones based on benthic or nekto-benthic organisms. Evolution of "group" A continues in onshore areas not yet affected by environmental change. Lineage B taxa migrate onshore from deeper—or open—oceanic environments and undergo diversification to fill niches vacated by extinction of lineage A taxa. Taxa used to define the base of each successive biozone are indicated by heavy lines. Use of "A" and "B" in the diagram is not related to the use of letters to designate Lower Silurian brachiopod biozones.

higher pressure, darker waters of a deeper environment to shallow, unstable, warmer, lighter, and lower pressure waters of depauperate habitats involves not only movement of the stock but also adaption (evolution) of the organism to different environmental conditions. The slow evolution of this genetically conservative group could easily take millions of years. It should be noted that the duration of the changing environment at a specific locality is short, perhaps less than 10,000 years (Palmer, 1979).

Figure 1 illustrates our concept of a biomere boundary. The boundary is diachronous and becomes progressively younger from the slope to the craton through time as extinctions of taxa followed migrating environmental changes. This diagram indicates that four significant features are associated with the biomere. First, in traditional interpretations, biozones A1 through A4 would all be considered geologically older than biozones B1 through B3, although portions of A3 and A4 are lateral biofacies (and temporally equivalent) to portions of B1, B2, and B3. Second, at any section (x, y, or z) one or more lineage biozones (based upon first occurrence) might be missing, and this might be ascribed incorrectly to the existence of a paraconformity. Third, taxonomic diversity is lowest just above the boundary, but then increases as new taxa evolve and occupy previously vacant habitats. Fourth, the time involved for the entire boundary event may encompass several biochrons and thus the boundary represents considerably more time than the acceptable diachroneity of chronostratigraphic boundaries; note that in any single location the event occurs much more rapidly. Attempts to use traditional methods of correlation for an interval characterized by a biomere event would yield spurious results since sections from geographically distant areas would contain differing biozonal sequences. This evidence might be used to suggest the existence of an unconformity or a paraconformity in areas where biozones appear to be "missing." Also, a stratotype for time intervals characterized by this type of boundary could be selected in a specific geographic location, but it could not be easily correlated with other regions.

Evidence from the fossil record for the Ordovician-Silurian boundary provides an example for the concepts presented above; studies for the last 100 years using traditional techniques and assumptions have not produced a satisfactory chronostratigraphic horizon. Three difficulties in illustrating the above concepts are: 1) paleontological studies are commonly confined to one system and do not treat changes in taxa across boundaries; 2) few studies treat shelf to slope paleoenvironments for refined time intervals; and 3) detailed stratigraphic data (such as for the Upper Cambrian strata in the southern Great Basin) often are inconclusive or unavailable.

ORDOVICIAN-SILURIAN BOUNDARY

Lapworth (1879) defined the Ordovician-Silurian boundary using graptolite successions occurring in a sequence of marine strata exposed in the British Isles. The graptolite successions used by Lapworth (1879) and by Ellis and Wood (1914–1918) are known from few sections and are poorly correlated with benthic fossils (Berry, 1976). In the last hundred years considerable efforts to correlate this boundary have resulted in the recognition of what appears to represent a worldwide unconformity in paleoenvironments of the shelf and craton (Berry and Boucot, 1970, 1972*a*, 1972*b*, 1973*a*; Ziegler et al., 1974; Talent et al., 1975). This unconformity coincides with an erosion surface in some areas, but is recognized solely by the absence of biozones in other areas, thus implying the existence of a paraconformity. Poorly understood benthic taxa associated with the boundary are of low diversity and have been assigned to the Ordovician Period or Silurian Period by various authors (review by Cocks and Price, 1975).

The Ordovician-Silurian boundary is characterized by the following features in various regions: 1) poorly distributed graptolite successions; 2) physical unconformity; 3) missing biozones (paraconformity); and 4) low diversity benthic faunas that have not been precisely correlated and appear to be diachronous. Recognition of a standardized boundary, synchronous or nearly synchronous on a global scale, has not been accomplished. We propose an alternative model that explains the apparent paraconformities and unusual temporal and spatial distribution of the benthic taxa, and that indicates the Ordovician-Silurian transition may represent a biomere boundary.

Graptolite Successions.—The Ordovician-Silurian boundary was originally defined on the basis of graptolite successions in western Europe, and similar successions have been reported from other areas (Berry and Boucot, 1970). The latest Ordovician is recognized by the occurrence of *Diplograptus anceps* and *Climatograptus prominenselongatus* (Riva, 1974; Williams, 1976). Basal Silurian graptolite biozones are *Akidograptus acuminatus* and, locally, *Glyptograptus persculptus* or other biozonal indicators. Other taxa, including conodonts, ostracodes, brachiopods, corals, trilobites, and cephalopods, have been correlated with the successions. A significant difficulty in correlation is that graptolites are rarely associated with shelly faunas, especially in Upper Ordovician and Lower Silurian rocks (Williams, 1969; Ingham and Wright, 1970; Berry, 1976). A further factor is that benthic shelly faunas were affected more strongly by bottom environmental conditions than were the graptolites, and different shelly faunas may be associated with the same graptolites. We have concluded that graptolites provide more accurate correlation for slope sequences (pelagic argillite-chert belt of Erdtmann, 1976) spanning the Ordovician-Silurian boundary. Recognition and correlation of this boundary in shallow-water carbonate or clastic sequences is difficult because graptolites were rarely preserved in these sequences.

Unconformities.—In areas containing shelly faunas, the Ordovician-Silurian boundary most commonly is considered to be unconformable (Berry and Boucot, 1970, 1972*a*, 1972*b*, 1973*a*; Ziegler et al., 1974; Talent et al., 1975). In many cratonic sections of North America the base of the Silurian reportedly rests unconformably on Upper Ordovician rocks (Berry and Boucot, 1970). This regional unconformity has been related to an Early Silurian regression associated with glaciation (Berry and Boucot, 1973*b*; Sheehan, 1973). In some areas evidence for an unconformity is based upon the reported absence of earliest Silurian (early and middle Llandoverian) fossils (Rexroad et al., 1965; Rexroad, 1967:15–16), thus suggesting the existence of a paraconformity. Shallowing and erosion of shelf areas has been reported by Lenz (1976) for the northern Cordillera. However, evidence reported by Johnson and Potter (1976), Miller (1976), Dunham (1977), and Miller and Walch (1977) indicates that deposition was continuous across the boundary interval in the southern Cordillera.

Considerable difficulty in recognition of the boundary has been noted for the Cellon section (shelf sequence) in the Carnic Alps and the Welsh borderland (Walliser, 1964, 1971; Schönlaub, 1971; Aldridge, 1972, 1975). Shallow-water sequences (based upon brachiopod communities) are characterized by the absence of early Llandoverian shelly faunas and by the existence of an unconformity separating Ordovician and Silurian rocks. However, as we have noted, shelly fauna biozones are poorly correlated with deeper water graptolite faunas and the existence and stratigraphic position of these unconformities is not well established (note especially Schönlaub, 1971:37, fig. 2 for Cellon section).

Diachronous Benthic Faunas.—An example of a diachronous benthic fauna is the "Hirnantian fauna." This fauna is typically a low diversity assemblage of brachiopods and trilobites with other minor shelly elements and is known from Europe, Asia, and North America (Wright, 1968; Nikitin, 1971, 1976; Schönlaub, 1971; Cocks and Price, 1975; Lesperance and Sheehan, 1976). This fauna was originally used by Bancroft (1933) to define a stage of post-Ashgillian age, but Ingham and Wright (1970) placed the Hirnantian Stage in the Ashgillian. Cocks and Price (1975) and Lesperance and Sheehan (1976) indicated that the Hirnantian fauna appeared to be diachronous and therefore could not be equivalent to the Hirnantian Stage.

Published information indicates that the fauna ranges in age from Ashgillian to medial Llandoverian (Nikitin, 1971, 1976; Schönlaub, 1971; Cocks and Price, 1975; Lesperance and Sheehan, 1976). Nikitin reported a Hirnantian fauna in the central USSR associated with the graptolite *Glyptograptus persculptus*, indicative of the *G. persculptus* Biozone (=Zone 16) of the earliest Llandoverian. Cocks and Price (1975) did not consider Nikitin's fauna to be Hirnantian, but the faunal list includes *Mucronaspis* (*Dalmanitina*) *macronata*, *Eostropheodonta* aff. *squamosa*, *Dalamanella testudinaria*, and *Hirnantia* species, which, at the generic level, represent common Hirnantian taxa.

Further evidence of the age relationships of the fauna is in the Carnic Alps of Austria and Italy. Schönlaub (1971: fig. 2) illustrated a Hirnantian fauna interbedded and coexisting with the conodont *Amorphognathus ordovicica*, diagnostic of Late Ordovician (Ashgillian) age. Cocks and Price (1975) discussed the Hirnantian fauna from the St. Martin's Cemetary Horizon in Wales, which occurs above strata of Rawtheyan age (Late Ordovician) and below faunas of early Llandoverian age. Lesperance and Sheehan (1976) discussed the occurrence of a Hirnantian fauna in Quebec that lies above lower or middle Ashgillian and below Llandoverian beds and is associated with the graptolite *Cliograptus rectangularismedius* of Early Silurian age. They also presented evidence (1976:721) from the type locality suggesting that the Hirnantian fauna may be of early and medial Llandoverian age. From the foregoing we conclude that the Hirnantian fauna is a diachronous "community," as suggested by Cocks and Price (1975), and should not be used to define a time-stratigraphic unit.

A second example of a diachronous benthic or nekto-benthic fauna is the distribution of conodont biozones. Detailed conodont biozones for latest Ordovician and earliest Silurian time in North America are not well established. Sweet et al. (1971) recognized Late Ordovician faunas (Faunas 10, 11, 12) and Nicoll and Rexroad (1968) and Pollock et al. (1970) recognized Early Silurian biozones (*Panderodus simplex, Icriodina irregularis, Neospathognathodus celloni* Assemblage Biozones). These have been recognized in mid-continental cratonic paleoenvironments but are poorly known from offshore (shelf or slope) paleoenvironments.

The *Panderodus simplex* Assemblage Biozone was named by Pollock et al. (1970:746) for conodonts occurring in a sequence of rocks below the lowest occurrence of *Icriodella discreta* or *Icriodella* new species or the genus *Icriocina* and above diagnostic Ordovician species. This biozone contains a low diversity assemblage of simple-cone species and, although considered earliest Silurian, also contains Ordovician species (Craig, 1969; Walliser, 1971; Barnes et al., 1973; Liebe and Rexroad, 1977:844). The *P. simplex* Biozone has not been recognized in rocks deposited in shelf or slope paleoenvironments, although Miller (1975, 1976) and Audell and Miller (1979) reported nondiagnostic simple-cone taxa above Upper Ordovician rocks and below upper Llandoverian rocks in the southern Great Basin (shelf).

From these examples we conclude that the Hirnantian fauna and the *P. simplex* Biozone are diachronous and geographically transgressive (and partially regressive) pioneer assemblages (definition of assemblage following Kauffman and Scott, 1976) that existed after other Ordovician taxa were eliminated. This pioneer assemblage is much like stage 4 (not time stratigraphic) of a biomere (Stitt, 1971*a*) or stage 1 of Palmer (1979), where the extinction of specialized forms occurred, but the generalists were not affected.

Brachiopod Distribution.—Sheehan (1973, 1975) discussed the abrupt changes in brachiopods that occurred across the Ordovician-Silurian boundary. He described Late Ordovician brachiopod faunas as containing many stenotopic species, especially those existing in shallow-water (cratonic) paleoenvironments. These species became extinct because of an "ecologic crisis" at the end of Ordovician time, although the precise dating is difficult to determine. New taxa in the Early Silurian were derived from taxa existing in the open ocean (off the continental platform) that migrated into the empty niches from offshore paleoenvironments. He also noted that the diversity of Early Silurian brachiopods was low and did not stabilize until late Llandoverian time. These abrupt faunal changes were attributed to the onset of glaciation and consequent regression that eliminated many Late Ordovician niches. However, the distribution and evolution of brachiopod taxa also provide significant support for our biomere model.

Discussion and Conclusions

The boundaries of time-stratigraphic (chronostratigraphic) units are based upon evidence from the fossil record. Implicit in their definition and recognition is the assumption that, despite homotaxis as described by Huxley in the 1800s, the boundaries are synchronous on a global scale. Since the first definition of the Ordovician-Silurian boundary by Lapworth (1879) to resolve previous conflict over the Cambrian-Silurian boundary, attempts to recognize and correlate this boundary on a worldwide scale have been difficult. This difficulty is reflected by the contradictory information that includes peculiar or unusual associations of taxa, and the ever-present "paraconformity" reported in the literature. We suggest that the paleontological evidence can be interpreted differently. The changes in biota were due to environmental changes that produced an episode of extinction with significant diachroneity but which are not necessarily related to changes in lithology. Therefore, the Ordovician-Silurian boundary may be interpreted as a biomere boundary.

In Figure 2 we show the traditional concept of the Ordovician-Silurian boundary (Fig. 2a) and two models (Figs. 2b, 2c) that illustrate the Ordovician-Silurian transition as a biomere boundary. Our interpretation of the traditional model (Fig. 2a) is based upon reported distribution of unconformities and biota. Using either of the two biomere boundary models (Figs. 2b and 2c), it is evident that in offshore areas (slope and shelf) currently recognized shelly faunas of Late Ordovician (Ashgillian) age would be absent

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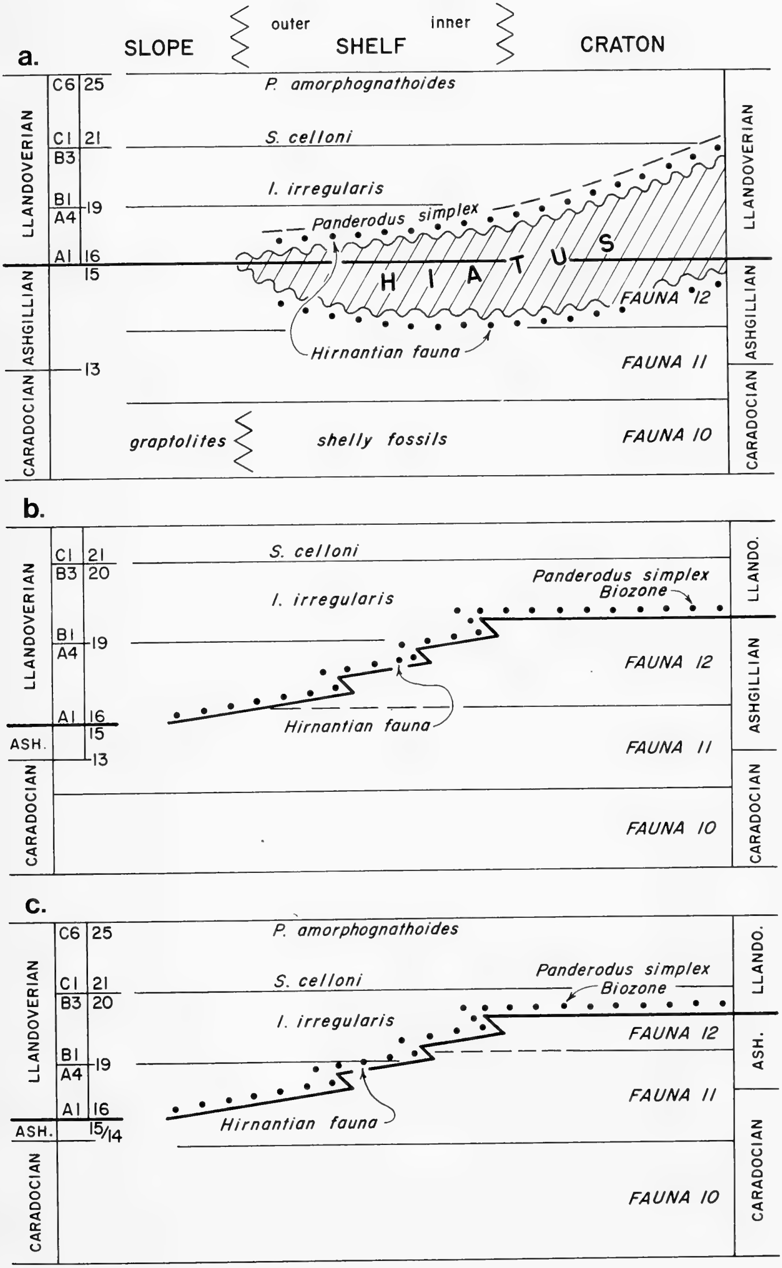
FIGURE 2. Three interpretations of the Ordovician-Silurian boundary. a) Traditional interpretation illustrating continuous deposition in deeper water (slope) and unconformity in shallow water (shelf and craton). b) Biomere boundary, illustrating diachroneity and relationships of established biozones to the boundary. c) Biomere boundary, illustrating greater diachroneity. The Hirnantian fauna (dotted line) and *Panderodus simplex* Biozone (dashed line) are low diversity time-transgressive associations and are found with Ordovician and Silurian taxa. Actual position of the biomere boundary is approximate.


a.
SLOPE
outer
SHELF
inner
CRATON
LLANDOVERIAN
ASHGILLIAN
CARADOCIAN
C6
25
C1
21
B3
B1
19
A4
A1
16
15
13
P. amorphognathoides
S. celloni
I. irregularis
Panderodus simplex
HIATUS
FAUNA 12
FAUNA 11
FAUNA 10
Hirnantian fauna
graptolites
shelly fossils
b.
LLANDOVERIAN
ASH.
CARADOCIAN
LLANDO.
ASHGILLIAN
CARADOCIAN
C1
21
B3
20
B1
19
A4
A1
16
15
13
S. celloni
I. irregularis
Panderodus simplex Biozone
Hirnantian fauna
FAUNA 12
FAUNA 11
FAUNA 10
c.
LLANDOVERIAN
ASH.
CARADOCIAN
LLANDO.
ASH.
CARADOCIAN
C6
25
C1
21
B3
20
B1
19
A4
A1
16
15/14
P. amorphognathoides
S. celloni
I. irregularis
Panderodus simplex Biozone
Hirnantian fauna
FAUNA 12
FAUNA 11
FAUNA 10

or only partially represented, but shelly faunas of Early Silurian (early and middle Llandoverian) age would be found. Onshore areas (craton) would contain faunas of Ashgillian age, but would lack currently recognized shelly faunas of early Llandoverian age. Not all of the data presented agree with the proposed models, but differences are generally minor and may be due to oversimplification in the diagrams. The influence of paleobiogeography was not taken into account; thus it may be necessary to construct other diagrams for different biotic provinces.

The existence of a biomere boundary would necessitate a redefinition of the systemic boundary. The most reasonable redefinition would establish the boundary at the base of the Ashgillian or at the base of the late Llandoverian and thereby employ well-established sequences of shelly faunas as well as graptolites. Another possibility would be to retain the traditional definition of the Ordovician-Silurian boundary based on typically "Ordovician faunas" and "Silurian faunas," and recognize that the boundary is diachronous, and therefore not a chronostratigraphic boundary. The recognition of the boundary would be based on different defining and/or characterizing taxa in different depositional settings (slope, outer and inner shelf, and craton).

Biomeres and biomere boundaries have been documented in the Cambrian and for the Cambrian-Ordovician boundary (Stitt, 1971*b*; J. F. Miller, *unpublished data*). In our study a biomere boundary is suggested for the Ordovician-Silurian boundary. Other boundaries in the Phanerozoic time scale may prove to be biomeres. Other possible biomere boundaries revealed by a brief survey of the literature include the Permian-Triassic, Triassic-Jurassic, Jurassic-Cretaceous, and Cretaceous-Paleogene.

Recognition of a major biomere boundary would require detailed measurements of strata and descriptions of taxa across the proposed boundary from a number of sections in deep-water (slope), shallow–water (shelf), and craton paleoenvironments. These sections should be taken as close as possible along a single paleolatitude; auxiliary sections should be located normal to the first line of sections and ideally should cover a significant band of latitude. Although suffering from a lack of many detailed studies, the widespread Paleozoic rocks in the western United States (Cordilleran region) represent slope, shelf, and craton paleoenvironments (Stewart et al., 1977); and these could provide the data necessary to document the existence of biomere boundaries.

Although biomeres currently have important stratigraphic implications only for Cambrian rocks, we suggest that the fossil record for younger strata supports expansion of the concept to include larger events on a global scale. These biomere boundaries represent major stratigraphic markers and have not been recognized through most of the Phanerozoic rock record, and they provide a new explanation for the lack of correlations of many traditionally defined chronostratigraphic and geochronologic boundaries.

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The origin of Darwin's finches (Fringillidae, Passeriformes)

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Abstract. Despite numerous studies of the group, the ancestry of Darwin's finches, consisting of the Cocos Finch (*Pinaroloxias inornata*) and the Galápagos finches (13 species of *Geospiza, sensu lato*), has never been adequately resolved. Striking similarities in osteology and plumage indicate that the Blue-black Grassquit, *Volatinia jacarina*, an emberizine finch of Central and South America, may be the direct ancestor of Darwin's finches. The Cocos Finch and the Galápagos finches evolved from independent colonizations of *Volatinia* from the Neotropical mainland, and thus their similarities are largely due to retention of ancestral characters present in *Volatinia*. Evidence for a supposed close relationship between Darwin's finches and *Tiaris* or *Melanospiza* of the West Indies either is unsubstantiated or involves characters that are found also in *Volatinia*. Geological data reveal very young ages for both the Galápagos (3–5 million years for the oldest islands) and Cocos Island (1 million years), thus limiting the possible age of terrestrial life on these islands. The ancestral relationship of living *Volatinia* to Darwin's finches is compatible with the relatively recent origin of the rest of the terrestrial avifauna of the Galápagos, whose nearest relatives also are in western South America and not in the West Indies. The strong resemblance between *Volatinia* and Darwin's finches is best expressed by including *Volatinia* Reichenbach 1850, in the genus *Geospiza* Gould 1837. Because of the intergradation among the various species of Galápagos finches and their similarity to the Cocos Finch and *Volatinia*, the genera *Pinaroloxias* Sharpe 1885, *Platyspiza* Ridgway 1897, *Camarhynchus* Gould 1837, *Cactospiza* Ridgway 1897, and *Certhidea* Gould 1837, are also treated as synonyms of *Geospiza*.

Resumen. A pesar de las investigaciones numerosas de group, la herencia de los pinzones Darwin, que incluyen el pinzón de Cocos (*Pinaroloxias inornata*) y los pinzones de Galápagos (13 especies de *Geospiza, sensu lato*), nunca ha sido adecuádamente resuelta. Semejanzas impresionantes en osteología y plumaje indican que el marinerito, *Volatinia jacarina*, un pinzón "emberizine" de América Central y América del Sur, tal vez es el ascendiente directo de los pinzones Darwin. El pinzón de Cocos y los pinzones de Galápagos evolucionaron de colonizaciones independientes de *Volatinia* desde el continente neotropical y, por eso, las semejanzas de ellos se deben mayormente a causa de la retención de características hereditarias presentes en *Volatinia*. La evidencia para una supuesta relación cercana entre los pinzones Darwin y *Tiaris* o *Melanospiza* de las Antillas Occidentales, uno de dos, es impalpable o envuelve caracteres que se encuentran también en *Volatinia*. Datos geológicos indican edades jóvenes, tanto para Galápagos (3–5 millones de años para las islas más antíguas), como Isla Cocos (1 millón de años), limitando, de este modo, la posible edad de vida terrestre en estas islas. La relación hereditaria de la viviente *Volatinia* con los pinzones Darwin es compatible con el origen relatívamente reciente del resto de la avifauna terrestre de los Galápagos, cuyos parientes más cercanos se encuentran en la parte occidental de Sur América y no en las Antillas Occidentales. La fuerte semejanza entre *Volatinia* y los pinzones Darwin se expresa mejor incluyendo a *Volatinia* Reichenbach 1850, en el género *Geospiza* Gould 1837. A causa de la intergraduación entre las varias especies de los pinzones de Galápagos y su semejanza con el pinzón de Cocos y *Volatinia*, los géneros *Pinaroloxias* Sharpe 1885, *Platyspiza* Ridgway 1897, *Camarhynchus* Gould 1837, *Cactospiza* Ridgway 1897, y *Certhidea* Gould 1837, también son mirados como sinónimos de *Geospiza*.

INTRODUCTION

Darwin's finches are small, drab birds that have been studied by many systematists, evolutionists, and ecologists since the collections and observations of Charles Darwin in 1835. Thirteen species of Darwin's finches live in the Galápagos Islands (Ecuador), while a single species, *Pinaroloxias inornata*, lives on Cocos Island (Costa Rica). The various forms of Darwin's finches in the Galápagos (*Geospiza, sensu lato*) exhibit a complete gradation between the morphological extremes in overall size and plumage, and their reproductive behavior and ecology are even more uniform. Their remarkable range of bill sizes and shapes provides the main basis for analysis of their evolution and systematics.

A logical first step in understanding the evolutionary radiation of Darwin's finches is to seek the identity of the ancestral species that first colonized the Galápagos or Cocos Island and subsequently gave rise to the 14 species generally recognized today, following Lack (1947). Progress in the search for this ancestor has been hampered by the fact that the four largest and most comprehensive publications on Darwin's finches (Swarth, 1931; Lack, 1945, 1947; and Bowman, 1961) have stressed the differences between Darwin's finches and mainland finches, while largely ignoring or not interpreting the similarities. This reluctance to attempt to relate Darwin's finches to mainland birds is perhaps due in part to the influence of Swarth (1929, 1931), who elevated Darwin's finches to familial rank (Geospizidae). Although Swarth (1929) could not see consistent similarities between Darwin's finches and any other family, his diagnosis of the "Family Geospizidae" contains no characters that are not also found in certain emberizine finches (Passeriformes: Fringillidae: Emberizinae). Swarth's "Geospizidae" generally has not been recognized by later authors, but is often maintained as a distinct subfamily (Geospizinae) within the Fringillidae (Emberizidae of some workers). This treatment, however, is not phylogenetically consistent with the ancestry of the group as proposed by several of the same authors (Bowman, 1961, 1963; Lack, 1947, 1961; and Harris, 1974), who leave open the possibility of an ancestor for Darwin's finches in the Parulidae (New World warblers; Mniotiltinae herein), and despair of the futility of determining the real ancestor. For example, Bowman (1961:135) remarked, "Whether or not the ancestral geospizine was a thin-billed form . . . or was more typically finchlike . . . or like any other 'type' represented in the subfamily, may never be known. The structural transition in the jaw musculature from one 'extreme' to another may be so clearly traced that conjecture about the precise nature of the ancestral geospizine is really quite meaningless . . . ." This statement contradicts others in the monograph where in several places (pp. 178–179) a relationship is suggested, at an unspecified level, between Darwin's finches and certain genera of Emberizinae, especially *Tiaris* and *Melanospiza*. Thus the problem of determining the ancestry of Darwin's finches is twofold. Firstly, one must determine their correct subfamilial position within the 9-primaried oscines (because of the similar nature of the myology [Raikow, 1978] and osteology of all 9-primaried oscines of the New World except vireos, I regard them all as constituting but a single family, the Fringillidae). Secondly, only after secure allocation to subfamily, one may search for closely related genera and species.

Mainly through detailed myological studies, Raikow (1977) showed that the Hawaiian finches (Drepanidini) evolved from a single primitive species of the Carduelinae, although he did not specifically state the ancestral genus or species itself. There is no *a priori* reason why the ancestry of Darwin's finches cannot also be determined with at least as much resolution, particularly because (1) the range of variation in bill shapes in Darwin's finches is much smaller than in the Drepanidini (*compare* pls. 9–12 of Bowman, 1961, with p. 101 of Raikow, 1977); (2) Darwin's finches consist of only 1 to 6 poorly differentiated genera, depending on the classification used, while the Hawaiian finches constitute 10 distinct genera, following Raikow (1977); (3) based purely on geographical considerations, we must look no farther than the New World for the ancestors of Darwin's finches, while the ancestor of the Drepanidini could have come from either the New World or the Old World; and (4) the Galápagos probably have not been available for colonization by land birds for as long a period as the Hawaiian Islands. The oldest islands in the Galápagos appear to be no more than 3–5 million years old (Cox, *in press*). The oldest ages for Hawaiian Islands inhabited by a diverse assemblage of drepanidines are about 5 million years for Kauai (McDougall, 1979); islands west of Kauai are even older.

My thesis is that Darwin's finches not only are clearly emberizines, but in fact are so closely related to the living mainland species *Volatinia jacarina* (Blue-black Grassquit) that *V. jacarina* singly gave rise to the entire array of Darwin's finches, both in the Galápagos and on Cocos Island. After a historical review of other proposed relationships of Darwin's finches, I will present anatomical data to support my hypothesis, followed by a discussion of nonanatomical evidence. Finally, the evolutionary scheme proposed herein will be analyzed zoogeographically in the chronological framework dictated by recent geological discoveries.

History of the Proposed Relationships of Darwin's Finches

Gould (1843) originally described the Cocos Finch, *Pinaroloxias,* as *Cactornis inornatus,* thus correctly placing it with the Galápagos finches. Since Gould's description, the close affinity of *Pinaroloxias* to at least certain of the Galápagos finches has seldom been questioned. Gray (1859) referred *Pinaroloxias* to the genus *Loxops,* thus implying that it is a member of the Drepanidini of Hawaii, while Salvin (1876) stated that the systematic position of *Pinaroloxias* is uncertain, although probably it is related neither to the Drepanidini nor to the Galápagos finches. Ridgway (1897) regarded *Pinaroloxias* to be related both to the Galápagos finches and to *Coereba.* All other authors either have remained neutral on this matter or have stated that *Pinaroloxias* is related to the Galápagos finches.

Volatinia has been mentioned twice in previous published accounts of Darwin's finches, but has never before been suggested as very closely related. Bowman (1961) noted a similarity in the pneumatization pattern of the skull in Darwin's finches, *Volatinia,* and several other emberizines. Harris (1972) mentioned the similar plumages in *Volatinia* and Darwin's finches, but then curiously proposed a possible relationship (also based largely on plumage) between Darwin's finches and *Coereba flaveola.* As stated even by Harris (1972), *C. flaveola* resembles Darwin's finches less in plumage than does *Volatinia*; both males and females are black in the melanistic phase of *C. flaveola,* while only males are black in Darwin's finches and *Volatinia.* Harris ignored evidence for the emberizine nature of Darwin's finches presented in Tordoff (1954*a*) in stating (1972:168), "To suggest a link between *Coereba* and the Geospizinae . . . may seem a little rash but it is at least as feasible as assuming an affinity with the Fringillidae or Emberizidae." Harris's hypothesis is further discredited on osteological evidence presented herein.

Various other non-Galápagos birds have been suggested to be related to Darwin's finches. Salvin (1876) proposed that *Camarhynchus* and *Geospiza* do not have a common ancestor, but instead that *Camarhynchus* is related to *Spermophila* (=*Sporophila*) or *Neorhynchus nasesus* (=*Sporophila peruviana*), while *Geospiza* is related to *Guiraca* (=*Passerina*). Rothschild and Hartert (1899) also subscribed to the closeness of *Geospiza* and *Guiraca.* Ridgway (1897) rejected Salvin's thesis of a *Camarhynchus-Neorhynchus* relationship, and suggested that *Camarhynchus* may be related to *Pyrrhulagra* (=*Loxigilla*). Ridgway (1897) also proposed possible close relationships between *Geospiza* and *Cyanoloxia* (=*Passerina*) and *Oryzoborus* (=*Sporophila*). Sushkin (1925) vaguely mentioned unspecified osteological similarities between *Geospiza* and various finches, including *Guiraca, Cyanocompsa,* and *Oryzoborus.* All of the hypothesized relationships in Salvin (1876), Ridgway (1897), Rothschild and Hartert (1899), and Sushkin (1925) are negated by the dissimilarities of Darwin's finches to *Coereba, Passerina* (*sensu lato*), *Sporophila* (*sensu lato*), and *Loxigilla* (*see* Osteological Comparisons).

The often-suggested close affinity of *Tiaris* to Darwin's finches is largely unsupported by real evidence. Most references discussed below deal with hypothesized relationships of *Tiaris* to the Galápagos finches and do not specifically mention *Pinaroloxias.* It may be inferred, however, that most or all of these authors regarded *Pinaroloxias* and the Galápagos finches as a monophyletic assemblage. Sushkin (1925:261) appears to be the first person to suggest such a relationship, stating with no supportive evidence, "*Tiaris* is most intimately related to the famous Galapagoes [sic] finches, *Geospiza* . . . ." The statement of Lowe (1936:317) is almost as uninformative.

"Finally, I might add that I found melanism a very striking feature among the small Finches of the genus *Euetheia* [=*Tiaris*], which I found extremely common on an extremely arid, cactus-grown, and isolated island named Blanquilla, a hundred miles from the coast of Venezuela. The physical conditions of Blanquilla must be remarkably similar to those obtaining in the Galapagos. Some of the Finches I shot there are so similar in appearance to certain species of Darwin's Finches that it would take an expert to distinguish them." Thus black plumage, a condition found in many 9-primaried oscines, is Lowe's only character. Yet Lack (1945:7) cited the "anatomical" studies of Sushkin (1925) and Lowe (1936) as indicating a relationship between *Tiaris* and Darwin's finches. Bond (1948, 1978) agreed with Lack but suggested that *Melanospiza* is also closely related.

Beecher (1953) studied the internal and external anatomy of a wide variety of oscines and concluded (p. 308), "In the [horny] palate and externally *Melanospiza richardsonii* [sic] . . . is similar to *Geospiza,* and both may have been derived from a widespread Caribbean form like *Tiaris.*" Beecher had no spirit specimen of *Melanospiza.* Beecher's study lacks detailed word descriptions for the states of various characters in Galápagos finches, *Volatinia, Tiaris,* or *Melanospiza,* among which only one species of Galápagos finch (*G. fortis*) is illustrated. As pointed out by Tordoff (1954*b*), there are no unique characters in Beecher's diagnosis (p. 308) of the "Geospizidae" that distinguish Galápagos finches from the Emberizinae. Tordoff (1954*a*:27) noted the presence of unfused or incompletely fused palatomaxillaries in a wide variety of emberizine genera, including the Galápagos finches and *Tiaris,* but not in *Volatinia.* In Tordoff's Appendix (pp. 35–39), however, the palatomaxillary in *Volatinia* is assigned to the same character state as that in all Darwin's finches and in *Tiaris olivacea.* I agree that *Volatinia* may have incompletely fused palatomaxillaries, which in fact resemble those of Darwin's finches more than do those of any species of *Tiaris.*

Bowman (1961:178, 179) noticed the similarity in pattern and placement of the posterior "windows" of incompletely "ossified" skulls in Darwin's finches, *Volatinia, Tiaris olivacea, T. bicolor, Melanospiza,* and *Loxigilla violacea,* as well as in the probable non-emberizines *Caryothraustes poliogaster, Chlorophanes spiza,* and *Cyanerpes cyanea.* Bowman cautiously used this character (pp. 179, 199–201) as evidence for a possible close relationship among Darwin's finches, *Tiaris,* and *Melanospiza,* while apparently ignoring the presence of the same condition in the other taxa. Because the pattern of cranial ossification (termed "pneumatization" herein) in Darwin's finches is not shared uniquely among emberizines with *Tiaris* and *Melanospiza,* it alone cannot be used to ally these three groups without also including *Loxigilla* and *Volatinia.*

Understandably, neither Bock (1963) nor Muller (1973) gave any evidence for their suggestions of a close relationship between *Tiaris* and Darwin's finches. Following a study in *Tiaris canora* and *T. olivacea* of "handedness" and use of the foot in holding, Baptista (1976:221) stated, "The genus *Tiaris* is regarded as closely related to the geospizines by some authors (*see* Sushkin, 1925; Paynter, 1970). A study of courtship and aggressive behaviour in Olive Finches [*T. olivacea*] revealed some striking similarities with displays of geospizines (Baptista, *in preparation*). Although holding is not unique to *Tiaris* spp. among continental emberizines, taken with other characters (anatomy, plumage, behaviour) it supports the affinity between grassquits and Darwin's finches." Several comments are warranted regarding Baptista's statement: (1) Sushkin (1925), as shown above, did not substantiate his claims; (2) Paynter and Storer (1970) [=Paynter, 1970] did not specifically mention *Tiaris* as a relative of Darwin's finches, but instead said only that Darwin's finches presumably evolved from a member of their "fourth group" of Emberizinae, which consists of 11 genera, including *Volatinia* as well as *Tiaris*; and (3) concerning the "other characters (anatomy, plumage, behaviour)" noted by Baptista, the palatomaxillary character of Tordoff (1954*a*) and the skull window character of Bowman (1961) are the only published anatomical characters to ally *Tiaris* with Darwin's finches, and both of these characters are also found in *Volatinia* and other emberizines. Additionally, the plumage pattern in primitive Darwin's finches is more closely matched by that in *Volatinia* than by that in any species of *Tiaris,* thus leaving only behavior as a possible link between Darwin's finches and *Tiaris.* Until published accounts of behavior appear that carefully compare Darwin's finches with both *Tiaris* and *Volatinia,* the behavior of these birds cannot be evaluated accurately in taxonomic terms.

The history of the proposed relationships of *Melanospiza* to Darwin's finches, already discussed in part, is very similar to that of *Tiaris* in its general lack of substantiation. Without reason or comment, Cory (1892) listed the St. Lucia Finch as *Geospiza richardsoni.* Ridgway (1897) subscribed to a close relationship between *Melanospiza* and *Geospiza,* but mentioned only differences rather than similarities between *Melanospiza* and *Geospiza.* Ridgway (1901:544–545) defines the similarities between *Melanospiza* and *Geospiza* no further than a superficial "remarkable resemblance" and a "close . . . general resemblance," leaving one to presume that black plumage in males is their main shared character. (The female plumage of *Melanospiza,* which was still unknown at the time of Ridgway's writings, is not streaked as in *Volatinia, Pinaroloxias,* and many of the Galápagos finches. It is solidly colored, largely brown above and buff below.)

Bond (1929:523), perhaps following Ridgway (1901), noted an undefined "remarkable, though superficial resemblance" to *Geospiza* in the male of *Melanospiza,* but maintained that the latter is "structurally close to *Tiaris.*" Bond (1945, 1950, 1956) reported that *Melanospiza* is very similar to *Geospiza,* but provided no details. Tordoff (1954*a*, 1954*b*), following Bond (1950), theorized that *Melanospiza* and *Geospiza* could have evolved from a common ancestor. Bowman (1961:162) noted that the configuration of the horny palate in *Geospiza fortis* is nearly identical to that in *Melanospiza.* Bowman also reported a great diversity in palatal relief among Darwin's finches, and because he did not characterize the palatal structure of other emberizines of similar size, it is not known if the resemblance in palatal relief in *G. fortis* and *Melanospiza* could be due to convergence associated with their similarity in bill size. Studies of the feeding habits of *Melanospiza* are lacking, and thus it is not possible to compare its feeding with that of any Darwin's finches, many of which have been well studied in this regard. Bowman (1961:179, 201) also used the similar cranial pneumatization to suggest cautiously a relationship between *Melanospiza* and Darwin's finches. Above I have noted that this character state cannot be used as evidence to unite Darwin's finches with *Tiaris* and *Melanospiza* exclusive of *Volatinia.* Bowman (1963:135) gave no details in his mention of "a striking resemblance" of *Melanospiza* to *G. fortis.*

In summary, it appears that black plumage in males has been the character responsible for most published accounts of the "remarkable" or "striking" resemblance of *Tiaris* and *Melanospiza* to *Geospiza.* The cranial pneumatization character of Bowman (1961) is not unique to *Tiaris, Melanospiza,* and Darwin's finches. The similar horny palates of *Melanospiza* and *G. fortis* (Bowman, 1961) and the similarities in behavior between *Tiaris* and *Geospiza* (Baptista, 1976) cannot be evaluated taxonomically until other emberizines, especially *Volatinia,* are included in the comparisons.

MATERIALS AND METHODS

Institutional abbreviations used: AMNH—American Museum of Natural History; ANSP—Academy of Natural Sciences of Philadelphia; CMNH—Carnegie Museum of Natural History; FMNH—Field Museum of Natural History; KU—University of Kansas Museum of Natural History; LSU—Louisiana State University Museum of Zoology; UA—University of Arizona; UCMVZ—University of California (Berkeley) Museum of Vertebrate Zoology; UMMZ—University of Michigan Museum of Zoology; USNM—United States National Museum of Natural History. Unless stated otherwise, all specimens listed below are from USNM.

Full skeletons or skulls examined in this study are as follows: Mniotiltinae—*Dendroica petechia* 502312, *Geothlypis trichas* 502315; Tanagrinae—*Piranga rubra* 492866, *Euphonia laniirostris* 500551, *Saltator maximus* 500546; subfamily *incertae sedis*—*Coereba flaveola* 500532; Fringillinae (Carduelinae)—*Carpodacus mexicanus* 498536, *Carduelis psaltria* 499754; Drepanidini—*Psittirostra cantans* 298283; Icterinae—*Molothrus aeneus* 288959, *Cacicus uropygialis* 428586; Emberizinae—*Spizella breweri* UA 10001, 10002, 10004–10010, 11742, *Pooecetes gramineus* UA 2219, 6221, 8693, 13067, 13415–13418, *Pipilo fuscus* UA 6234, 8684, 8685, 8689, unnumbered, *Phrygilus fruticeti* 227537, *Melanodera xanthogramma* 491023, *Poospiza nigrorufa* 499056, *Sicalis luteola* 227533, *Emberizoides herbicola* 428724, *Catamenia inornata* 428755, *Pezopetes capitalis* 429814, *Passerina cyanella* 492771, *Sporophila nigricollis* 500557, *S. americana* 500550, *S.* (=*Oryzoborus*) *angolensis* 428813, *S.* (*O.*) *crassirostris* 321748 (merger of *Oryzoborus* into *Sporophila* follows Olson, 1981), *Melopyrrha nigra* 322174, *Loxipasser anoxanthus* 502866, *Tiaris bicolor* 292670–292672, 487950, 487951, 488014, 488016, 488019, 488021, 488022, 488034, 500684, *T. canora* 226045–226048, 320952, 320957, 322662, 343399, 343426, 343817, 498963–498965, *T. olivacea* 289017, 291027, 291028, 292664, 292665, 292667, 292668, 318684, 318930, 318931, 428023, *T. obscura* 253464, *Melanospiza richardsoni* UMMZ 136174 (same specimen as examined by Bowman, 1961), *Loxigilla noctis* 487995, *Volatinia jacarina splendens* USNM 289016, 344324, 344325, 344926, 347234, 347235, KU 23689, 23691, 33218, 35306, 36598–36600, 37704, 37706, *V. j. peruviensis* AMNH 8334, 9000–9009, 10235, 10236, LSU 70296, 84138, *Pinaroloxias inornata* 318774, 318775, 321071, 321072, *Geospiza nebulosa* (use of *nebulosa* to replace *difficilis* follows Sulloway, *in press*) UCMVZ 141033, *G. fuliginosa* UCMVZ 130299, USNM 345595, *G. fortis* UCMVZ 130248, *G. magnirostris* UCMVZ 130170, *G. scandens* UCMVZ 93115, *G. conirostris* UCMVZ 141044, *Platyspiza crassirostris* UCMVZ 93207, *Camarhynchus psittacula* UCMVZ 130414, *C. pauper* UCMVZ 141054, *C. parvulus* UCMVZ 130438, USNM 20533, *C. palidus* UCMVZ 130530, *Certhidea olivacea* UCMVZ 130567, USNM 345598. The specimens listed above form the main basis for my comparisons. However, from 1 to 7 additional skeletal specimens of most species of Darwin's finches were used to verify certain characters. I also examined skins in the USNM collection of all species of *Melanospiza, Tiaris, Volatinia,* and Darwin's finches, as well as all other genera of the Emberizinae.

To facilitate comparisons, descriptive nomenclature of the skull and mandible generally follows that of Bowman (1961). However, descriptions and comparisons of osteology and plumage are based solely upon my own examinations of specimens.

OSTEOLOGICAL COMPARISONS

I compared 1 to 8 skeletal specimens of each species of Darwin's finch (except *Camarhynchus heliobates*) with representative species of other groups of New World 9-primaried oscines (*see* MATERIALS AND METHODS). All Darwin's finches, both of the Galápagos and of Cocos Island, were found to resemble members of the Emberizinae and to differ from other 9-primaried oscines in the following characters: from Mniotiltinae—(1) relatively small ventral lobe of the ectethmoid, (2) relatively small nares, (3) narrow median ridge on the ventral surface of the premaxilla, (4) more acute angle at the jugal–maxillary junction, (5) dentary much thicker than the surangular; from Tanagrinae—(1) broad transpalatine process, (2) small ectethmoid, (3) more acute angle at the jugal–maxillary junction, (4) ventral surface of the premaxilla less concave and without large mediolateral ridges; from *Coereba flaveola* (in response to Harris, 1972, 1974)—(1) broad transpalatine process, (2) small retroarticular process, (3) dentary more curved and less pointed; from Fringillinae—(1) interorbital septum thinner (*see* Zusi, 1978), (2) interorbital area of the frontals narrower, (3) no extensive fusion of the prepalatine bar with the palatomaxillary process or the jugal, (4) nares oriented more laterad, (5) ventral surface of the premaxilla less concave, (6) retroarticular process large; from Drepanidini—(1) interorbital septum thinner (*see* Zusi, 1978), (2) no extensive fusion of the prepalatine bar with the palatomaxillary process or the jugal, (3) ventral surface of the premaxillary less concave; from Icterinae—(1) transpalatine process extending much posterior to the ectethmoid, (2) small retroarticular process,

(3) dentary more curved and less pointed. (I am not convinced of the monophyly of the "Cardinalinae." For example, tanager-like cranial characters are present in *Saltator* and *Cardinalis,* while *Passerina* is emberizine-like in certain cranial features. Using the characters stated above, *Saltator* would have to be regarded as a thraupid, while *Passerina* would be an emberizine.)

Further evidence to support the allocation of Darwin's finches in the Emberizinae is in Tordoff (1954*a*: Table 1), who found the "Geospizinae" not consistently different in any behavioral or morphological characters from the Richmondeninae (=Cardinalinae), Emberizinae, or "Fringillinae" (=*Fringilla*), but substantially different from the Carduelinae and the Old World Estrildinae. In his own classification, Tordoff (1954*a*) lists Darwin's finches in his expanded Fringillinae, which includes all genera that now are usually relegated to the Emberizinae. Recent classifications that do not recognize the distinctness of the Geospizinae and place Darwin's finches in the Emberizinae are those of Paynter (1970), Sibley (1970), Morony et al. (1975), and Raikow (1978), although the definition of Emberizinae is not identical in each of these treatments.

Having concluded that Darwin's finches indeed belong in the Emberizinae, the next step is to determine which emberizine is most similar morphologically and therefore probably their closest relative. I compared the skulls and mandibles in any genus of emberizine that I suspected might be even remotely related to Darwin's finches (*see* MATERIALS AND METHODS). No attempt was made to compare in detail the genera of "sparrows" (*Zonotrichia, Aimophila,* etc.) in the "first group" of Emberizinae of Paynter (1970) because these forms are very different from Darwin's finches in plumage and in their generally very large, bulbous squamosal region. Likewise, members of the second, sixth, and seventh "groups" of Emberizinae of Paynter (1970) are very different in cranial osteology and in coloration and pattern of plumage from Darwin's finches and tropical seed finches (the fifth and fourth "groups" of Emberizinae, respectively, of Paynter), thus necessitating only a few comparisons.

The states of the characters below are careful, nonquantified observations, which are just as meaningful or better than quantified characters; many systematic problems simply are not readily solved by a quantitative treatment. Among the Galápagos finches, *Geospiza nebulosa* and *G. fuliginosa* have been suggested to be the most primitive living species (Lack, 1945, 1946, 1947), a hypothesis supported by their generalized cranial morphology. The characters of these two species are therefore stressed in comparisons that follow. Details of the primitive nature of *G. nebulosa* and *G. fuliginosa* are found in EVOLUTION AND ZOOGEOGRAPHY.

In the comparisons below, if the skull or mandible of an emberizine species had an allometric character state that roughly matched that of a *Geospiza* of similar size (based on character states of *G. nebulosa* and the closely related series of *G. fuliginosa, G. fortis,* and *G. magnirostris*; *see* Fig. 1), then no evidence against a close relationship was produced. If, however, the character state of the skull or mandible did not resemble that of a *Geospiza* of similar size, this was taken as evidence against a close relationship to Galápagos finches. Some extrapolation was necessary when dealing with species smaller than any of the *Geospiza.*

I evaluated characters of *Pinaroloxias* independently from those of the Galápagos finches. Unlike in primitive species of Galápagos finches, the bill in *Pinaroloxias* is relatively thin and elongated, presumably correlated with its insectivorous, nectarivorous, graminivorous, and frugivorous feeding habits (Smith and Sweatman, 1976). Also, because only one species of finch lives on Cocos Island, no directional allometric trends can be determined for *Pinaroloxias,* unlike the Galápagos finches. Nevertheless, *Pinaroloxias* closely parallels *G. fuliginosa* and *G. nebulosa* in its similarities and dissimilarities to various finches of the mainland.

As already demonstrated, Darwin's finches and other emberizine finches share a suite of osteological characters that distinguish them from other groups of New World 9-primaried oscines. The osteological characters by which emberizine species differ from Darwin's finches, both of the Galápagos and of Cocos Island, are as follows (characters in quotation marks are defined on pp. 205–206 of Bowman, 1961; abbre-

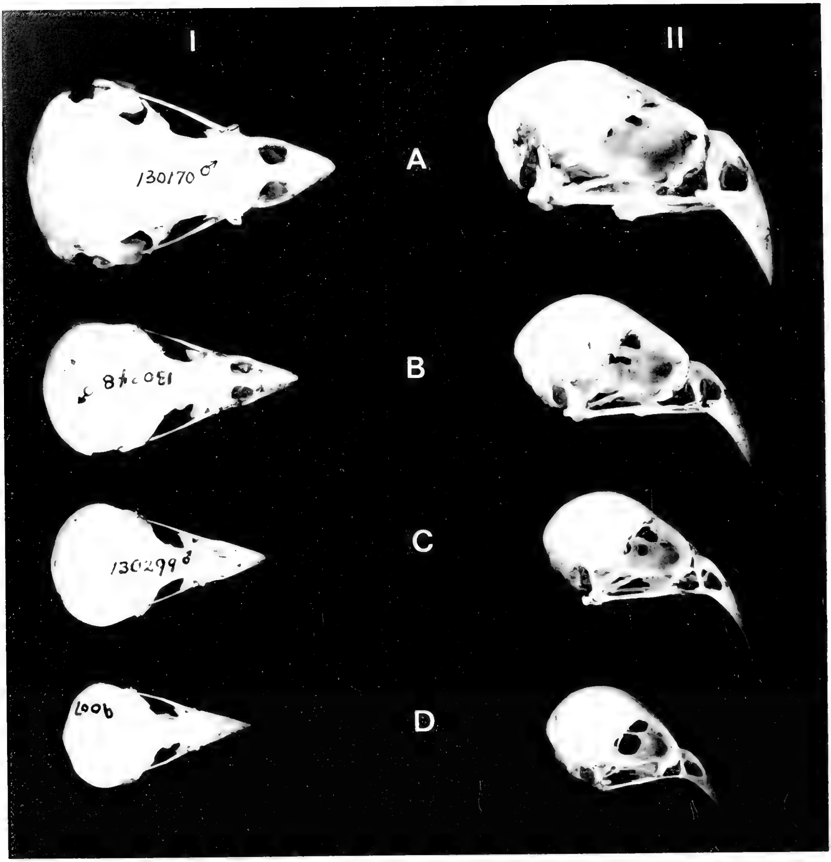

FIGURE 1. Skulls in dorsal (I) and lateral (II) aspect. A. *Geospiza magnirostris* UCMVZ 130170. B. *G. fortis* UCMVZ 130248. C. *G. fuliginosa* UCMVZ 130299. D. *Volatinia jacarina peruviensis* AMNH 9007. All *Geospiza* are from Isla Santa Cruz, Galápagos. Obvious allometric changes associated with increasing overall size include: dorsal view—larger attachment of temporal muscle, wider interorbital and internarial areas; lateral view—greater ossification of interorbital septum, stouter jugal bar, decreased slope of frontals, decreased relative size of nares, larger and more perpendicularly oriented bill. All figures are 1.9×.

viated geographical ranges are: CA = Central America; SA = South America; WI = West Indies): *Phrygilus fruticeti* (SA)—nares large and elongate, transpalatines expanded laterad, interorbital area narrow, "slope of upper mandible" small, dentary short; *Melanodera xanthogramma* (SA)—nares large, transpalatines and rostrum expanded laterad, rostrum with distinct sharp bend near anterior end of nares, auditory bullae large and bulbous, mandibular foramen large, "slope of lower mandible" large, posterior margin of dentary expanded laterad; *Poospiza nigrorufa* (SA)—nares oblong, transpalatines expanded laterad, "slope of upper mandible" small, maxillopalatine process located ventrally; *Sicalis luteola* (CA, SA)—prepalatine bar and transpalatine process expanded laterad, middle portion of jugal expanded dorsoventrad and compressed laterad, "slope of posterior border of surangular process" large; *Emberizoides herbicola* (CA, SA)—nares large and elongate, transpalatines protrude ventrad, "slope of upper mandible" small, "slope of nasal bone" small; *Catamenia inornata* (SA)—nares large, transpalatines expanded laterad, "slope of upper mandible" large; *Pezopetes capitalis* (CA)—nares large and elongate, transpalatines expanded laterad, "slope of upper mandible" small, temporal fossa poorly developed, interorbital septum thin and foraminate; *Sporophila nigricollis* (CA, SA, WI) and *S. americana* (CA, SA)—dorsal surface of culmen decurved, palatines stout, transpalatines directed laterad, entire mandible stout with much lateral expansion at posterior margin of dentary, internal angular process large and tapers much (wide at base, narrow at distal end); *Sporophila* (*Oryzoborus*) *angolensis* (CA, SA) and *S.* (*O.*) *crassirostris* (CA, SA)—nares small (*S. crassirostris* only), rostrum stout and expanded laterad, palatines stout, transpalatines directed laterad, "slope of upper mandible" large, entire mandible stout with much lateral expansion at posterior margin of dentary, internal angular process large and tapers much (wide at base, narrow at distal end); *Melopyrrha nigra* (WI)—nares small, dorsal surface of culmen decurved, transpalatines with a long thin posterior process, entire ectethmoid large, mandibular foramen small, posterior "slope of border of the surangular process" large; *Loxipasser anoxanthus* (WI)—dorsal surface of rostrum decurved, "slope of upper mandible" large, transpalatines with a long thin posterior process, entire ectethmoid large, posterior "slope of border of the surangular process" large, "slope of lower mandible" large; *Tiaris bicolor* (SA, WI)—"slope of upper mandible" large, transpalatine process long; *T. canora* (WI)—"slope of upper mandible" large, transpalatine process long, entire ectethmoid large and bulbous, zygomatic process large; *T. olivacea* (CA, SA, WI)—"slope of upper mandible" large, rostrum with a distinct lateral protrusion where it meets jugal, transpalatine process long, entire ectethmoid large and bulbous, dentary short with posterior margin (at dentary–surangular junction) expanded dorsad and laterad; *T. obscura* (SA)—"slope of upper mandible" large, ventral lobe of ectethmoid large, flaring posteriad and laterad; *Melanospiza richardsoni* (WI)—nares large, "slope of upper mandible" small, transpalatine process long and slender, palatomaxillary process long and narrow; "width of frontal bridge" small, "slope of lower mandible" large; *Loxigilla noctis* (WI)—transpalatine process thin, "slope of upper mandible" slightly small, ventral lobe of ectethmoid large, supraoccipital bulbous, "slope of lower mandible" large; *Volatinia jacarina* (CA, SA, WI)—no consistent differences noted.

Volatinia is clearly more similar than any other emberizine to Darwin's finches in cranial osteology (*see* Fig. 1). However, I included grassquits of the genus *Tiaris* and the St. Lucia Finch (*Melanospiza richardsoni*) in additional, more quantitative comparisons with Darwin's finches because these birds have so often been mentioned as perhaps the closest living relatives of Darwin's finches. I made 10 linear and 9 angular measurements of the skulls and mandibles of *Melanospiza, Tiaris,* and *Volatinia,* exactly as described in Bowman (1961:205–206) for Darwin's finches, in an attempt to discover further evidence of the relationships of these genera to Darwin's finches. These data are not presented here because of their apparent lack of useful systematic information, but are available on request. *Spizella breweri, Pooecetes gramineus,* and *Pipilo fuscus* were included for "out-group" comparisons. Within the Emberizinae, these three species are only distantly related to *Melanospiza, Tiaris, Volatinia,* or *Geospiza* and are thus expected to show differences from the latter group that cannot be attributed simply to allometric changes. When each linear measurement was plotted against the cube root of body weight, however, only *Pooecetes* and *Pipilo* were consistently different from the Galápagos finches in proportions of the skull and mandible, while all of the smaller species (*Tiaris bicolor, T. olivacea, V. jacarina,* and *S. breweri*) were generally very similar to *Geospiza*. (Body weights were not available for *G. nebulosa* or *Pinaroloxias*.) Plotted points that represent these smaller species were usually very near to regression lines based on the values for *G. fuliginosa, G. fortis,* and *G. magnirostris,* with no discernible trend to argue for or against a close relationship between *Geospiza* and any of the small species with which they were compared. Structural restraints may place severe limitations on cranial morphology in the smaller seed-eating emberizines, with the result that similar proportions are found in distantly

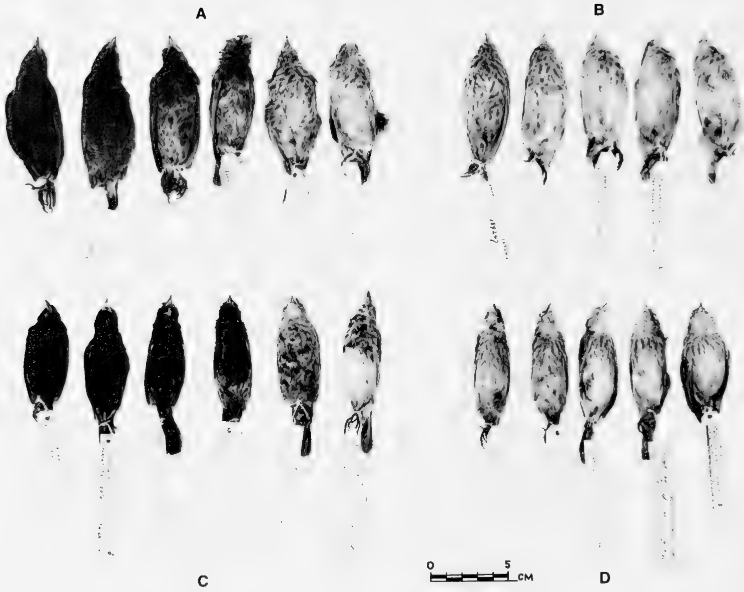

FIGURE 2. Skins in ventral aspect. *Geospiza fuliginosa* (A—males, B—females). *Volatinia jacarina peruviensis* (C—males, D—females). Specimens are from ANSP, CMNH, FMNH, LSU, and USNM.

related forms. The relationship of linear measurements to body weight appears to be of little value in the search for potential relatives of Darwin's finches.

The angular measurements of *Pooecetes* and *Pipilo* are often very different from those of species of *Geospiza* of a similar size, while these angles in *Spizella* often resemble those in *Tiaris, Volatinia, G. nebulosa,* or *G. fuliginosa.* Once again it is clear that certain "out-group" species may not differ strongly from "in-group" species in many quantitative characters. Nevertheless, the angular measurements of *Spizella* differ somewhat more from those expected of a small Darwin's finch than do those of *Volatinia.* Keeping in mind that *Volatinia* and the species of *Tiaris* are smaller than *G. nebulosa* or *G. fuliginosa,* while *Melanospiza* is about the size of *G. fortis,* the angular measurements of *Volatinia* resemble those of *Geospiza* more than do those of *Melanospiza* or any species of *Tiaris.* The angular measurements of *Pinaroloxias,* however, are not clearly more similar to those of *Volatinia* or *Tiaris,* as they fall within the range of *Volatinia* and at least one species of *Tiaris* in every case except one.

I found only 3 characters in the postcranial skeleton that might shed some light on the relationships among Darwin's finches, *Volatinia, Tiaris,* and *Melanospiza.* The humerus and ulna in all Darwin's finches and in *Volatinia* are more delicate, especially in the slenderness of the shaft, than are those in *Melanospiza* or *Tiaris.* Also, the medial pneumatic fossa of the humerus in Darwin's finches, *T. canora,* and *Volatinia* is deeper than that in *Melanospiza, T. olivacea,* or *T. bicolor.* I found no characters shared between Darwin's finches and *Melanospiza* or *Tiaris* that are lacking in *Volatinia.* These few postcranial characters lend support to the proposed very close relationship of *Volatinia* to Darwin's finches, and their apparent distinctness from *Tiaris* and *Melanospiza.*

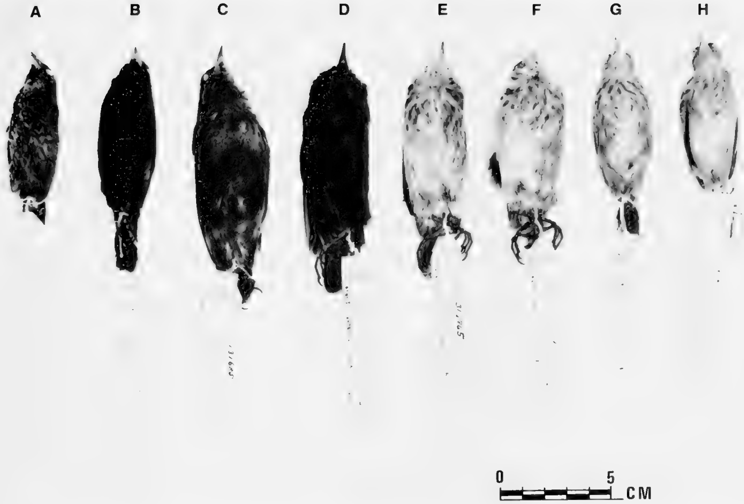

FIGURE 3. Skins in ventral aspect. *Volatinia jacarina splendens* (A, B—males; G, H—females). *Pinaroloxias inornata* (C, D—males; E, F—females). All specimens are from USNM.

NON-OSTEOLOGICAL CHARACTERS

Plumage.—*Geospiza nebulosa*, *G. fuliginosa*, *G. fortis*, and *G. magnirostris* (the species of Galápagos finches with seed-eating bills, black plumage in adult males, and streaked plumage in females) differ from *Volatinia* mainly in their larger body sizes, relatively shorter tails, larger bills, and duller black plumage in adult males. Rather similarly, *Pinaroloxias* differs from *Volatinia* in its larger body size, slightly shorter tail, more elongate bill, and duller black plumage in adult males. None of these differences warrants generic separation. The similarity in plumages among these species is apparent from Figures 2 and 3. Unlike in *Tiaris* and *Melanospiza*, the females of *Volatinia*, *Pinaroloxias*, and primitive species of Galápagos finches (*G. nebulosa*, *G. fuliginosa*) have streaked breasts and wing bars.

The pattern by which the adult male plumage is acquired in Galápagos finches is very similar to that in *Volatinia jacarina peruviensis*, the subspecies that occurs on the arid Pacific slope from southern Ecuador through Perú to northern Chile (which, incidentally, was originally described by Peale [1848] as *Geospiza peruviensis*). As illustrated in Figure 2, the area of the under-tail coverts is the last to attain black plumage in both *V. j. peruviensis* and *G. fuliginosa*. Fully black under-tail coverts seldom, if ever, occur in Darwin's finches, and only very rarely in *V. j. peruviensis*. The under-tail coverts in adult males of other races of *V. jacarina*, however, are completely black, as is often the case in *Pinaroloxias*. Adult males of *V. j. peruviensis* further resemble *Geospiza* in that they are never as glossy in plumage as males of other races of *V. jacarina*. Of the 99 skins of males of *V. j. peruviensis* that I have examined, not one is blue-black, or even completely black, whereas adult males in other races of *V. jacarina* are normally completely blue-black.

No detailed study of molt is available for *Pinaroloxias*, but Lack (1945, 1947) noted that the males acquire the black plumage irregularly all over the body, instead of initially in the head region and then posteriorly, as in Galápagos finches. Males of *V. j. splendens* (the race that occurs, among other areas, along the Pacific coast from northern México through central Ecuador) generally attain their black plumage in the same way as *Pinaroloxias* (Fig. 3). Thus the difference in the pattern and acquisition of black plumage in *Pinaroloxias* versus the Galápagos finches is paralleled in *V. j. splendens* versus *V. j. peruviensis,* and suggests that *Pinaroloxias* and the Galápagos finches evolved from different races of *V. jacarina,* namely from *splendens* and *peruviensis,* respectively. Within *V. jacarina,* one of these conditions of plumage development is presumably primitive and the other derived, but I have no evidence for which is which. In this example, I see nothing wrong in suggesting ancestry of *Pinaroloxias* from *V. j. splendens,* and the Galápagos finches from *V. j. peruviensis,* based on shared characters, even though the shared character state in one of these groups is obviously primitive.

Life History.—The short, thin, buzzy song of *Volatinia* is reminiscent of that in various Darwin's finches; a comparative analysis of songs in *Volatinia* versus its insular derivatives could be valuable, although vocalizations may be unreliable as indicators of generic relationships and are best used at the species level.

Volatinia is well known for its unusual song-flight, in which the reproductively active male jumps vertically (aided by the wings) while singing. Alderton (1963) found the height of these vertical maneuvers to vary from a norm of 30 to 45 cm up to 1.5 m. Vertical jumps are not necessarily accompanied by a song, nor the song with a jump. Such a flight display is absent in Darwin's finches (and all other emberizines for that matter); it may have been secondarily lost. Nevertheless, Darwin's finches have what may be a modified remnant of the song-flight of *Volatinia.* It is described by Lack (1945:23) as follows: "The song is delivered from perches in the territory, also, in all except *Certhidea* [P. R. Grant (*personal communication*) has seen *Certhidea* singing in flight], during a special flight, slower with more rounded wings, usually descending from a higher branch to a lower. This song-flight is also common when going to or from the nest during display-building. In *Cactospiza pallida,* as in the other species, the song-flight is normally from one branch to another below the canopy of the forest trees. However, where this species occurs in the six to ten foot [1.8–3 m] scrub in the higher hills, the same movements result in an aerial song-flight above the low trees, which makes the bird conspicuous for a long distance." The major differences in song-flights are the vertical movement accompanied by a jump in *Volatinia* versus the horizontal or diagonal movement without a distinct jump in Darwin's finches (P. R. Grant, *personal communication*). These differences neither confirm nor refute the suggestion of homology in song-flights of *Volatinia* and Darwin's finches.

Basic life history data are quite limited for *Pinaroloxias,* although the following passage from Slud (1967:292) suggests that, as in the Galápagos finches, it may still retain a modified song-flight: "Hundley observed (*loc. cit.*): '. . . a black Cocos Finch with ruffled feathers was hopping up and down. The behavior of the female beside him was that of a young bird begging for food [and]. . . one black male only gave a sort of "chee" as it prepared to fly, and repeated 2 or 3 times as it flew away.' "

The nests of Galápagos finches are usually globular, domed structures with a side entrance (Lack, 1947), but open cup nests are occasionally built. The domed nest of *Pinaroloxias* appears to be similar, although descriptions are few (Slud, 1967). The nest of *Volatinia* is a small, open cup (Belcher and Smooker, 1937; Alderton, 1963; Bond, 1971), while *Melanospiza* and the species of *Tiaris* build globular nests with side entrances (Belcher and Smooker, 1937; Skutch, 1954; Bond, 1971). Globular nests are characteristic of the apparently related complex of West Indian finches that includes *Loxipasser, Loxigilla,* and *Melopyrrha,* as well as *Melanospiza* and *Tiaris* (Steadman and Olson, *in preparation*). Nest structure in these finches may vary intraspecifically, however, as Bond (1971) noted that both *Loxigilla portoricensis* and *L. violacea* build either cup-shaped or globular nests. Thus the normally globular nests of Darwin's finches may have evolved independently after the initial colonization of Cocos Island and the Galápagos by *Volatinia.* An alternative hypothesis is that *Volatinia* originally built a globular nest and has evolved the use of a cup-shaped nest on the mainland since it colonized Cocos and the Galápagos.

The eggs of Darwin's finches give no clear evidence of their affinities. Galápagos finches, *Volatinia,* and *Tiaris* all have lightly colored eggs that are spotted in various shades of brown or red. This is also apparently true of *Pinaroloxias* (Slud, 1967) and *Melanospiza* (Bond, 1971), although the ground color has not been specifically noted.

Evolution and Zoogeography

The osteological discrepancies between Darwin's finches and emberizines other than *Volatinia* are of a magnitude that precludes a relationship close enough to suggest potential ancestry. Lack (1945, 1946, 1947) suggested other characters of *Geospiza fuliginosa,* and especially of *G. nebulosa,* that are primitive within Galápagos finches; namely, black plumage in males, streaked underparts and a rufous wing-bar in females, a finch-like bill, a diet of seeds, and a habitat in the arid lowlands. Each of these characters is present in *Volatinia,* whose cranial morphology also resembles that in *G. nebulosa* and *G. fuliginosa* more than that in any other Galápagos finch.

Although Bowman (1961) claimed that Lack (1947) was unjustified in assuming that *G. nebulosa* or *G. fuliginosa* represents the most primitive living Darwin's finch, Bowman did not himself clearly suggest which species may be primitive within the group, perhaps because of his reluctance to relate Darwin's finches to any mainland birds. The fact that males of *Volatinia* are black supports the hypothesis of Lack (1945, 1947) on the primitiveness of black plumage in males of Darwin's finches.

Volatinia, G. nebulosa, and *G. fuliginosa* all have finch-like bills adapted for seed eating, and not thin bills such as in *Certhidea* or *Pinaroloxias.* Like Tordoff (1954*a*:31), I disagree with Amadon (1950) in seeing ". . . no justification for considering a heavy, seed-crushing bill an evolutionary dead end." Additional evidence for this view is found in the well substantiated conclusion of Raikow (1977) that the entire assemblage of Drepanidini evolved from a single species of Carduelinae with a finch-like bill.

I believe that the overall similarity of *Pinaroloxias* to the Galápagos finches can be attributed to the retention of primitive characters found in *Volatinia,* their probable common ancestor. Lack (1947:104) noticed the similarity in plumage between *Pinaroloxias* and *Geospiza nebulosa* and suggested that it presumably was due to the retention of primitive characters. Parallel evolution would account for the larger size and the reduction in glossiness of the black plumage in adult males of *Pinaroloxias* and *G. nebulosa* as compared to *Volatinia.* That the most primitive Darwin's finches (*Pinaroloxias, G. nebulosa,* and *G. fuliginosa*) are larger than *Volatinia* is paralleled by other herbivorous vertebrates of the Galápagos, such as the tortoises (*Geochelone*) and the extinct giant thomasomyine rodent (*Megaoryzomys*), which are also larger than their nearest mainland relatives. As with Darwin's finches, an increase in size in the tortoises and rodents probably enabled them to use a wider range of food plants.

That *Pinaroloxias* has been derived independently of the Galápagos finches makes sense zoogeographically. It has always perplexed me that Darwin's finches would have colonized Cocos Island from the Galápagos or *vice versa,* a prerequisite for their supposed monophyly. Modern wind patterns (Alpert, 1963) are not favorable for such interisland movements, and Pleistocene wind patterns are not precisely known. It seems much more likely that the ancestors of both *Pinaroloxias* and the Galápagos finches came independently from the mainland rather than crossing some 600 km of open ocean between the Galápagos and Cocos Island, probably unaided by wind in either direction. Further, no other land birds from Cocos Island are more closely related to those of the Galápagos than to forms on the mainland, except possibly the Yellow Warbler, *Dendroica petechia.* The similar plumage of the Yellow Warbler of Cocos and the Galápagos, *D. p. aureola,* strongly resembles that of populations on certain West Indian islands, particularly the Lesser Antilles except Martinique. Olson (1980) has noted that *D. p. aureola* resembles *D. p. peruviana* of coastal Perú, Ecuador, and southern Colombia more than other mainland forms, and has suggested that the similarity between the Yellow Warblers of the West Indies and *D. p. aureola* may have evolved independently. Likewise, I believe that the similar plumage of *D. p.*

aureola on Cocos and the Galápagos may have evolved independently. As pointed out by Steadman and Ray (*in press*), it is not historically sound to hypothesize a close relationship between terrestrial vertebrates that are found in the Galápagos and the West Indies but not on the Neotropical mainland. The Panamanian water gap closed approximately 3 million years ago (Marshall, 1979), when the Galápagos were probably composed of only 2 or 3 very small islands which were farther from the mainland than today (Cox, *in press*) and were undoubtedly very active volcanically and without a well-developed flora to support terrestrial vertebrates. Porter (1976), following a modern, comprehensive review of the flora of the Galápagos, concluded (p. 745): ". . . as the tropical American flora has become better known, most Galapagos species once thought to be only Mexican, Central American or West Indian in their extra-Galapagean distribution also have been found to occur in northern and western tropical South America . . . or to have been incorrectly identified . . . . West Indian relationships do not exist.

"Ninety-nine per cent of the non-endemic vascular plant taxa in the Galapagos Islands also occur in South America. The remaining 1% occurs in Mexico and Central America. All but four of the 286 indigenous non-endemic taxa in the islands are known from the land area nearest the archipelago . . . . The endemics have their closest known relatives in South America as well." My studies of the terrestrial birds and mammals of Galápagos agree with Porter (1976) in finding the nearest relatives in South America, not in the West Indies.

The Blue-black Grassquit occurs today essentially throughout the lowlands of the Neotropical region, including the Pacific slope from northern México to northern Chile. Thus nothing in its modern distribution presents any difficulty to the theory that it is the direct ancestor of both *Pinaroloxias* and the Galápagos finches. That *Volatinia* has some ability to disperse over water is shown by its occurrence on Grenada in the Lesser Antilles. Also, Clark (1905) reported an individual *Volatinia* landing on a ship midway between Trinidad and Grenada.

Neither the habitat nor mode of feeding in *Volatinia* differs from those of its insular counterparts in the Galápagos. *Volatinia* inhabits unforested areas such as grasslands, savannas, open brushlands, and all sorts of artificial clearings, where it feeds largely on seeds on or near the ground. *Geospiza fuliginosa* and *G. nebulosa* eat seeds and fruits, mainly on the ground (Bowman, 1961; Abbott et al., 1977), and live in the arid, scrubby lowlands of the Galápagos, although on larger, higher islands, *G. nebulosa* may be largely restricted to the humid, more densely forested uplands, at least during the nesting season. The accounts of Slud (1967) and Smith and Sweatman (1976) show that *Pinaroloxias* has a wide tolerance of habitat (cultivated areas to virgin forest), feeding heights (ground to the tops of trees), and food items (insects, nectar, seeds, fruits), thus providing few clues to the habitat and feeding ecology of its ancestor. The cranial morphology of *Pinaroloxias*, however, is clearly that of an emberizine, implying that its ancestor was a finch-like, largely seed-eating, ground-dwelling bird.

Because of recent geological evidence unavailable to earlier authors, Darwin's finches can now be put into a more meaningful chronological framework. Dalrymple and Cox (1968) reported three potassium-argon ages of about 2.0 million years for Cocos Island, cautioning that these ages are not necessarily the oldest potential ages for Cocos Island and do not certainly represent the actual time of emergence above the ocean. Cox (*in press*) has summarized the geochronology and paleogeography of the Galápagos, concluding that the oldest islands emerged 3 to 5 million years ago and were never linked to the mainland or to Cocos Island by a landbridge or a chain of islands, as suggested by many biologists in the past. In fact the Galápagos are moving toward South America and were farther from the mainland in the past than at present. The ancestral finch probably colonized the Galápagos significantly later than the initial emergence of barren basaltic rock, and probably only after an increase in land area and in the number of emergent islands (*see* the paleogeographic maps in Cox, *in press*). Also, the development of soil and some sort of structured vegetation was necessary for the successful emberizine invasions of the Galápagos and Cocos. In my opinion, this occurred much later than the ages of the islands, themselves, particularly in light of the potential for very rapid evolution on islands. Certainly any suggestion of a colonization of these islands in the early or middle Tertiary Era is totally inconsistent with modern geological information. I would not be surprised if Cocos and the Galápagos were both totally without finches as recently as 100,000 years ago.

Generic Limits.—The generic status of Galápagos finches has been subject to much controversy. In the original description of most species of Galápagos finches, Gould (1837) recognized but a single genus, *Geospiza,* with *Camarhynchus, Cactornis,* and *Certhidea* as subgenera. Most subsequent workers have used 3–5 genera, although Rothschild and Hartert (1899, 1902) and Snodgrass and Heller (1904) recognized only *Geospiza* and *Certhidea.* Even those who use as many as 5 genera (Swarth, 1931; Lack, 1945; Bowman, 1961, 1963) generally have noted that one "genus" grades into the next, so that arbitrary limits must be made to split these finches into more than one genus. As a result, the various "genera" are very difficult to define because they have few, it any, characters that distinguish them consistently from the other supposed genera. In addition, no species of finch in the Galápagos is clearly very distinct from all of the others. Nearly every species grades into one or two other species through specimens that are intermediate in size, plumage, and bill morphology. (For measurements and discussion of intermediate specimens, *see* Section I and Table 16 in Lack [1945], and pp. 23, 97–99 and Table XXXII in Lack [1947].)

Using the genera recognized by Bowman (1961), *Geospiza* grades into *Platyspiza,* which grades into *Camarhynchus,* while *Camarhynchus* grades into *Cactospiza,* which in turn grades into *Certhidea.* New evidence for the closeness of *Platyspiza* to *Geospiza* is provided by fossils from Isla Santa Cruz of a finch that is apparently intermediate between *P. crassirostris* and *G. fortis* (Steadman, 1981). Adult males of *Platyspiza* can be very nearly as uniform black as in *Geospiza* (Swarth, 1931:211), while the extreme similarity in plumage between *Platyspiza* and *Camarhynchus* has long been recognized by many systematists. Likewise the plumage in *Cactospiza* is similar to that in *Platyspiza* and *Camarhynchus,* although showing some *Certhidea*-like tendencies. The Warbler Finch, *Certhidea olivacea,* is often considered the most "aberrant" form of Galápagos finch, but it can be allied to *Camarhynchus* and *Cactospiza* through intermediate specimens from Isla Santa Cruz (*Cactospiza "giffordi"*), Isla Floreana (*Camarhynchus "conjunctus"*), and Isla San Cristóbal (*Camarhynchus "aureus"*), each of which was described by Swarth (1929) from one or two individuals. Lack (1945) and subsequent authors have not recognized these forms as distinct species, suggesting instead that they are either hybrids or freak individuals. Regardless, these specimens are clearly intermediate between *Camarhynchus* or *Cactospiza* and *Certhidea* in measurements of both the bill (*see* Swarth, 1931: Fig. 55) and the body, as well as in coloration of the plumage.

I do not agree with Bowman (1961:156) that the similarity of plumage in *Platyspiza, Camarhynchus,* and *Cactospiza* is the result of convergent evolution. If, as essentially all modern researchers agree, the Galápagos finches are a monophyletic group (i.e., all derived from a single ancestor), Bowman's hypothesis would necessitate an initial divergence of plumages after colonization, followed by convergence. I cannot come up with a reasonable selective scheme to produce divergence and subsequent convergence in these plumages. Instead these finches seem clearly to be diverging both in plumage and in bill shape and size, into different habitats and life styles.

For example, although *G. magnirostris* and *Certhidea* are by themselves very different from each other, even these extremes can be united by a gradational series of intermediates. Further, the juvenal plumage of *Certhidea* is similar to that in other Galápagos finches, being olive-brown on the dorsum and vaguely streaked on the throat, breast, and upper belly. If *G. magnirostris* and *Certhidea* were the only finches in the Galápagos, one would almost surely assign them to a different genus. Their union through intermediate taxa and individuals, however, argues for congeneric status for Galápagos finches, as does their uniformity of breeding ecology and behavior. Thus I synonymize *Camarhynchus* Gould 1837, *Certhidea* Gould 1837, *Cactospiza* Ridgway

1897, and *Platyspiza* Ridgway 1897, with *Geospiza* Gould 1837. Because the Galápagos finches (*Geospiza*) are so similar in osteology and plumage to *Pinaroloxias* and *Volatinia,* I further regard *Pinaroloxias* Sharpe 1885, and *Volatinia* Reichenbach 1850, as synonyms of *Geospiza* Gould 1837.

I fully realize that this generic treatment will be controversial and may not be followed by many ornithologists, who would prefer instead to abide by the traditional generic limits of Swarth, Lack, and Bowman. With all respect to these and other researchers who have studied Darwin's finches, I conclude that an objective survey of the anatomy of Darwin's finches simply does not permit recognition of more than one genus. My treatment stresses the close relationship among these finches, which is masked by their maintenance in separate genera.

Summary

Darwin's finches have been the subject of a variety of systematic, evolutionary, and ecological studies since the time of Charles Darwin, yet there has never been a thorough attempt to determine their relationships to birds outside of Cocos Island and the Galápagos. On the basis of strong similarities in osteology and plumage, the Neotropical Blue-black Grassquit, *Volatinia jacarina,* appears to be so closely related to Darwin's finches that I propose it to be the species that singly gave rise to the entire radiation of Darwin's finches. Among all Darwin's finches, the Cocos Finch (*Pinaroloxias*) and the small Galápagos ground finches (*Geospiza nebulosa, G. fuliginosa*) are the most similar in plumage and osteology to *V. jacarina.* My review of other hypotheses of relationships of Darwin's finches shows that no other proposed relative, including the often-mentioned *Tiaris* and *Melanospiza,* is as similar to Darwin's finches as is *Volatinia.*

I believe that *Volatinia* colonized Cocos and the Galápagos independently from the mainland at some time late in the Quaternary Era. It is very unlikely that the Galápagos or Cocos would have been inhabitable by land birds before 1–2 million years ago, and the actual colonizations by *Volatinia* probably occurred even later. The close relationship of *Volatinia* to Darwin's finches is further evidence for a South American derivation of the fauna and flora of the Galápagos, whose nearest relatives are not in the West Indies.

I regard *Volatinia* and all species of Darwin's finches, both on the Galápagos and Cocos Island, to be members of a single, expanded genus *Geospiza,* since no single species or group of species within this assemblage is clearly distinct from any of the others.

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