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# Notes on Rare Species of *Munidopsis* (Anomura: Galatheidae) and *Ethusina* (Brachyura: Dorippidae) Collected by the USNS Bartlett in the Venezuela Basin, Caribbean Sea

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ABSTRACT. — Trawling in bathyal and abyssal depths of the Venezuela Basin by USNS BARTLETT produced 107 specimens in four species of the anomuran genus *Munidopsis* (Galatheidae), and 6 specimens of the brachyuran crab *Ethusina abyssicola* (Doripiidae). Taxonomic analysis shows that *Munidopsis aries* (A. Milne Edwards 1880) is a senior synonym of *Munidopsis sundi* Sivertsen and Holthuis 1956, and that *Munidopsis geyeri* Pequegnat and Pequegnat 1970 is not synonymous with *Munidopsis subsquamosa* Henderson 1885 as recently suggested by Ambler (1980). Biological data on gut contents, sediment preference, and parasitism are provided for these species, as well as for *Munidopsis bermudezi* Chace 1939 and *Munidopsis crassa* Smith 1885. The question of deep sea basin endemicity is considered in relation to the known Atlantic distribution of the species; primary isolating mechanisms seem to be both geological and chronological in origin. [abyssal, bathyal, Decapoda, Dorippidae, *Ethusina*, Galatheidae, *Munidopsis*, Venezuela Basin, zoogeography]

During October and November 1981 the U.S. Navy research vessel USNS BART-LETT conducted a series of deep water trawls at a 3-station site in the Venezuela Basin (Fig. 1), as part of a longer term study on the hydrography, geology, biology, and selected oceanographic parameters in this region. The bathyal and abyssal benthic and pelagic decapod crustaceans comprised a substantial portion in several trawls over 3000 m in depth. Members of at least 11 families were represented in these collections, and many of the species were rare forms, known from few individuals.' Many of the individual specimens were obtained in excellent condition, a consequence of small siliceous sponges protecting the crustaceans from damage during trawling operations.

Systematic and ecological studies were carried out on each of the families obtained,

and this is the first of a series of reports on the taxonomic, zoogeographic, and ecological relationships of the decapod crustaceans from the bathyal and abyssal waters of the Venezuela Basin. Here I report on anomuran and brachyuran crabs. Future reports will deal with epibenthic and benthic families Polychelidae, Crangonidae, Glyphocrangonidae, Penaeidae, and Aristeidae, and also the Oplophoridae, Nematocarcinidae, Pasiphaeidae, and Sergestidae, most of which inhabit midwater areas over the Basin.

The crab material collected from USNS BARTLETT, although sparse, nevertheless contained rare and interesting material from a region heretofore little explored. The Galatheidae (107 specimens) were represented by a single genus, *Munidopsis*, and 4 species. The dorippid crab genus *Ethusina* (6 specimens) was represented by a single species.

Although it is somewhat surprising that more anomuran or brachyuran crabs were not collected, the samples obtained from the

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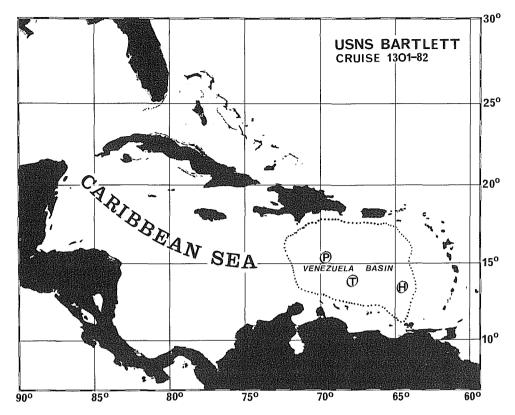


FIG. 1. Map of the Caribbean Sea showing the general location of the pelagic (P), hemipelagic (H) and turbidite (T) sediment areas within the Venezuela Basin. USNS BARTLETT stations were conducted in these areas. Dotted line marks the approximate boundary of the 2000 fm line, as determined from H.O. chart No. 1290.

BARTLETT probably are representative of the trawling areas. Trawl samples were almost always very ample and rich in both benthic and midwater vertebrates and invertebrates, and included a wide size range. Judging from the numerous polychelid lobsters, penaeid shrimp, and aristeid shrimp found in every benthic tow, galatheid and dorripid crabs are a small part of the total decapod fauna in the Venezuela Basin. Their relative importance within this fauna, however, is probably greater than their numbers indicate.

## MATERIALS AND METHODS

All of the material was taken using a 45 ft balloon net shrimp trawl, with 1.5 inch

stretch mesh net, and 0.5 inch stretch mesh in the cod. Selected examples of specimens were isolated immediately from the trawl catch in pre-cooled (5° C) surface seawater (36-37% salinity) obtained in situ prior to trawl operations. This material was usually photographed within 5–15 minutes of arriving on deck, using either Ektachrome 400, or Tungsten flash color-corrected film. Additional notes on color and morphological features were made at this time. Specimens were then preserved in 70% etoh and stored in plastic bags inside large specimen containers under air conditioning until shipped to the laboratory.

Measurements were made on shore using dial calipers to record carapacial and ab-

Sta- tion	Date	Coordinates (gear on bottom)	Depth (m)	Sediment type	Species
36	25-26 Oct	15°07.37'N, 69°08.18'W	3952-4044	Pelagic	Ethusina abyssicola
37	26-27 Oct	15°04.51'N, 69°08.34'W	3995-4095	Pelagic	Munidopsis aries
38	27 Oct	15°08.76′N, 69°13.20′W	3934-4013	Pelagic	M. aries, bermudezi, crassa, E. abyssicola
39	27–28 Oct	15°08.93'N, 69°13.33'W	3993–4064	Pelagic	M. aries, bermudezi, crassa
40	28 Oct	15°05.60'N, 69°11.48'W	3957-4013	Pelagic	Ethusina abyssicola
58	04 Nov	13°42.50'N, 67°41.08'W	4044	Turbidite	M. crassa
60	06 Nov	13°48.13'N, 67°46.92'W	4046	Turbidite	M. crassa, E. abyssicola
62	07 Nov	13°50.76'N, 67°37.17'W	5050-5055	Turbidite	M. crassa
63	08 Nov	13°49.09'N, 67°55.00'W	5046	Turbidite	M. crassa
64	08 Nov	13°48.25'N, 67°37.68'W	5046	Turbidite	M. crassa
65	09 Nov	13°51.80'N, 67°52.40'W	5046	Turbidite	M. crassa
87	25 Nov	13°36.60'N, 64°46.20'W	3481-3517	Hemipelagic	M. bermudezi
88	26 Nov	13°33.60'N, 64°46.90'W	3517–3549	Hemipelagic	M. bermudezi, M. geyeri
90	26 Nov	13°26.90'N, 64°42.70'W	34223464	Hemipelagic	M. bermudezi, M. geyeri
91	27 Nov	13°27.64'N, 67°47.56'W	3459–3507	Hemipelagic	M. bermudezi, E. abyssicola
92	28 Nov	13°30.60'N, 64°44.90'W	3475-3517	Hemipelagic	M. aries, M. bermudezi
93	28 Nov	13°32.30'N, 64°40.90'W	3411-3459	Hemipelagic	M. bermudezi
94	28–29 Nov	13°32.20'N, 64°42.00'W	3427-3475	Hemipelagic	M. bermudezi
96	30 Nov	14°16.70'N, 67°06.20'W	5059	Turbidite	M. crassa
97	01 Dec	14°34.10′N, 67°26.30′W	5055-5060	Turbidite	M. crassa
99	03 Dec	14°51.70′N, 67°27.80′W	4956–4997	Turbidite	M. crassa

TABLE 1. Station data, bottom characteristics and galatheid and dorippid crab species from USNS BARTLETT Cruise 1301-82, October–December 1981.

dominal measurements, and included rostral carapace length (Rcl), carapace length (cl), carapace width (cw), and total length (tl). All identifiable material was sexed and weighed on a Mettler automatic balance to the nearest 0.1 g. Gut contents were analyzed in selected specimens by excising a rectangular piece from the gastric region dorsally, removing the stomach, and making a smear slide of gut and contents. Ingested material was identified as far as possible to a recognizable taxonomic level, and percent content of identifiable items was estimated from the smear slide. There is no way to be certain, however, what percentage of gut contents are indicative of total ingested material because many (if not all) specimens may have regurgitated stomach contents either during collection, in the water column on the way up, on the deck of the ship, or when placed in preservative. Moreover, many specimens may continue to feed in the trawl during capture, so that the ingested items may reflect adventitious feeding instead of what had been eaten in situ.

Specimens will be deposited at the Academy of Natural Sciences of Philadelphia (ANSP), National Museum of Natural History, Washington D.C. (USNM), Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), British Museum, Natural History (BMNH), and the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF). In addition, a voucher se-

ries of specimens will be returned to Naval Ocean Research and Development Activity (NORDA), code 334, NSTL Station, Bay St. Louis, Mississippi.

For the galatheid and dorippid crabs discussed here, carapace measurements consist of Rcl for the Galatheidae, and  $cl \times cw$  for the Dorippidae. Rcl was measured from the tip of the intact rostrum to the posterior dorsodistal margin of the carapace, cl was measured similarly from the most advanced frontal margin, and cw was taken across the widest part of the carapace.

Information for each USNS BARTLETT station where taxa considered here were collected is provided in Table 1.

# FAMILY GALATHEIDAE SAMOUELLE 1819

# Genus Munidopsis Whiteaves 1874

Munidopsis aries (A. Milne Edwards 1880)

- Orophorhynchus aries A. Milne Edwards 1880: 58. A. Milne Edwards and Bouvier 1894: 209, 223, 284, 286 [discussion], 287 [key]; 1897: 2 [table], 111, pl. 9, figs. 7–11, pl. 10, figs. 1–2; 1900: 340 [discussion]. Faxon 1895: 82 [designation of species as type of genus].
- Munidopsis aries: Benedict 1902: 316 [listed]. Doflein and Balss 1913: 175 [listed], 177 [table]. Chace 1942: 70 [discussion], 74 [key]. Pequegnat and Pequegnat 1970a: 139 [key]; 1971: 5 [key], 21 [discussion], fig. 12B. Not Munidopsis aries: Ambler 1980: 17, 30 [table, graph], 31 [discussion] [= Munidopsis albatrossae Pequegnat and Pequegnat 1973].
- *Munidopsis sundi* Sivertsen and Holthuis 1956: 44, pl. 4, figs. 2 [not 3], 4. Pequegnat and Pequegnat 1971: 7 [key], 22, fig. 13; 1973: 163 et seq., fig. 3.
- Munidopsis n. sp.: Murray and Hjort 1912: 420 [fide Sivertsen and Holthuis 1956, p. 44].

MATERIAL EXAMINED. Stn 37, 1º juv, 26.7 mm, RMNH D00000;<sup>1</sup> Stn 38, 1å, 1å molted carapace pieces, ca. 80 mm (rostrum broken in whole specimen, molt not measured), AHF 2490-01, BMNH 1983-355; Stn 39, 1å, 1å juv, 86.0 and 44.2 mm, respectively, USNM 204591; Stn 92, 1å, 82.8 mm, NORDA.

REMARKS. The 3 largest males measured 134.4 to 148.8 mm total length, and well within the size range noted for two speci-

mens listed by Pequegnat and Pequegnat (1971) as M. sundi, but not nearly as large as the female holotype (218 mm tl) described by Sivertsen and Holthuis (1956) as M. sundi. As they have suggested, the species may well be the largest galatheid known.

DISCUSSION. Munidopsis aries was previously known from the male juvenile holotype described by Milne Edwards in 1880 from off the Lesser Antilles and three adult specimens later described or identified as M. sundi. The latter specimens include the female holotype of *M. sundi* (102 mm Rcl, 218 mm tl) collected south of the Azores which is the largest specimen known. One large male (88.5 mm Rcl, 162 mm tl) from the Colombia Basin and one ovigerous female (119 mm Rcl) from the northwestern Gulf of Mexico were reported by Pequegnat and Pequegnat (1973). The report of M. aries off the Oregon coast by Ambler (1980) is based on a specimen of a juvenile female (USNM 171346) of M. albatrossae (holotype, USNM 141453). Although Ambler recognized M. sundi and M. albatrossae were similar to *M. aries*, she failed to appreciate their exact relationships.

A comparison of the juvenile material from the BARTLETT collections with literature descriptions and illustrations of M. aries and M. sundi (Milne Edwards 1880; Milne Edwards and Bouvier 1897; Sivertsen and Holthuis 1956; Pequegnat and Pequegnat 1971) show very close agreement. More importantly, there are no appreciable differences between the BARTLETT material and the holotype of *M. aries* (MCZ 4761, see Fig. 2) that cannot be attributed to variations caused by age. The chief morphological changes appearing in growth are in the granulation and spination development on the anterior and anterolateral carapace margins, with the younger forms showing fewer, less crowded spines, and having less marked marginal crenulation than the older. The ontogenetic progression from juvenile to adult is easily seen in BARTLETT specimens, and in the mate-

<sup>&</sup>lt;sup>1</sup> Catalogue nos. for Rijksmuseum specimens were unavailable at printing deadline.

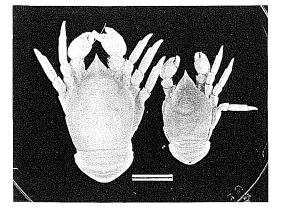


FIG. 2. Munidopsis aries (A. Milne Edwards). Left, 9 juv, USNS BARTLETT Cruise 1301-82, Stn 37, 26– 27 October 1981, 15°04.56'N, 69°08.34'W, 3979–4078 m, RMNH D00000;' right, HOLOTYPE & juv, USCS BLAKE, Stn 236, off Bequia, 1591 fm (2912 m), MCZ Harvard 4761. Scale line equals 10 mm.

rial, descriptions, and illustrations discussed above.

COLOR. Freshly collected specimens were pearly white, with pale golden yellow eyes, apparently lacking a darkened cornea. The carapace, abdomen, and pereopods had scattered golden setae, the latter forming a fine, bushy comblike tuft on the propodi of the first two walking legs.

ECOLOGY. Munidopsis aries was collected within the Venezuela Basin exclusively on pelagic carbonate sediments, with the exception at Stn 92 where a single male occurred on hemipelagic sediments (Table 1). It was never taken on turbidite sediments, and thus may be excluded from such sediments usually found about 5000 m deep or deeper. The species was found with Munidopsis bermudezi Chace and M. crassa Smith (q.v.).

GUT CONTENTS. Single male specimens from Stn 38 and 92 had empty foreguts but some material in the hindguts. The male from Stn 38 had large amounts of very finely divided and triturated fragments of plant and other fibrous matter, foraminiferans, siliceous sponge and holothurian spicules, and what appared to be fragments of wood. In the male from Stn 92 the material was a very finely divided, flocculent amorphous mass in which little could be distinguished. Identifiable animal remains appeared as a substantially smaller fraction than did plant or detrital material in both animals. The chelae of this species are strongly spatulate at the tips, and rimmed with small toothlike crenulations. They appear to be scraping and grasping claws rather than armed for rapacious predation.

DEPTH AND DISTRIBUTION. The USNS BARTLETT specimens were trawled in 3475-4095 m. Literature records indicate a depth of 2615 m off of the Azores (holotype of M. sundi), about 3200 m off Bequia, Lesser Antilles (holotype of *M. aries*), and about 4151 m in the Colombia Basin (Pequegnat and Pequegnat 1971). The eastern Pacific analog, M. albatrossae is known from off Oregon, the lower Baja peninsula, and Central America. The present distribution of M. aries is predominantly in deep Atlantic waters, from the eastern Atlantic to the northwestern Gulf of Mexico, and the Colombia and Venezuela Basins of the Caribbean Sea. There are no records of other possible analogs from the Indo-West Pacific, but their occurrence would not be surprising.

## Munidopsis bermudezi Chace 1939

Munidopsis bermudezi Chace 1939: 46; 1942: 73 [key], 83, figs. 29, 30. Sivertsen and Holthuis 1956: 44, pl. 4, fig. 3 [not fig. 2 as listed]. Pequegnat and Pequegnat 1970a: 139 [key], 145, figs. 5-1, 5-8, table 5-2; 1971: 5 [key], 22. Türkay 1975: 68, fig. 4a, b. Laird et al. 1976: 462, 463. Ambler 1980: 22 et seq. [discussion]. Munidopairs Marguere and Minet 1012, 420 [6 Ja Simon 2013]

Munidopsis: Murray and Hjort 1912: 420 [fide Sivertsen and Holthuis 1956: 44].

MATERIAL EXAMINED. **Stn 38**, 299, 23.1 mm, carapace missing on second, AHF 2490-02; **Stn 39**, 1å, 399, 38.4 mm, 29.8–35.0 mm, respectively, NORDA; **Stn 87**, 4åå, 19 juv, 24.4–36.4 mm, 7.0 mm, respectively, BMNH 1983-354; **Stn 88**, 1å, 24.7 mm, USNM 204592; **Stn 90**, 4åå, 699, 14.2–40.9 mm, 12.7–39.7 mm, respectively, ANSP CA4530; **Stn 91**, 5åå, 19, 31.1–

45.1 mm, 39.6 mm, respectively, AHF 2492-01; **Stn** 92, 46ô, 599 (2 ovig), 30.5-40.7 mm, 18.2-36.3 mm, smallest ovigerous 9 33.0 mm, respectively, USNM 204593; **Stn 93,** 1ô, 299 (1 ovig), 1 neuter, 30.7 mm, 27.0 mm, 29.0 mm (ovig), 35.9 mm, respectively, RMNH D00000;<sup>1</sup> **Stn 94,** 4ôô, 299 (1 ovig), 22.0-38.8 mm, 31.8 (ovig)-33.7 mm, respectively, RMNH D00000.<sup>1</sup>

REMARKS. *M. bermudezi* is easily distinguished from most other Atlantic *Munidopsis* in having a noticeably furred carapace and abdomen, 2 strong gastric tubercles or spines, and hirsute chelipeds much shorter than the body. All the specimens agreed well with Chace's (1942) description and illustration. Many of the specimens, however, had more than a single ventral spine on the cheliped ischium (up to 6 or 7 in some cases), but this was the only notable difference from Chace's material, and is undoubtedly a consequence of the few individuals available to him when he made his original description.

The only specimen seen parasitized, a female (31.4 mm) from Stn 92, had what appeared to be a large (?commensal) hydroidlike growth on the ventral surface of the abdomen. Another obviously fully grown specimen (Stn 93) had no gonopores or male pleopods, and appeared to be anatomically (although not necessarily functionally) neuter. This might have been a previously parasitized specimen exhibiting the latent effects of parasitic castration; it appeared normal in other respects.

*Munidopsis bermudezi* begins to exhibit sexual characters at a very small size, with females easily distinguished by gonopores at 12.7 mm Rcl and males by pleopod differentiation at 14.2 mm Rcl.

DISCUSSION. The species is rather rare, being known previously from 8 specimens. Ambler (1980) erected a new species, *Munidopsis cascadia*, for a series of specimens from the Cascade Basin off Oregon in the eastern Pacific that closely resemble *M. bermudezi*, but the eastern Pacific species is not as spiny, and the carapace appears more rounded and not as angular as in the Atlantic form. It also seems to be a generally larger crab. The 2 species are apparently eastern Pacific (*M. cascadia*) and Caribbean Atlantic (*M. bermudezi*) analogs.

COLOR. *M. bermudezi* is cream to ivory white underneath a dirty brown or gray tomentum, the latter colored by the type of sediment that the animal inhabits.

ECOLOGY. Mayo (1974) listed bottom characteristics for the material she examined as being clay, or with sponges and solitary corals. The BARTLETT material was taken on pelagic and hemipelagic sediments; the species was not collected on turbidites.

GUT CONTENTS. A male and female each, from stations 39 and 91 (NORDA and AHF 2492-01, respectively) were examined. Stn 39 was a pelagic sediment area and the guts of both the male and female specimen were packed with a dark brown amorphous mass. In the male this consisted of detrital particles and some small amount of shredded plant matter, an occasional spicule (holothurian), and several small setae. The female had what appeared also to be shredded plant material and an occasional sponge or holothurian spicule. The male from the hemipelagic station (91) had a nearly empty gut with small amounts of unidentifiable matter; the female from the same station had a gut packed with dark brown flocculent material in which was interspersed numerous siliceous sponge spicules. The finely divided and triturated material seen in the guts of these four specimens is not surprising, given the extremely well-developed gastric mill in this species.

DEPTH AND DISTRIBUTION. The species occurs in waters 2434–3020 m (1130–1650 fm) deep off southern Cuba, 2750 m off the Bahamas, 3119 m (1733 fm) off the Azores (fide Holthuis and Sivertsen 1956 for a 69 mm (tl) specimen first recorded by Murray and Hjort 1912), 3240+ m in the Gulf of Mexico, 3400–4000 m in the Venezuela Basin, and 5180 m off the Virgin Islands. The species is thus rather widely distributed in the Atlantic Ocean and relatively more common than some other *Munidopsis*.

# Munidopsis crassa Smith 1885

Munidopsis crassa Smith 1885: 494; 1886: 645, pl. 4.
A. Milne Edwards and Bouvier 1894: 275 [key]; 1899:
82, 85 [discussion]. Benedict 1902: 276 [key], 318
[listed]. Fowler 1912: 574. Doflein and Balss 1913:
176 [listed], 177 [table]. Bouvier 1922: 47, pl. 1, fig.
5. Nobre 1931: 187, 188 [discussion]; 1936: 117.
Chace 1942: 73 [key]. Gordon 1955: 237, text-figs.
1A, 2A, 2A', 3A, pl. 1. Sivertsen and Holthuis 1956:
46, pl. 4, fig. 1. Zariquiey Alvarez 1968: 268 [key],
269 et seq., fig. 95b. Miyake and Baba 1970: 89, 93,
94 [listed]. Pequegnat and Pequegnat 1970a: 139
[key], 151 [discussion]; 1971: 5 [key], 18, 19 [discussion].
Türkay 1975: 67, 68 [discussion], fig. 2a,
b. Ambler 1980: 24, 26, 27 [discussion].

MATERIAL EXAMINED. **Stn 38**, 1 juv, 9.3 mm, AHF 2490-03; **Stn 39**, 3&, 19 juv, 21.5–36.6 mm, 17.1 mm, respectively, BMNH 1983-352; **Stn 58**, 2&, 19 molt, 24.9, 29.8 mm, molt damaged, not measured, RMNH D00000;' **Stn 60**, 2&, 20.0, 43.2 mm, BMNH 1983-357; **Stn 62**, 5&, 19, 23.9–37.3 mm, 41.2 mm, respectively, ANSP CA4531; **Stn 62**, 1 intersex, 29.5 mm, USNM 204594; **Stn 63**, 2&, 499, 18.6, 41.9 mm, 25.5– 53.1 mm, respectively, ANSP CA4532; **Stn 64**, 19, 28.2 mm, NORDA; **Stn 65**, 4&, 599 (3 ovig), 1 intersex, 36.4–45.2 mm, 41.2–57.1 mm (smallest ovigerous 9 48.6 mm), 38.5 mm, respectively, AHF 2491-01; **Stn 96**, 5&, 19, 28.7–57.7 mm, 42.2 mm, respectively, NORDA; **Stn 97**, 19 damaged, 24.7 mm, NORDA; **Stn 99**, 399, 17.4–47.8 mm, USNM 204495.

REMARKS. *Munidopsis crassa* appears to be moderately common and not as scarce in collections as other species in this report. The BARTLETT material all showed minor variation in the development of the gastric and anterolateral spines and tubercles, primarily in uneven sizing. In many of the specimens the short inner (mesial) spine on the eyestalk was extremely reduced or lacking altogether. Sivertsen and Holthuis (1956) noted this variation in their material from the Bay of Biscay, and drew attention to a similar absence in Bouvier's animal from the same area. The reduction or loss of this spine is not correlated with geography, however, because Mayo (1974) noted similar variation, and the BARTLETT material might have the mesial spinule well developed, reduced, lacking altogether, or present on one eye and absent on the other.

Another type of variation commonly seen is in the degree of curvature of the rostrum. which (based on comparison of literature records and BARTLETT specimens) may be nearly straight to distinctly upswept distally. As pointed out by Mayo (1974) Gordon (1955) addressed this problem in considering whether or not *M. crassa* was merely a variant of the Munidopsis subsquamosa complex from the Indo-West Pacific area and thus a more widely distributed but variable species. Gordon concluded that the forms should remain separate, an opinion with which I concur. Mayo's (1974, pp. 116, 117) illustrations admirably show the spination and rugosity that characterizes this form. It should be noted, however, that smaller juvenile specimens in the BART-LETT material look remarkably like Munidopsis geyeri Pequegnat and Pequegnat 1970a (q.v.) except for the presence of at least a minute but discernible mesial eye spinule, and the noticeably less prominent and less piliferous rugae that characterize that species. In juvenile material the rostral spine also shows a variable degree of curvature, but could always be characterized as more or less curved to upswept.

Kensley (1968), however, noted that the rostrum in the type specimen (USNM 8563) was nearly horizontal, and used this as one feature in distinguishing his new species, *Munidopsis barnardi* from *M. crassa.* I have also examined Smith's holotype, which is completely fragmented in the jar, but the rostral base and part of the rostrum proper does exhibit some slight curvature. Unfortunately, the rostral tip was not discernible among the debris in the jar.

I compared *M. crassa* to *Munidopsis tuft-si* Ambler 1980 (USNM 171336, 171337,

holotype and paratype, respectively). The two species are almost identical in their general range of variation in spination on the gastric region, and along the anterior and anterolateral margins of the carapace. Even the large raised rugae on the branchial and cardiac areas were nearly identical. However, as Ambler noted, the first anterolateral spine is about equal to the first lateral spine in her species, but is invariably smaller in M. crassa. Another feature that I noted is that the telson plate in M. crassa is often subdivided into more pieces (8-9 plus a small center piece) than in M. tuftsi (7 plus a center piece). The other characters listed by Ambler in her Table 5 show too much variability to be of much use in distinguishing between the species. Thus, locality data becomes important in determining the taxa.

DISCUSSION. Munidopsis crassa belongs to a complex of species which show some degree of morphological relationships, and include *M. subsquamosa* Henderson 1885, *M.* aculeata Henderson 1888 (as M. subsquamosa aculeata), and M. barnardi Kensley 1968. One problem is that although Henderson often described and illustrated his species well, he did not recognize as clearly the limits of morphological variation in delimiting his varieties, which has led to some confusion. Therefore, all of the material in the subsquamosa-aculeata-crassa-barnardi complex will eventually have to be re-examined to determine whether a single variable species is being treated (sensu Henderson), or several subspecies of *subsquamosa*, or 4 or more distinct and widespread species exist.

PARASITISM. Mayo (1974) found a single female specimen of M. crassa collected from south of the Caicos Islands in the southern Bahamas to be parasitized by a peltogastrid barnacle. She pointed out that no other records of parasitism existed for the species. In contrast, I found that M. crassa was the most heavily parasitized of all the BART-LETT galatheids. Of 45 specimens, 7 (583,

299, or nearly 15%) had either rhizocephalan or bopyrid parasites. One female (Stn 99) had a remarkable isopod parasite (Dajidae?) in the form of a small, sponge-like ball enclosing the distal antennular peduncular and flagellar articles. When cut slightly and pressed this sac (undoubtedly a highly modified female) emitted several small, embryonic or nearly developed manca-type larvae having long antennae. Another individual, the intersex specimen from Stn 62, carried an ?akentrogonid parasite, and had the pleura of the second abdominal somite ballooned laterally outward and twisted, instead of being directly obliquely ventrad as is normal in the species.

COLOR. Freshly collected material was glossy, ivory white. Live material did not noticeably exhibit the rusty tint on the pereopods that was noted by Bouvier (1922) in his eastern Atlantic material.

ECOLOGY. Mayo (1974) characterized the benthos where various specimens were taken as consisting of coral and cinders, sponges, globigerina ooze and grey mud and sand. The BARTLETT material was taken at stations having pelagic carbonate (few specimens) or turbidite sediments (the majority of the material, see Table 1), so the species is apparently not completely selective in regard to substratum, although clearly preferring turbidites over carbonates.

GUT CONTENTS. The 4 largest specimens from Stn 92 (NORDA), consisting of 3 males and 1 female, were examined. The contents of the completely packed guts consisted entirely of dark chocolate brown flocculent material in which was embedded numerous sharp axon-type spicules, suggesting *M. crassa* feeds predominately on sponges. Alternatively, the species may be a detrital feeder with large numbers of spicules adventitiously eaten during ingestion of sediments, but little of the plant and other detrital fibers seen in other members of the genus were present in the individuals examined. As in *M. aries* and *M. bermudezi*, the chelae are definitively spatulate with dentocrenulated margins along the gape, although the fingers in *M. crassa* are nearly twice as long in relation to the palm as those in the former 2 species. This type of cheliped seems well adapted for both scraping away the relatively soft sponge tissue, or spooning up the detrital material on the sea floor.

DEPTH AND DISTRIBUTION. Munidopsis crassa occurs from about 2514 m (Mayo 1974) to a maximum depth of 5275 m (Türkay 1975) with the majority of specimens falling within 3100-4800 m based on literature records. The species is the most widely distributed of those collected in this study, being found from off the eastern coast of the United States, the Gulf of Mexico, the Caribbean Sea including the Yucatan. Colombia, and Venezuela Basins, eastward across the Atlantic Ocean, and from the Azores, Canary Islands, the Bay of Biscay, and off Portugal (summary in Mayo 1974). Analogous species occur in the eastern Pacific (*M. tuftsi* Ambler 1980), the southeastern Atlantic off South Africa (M. barnardi Kensley 1968), and the Indian Ocean (M. aculeata Henderson 1888). The latter species also allegedly occurs in the eastern Pacific, comprising part of the type series described by Henderson, and noted from one of those specimens (Gordon 1955) and other material (Faxon 1895). Türkay (1975) described another closely related species, Munidopsis thieli from over 5300 m off the Spanish coast, and commented on the relative rarity of M. crassa in this area as opposed to the more abundant M. thieli.

Munidopsis geyeri Pequegnat and Pequegnat 1970

- Munidopsis geyeri Pequegnat and Pequegnat 1970a: 149, fig. 5-1, 5-9, 5-10a, b; 1971: 5 [key], 19. Ambler 1980: 13 [abstract], 26 et seq. [discussion].
- Munidopsis subsquamosa: Ambler 1980: 26 (Atlantic and eastern Pacific specimens and references) [not Munidopsis subsquamosa Henderson 1885].

MATERIAL EXAMINED. **Stn 88**, 1º, 33.1 mm, RMNH D00000;<sup>1</sup> **Stn 90**, 1*å*, 35.0 mm, BMNH 1983-353.

REMARKS. The species was previously known from 8 specimens. The 2 individuals in the BARTLETT material agree in every detail with Pequegnat and Pequegnat's original (1970) description, as well as the more expanded annotation provided by Mayo (1974). *Munidopsis geyeri* is easily separated from *M. crassa* Smith by the presence of only 2 spines on the gastric dorsum, and by the very noticeable piliferous rugae across the gastric, cardiac, and branchial regions of the carapace. These rugae are very similar to those seen in the porcellanid crab *Petrolisthes galathinus* (Bosc 1802) and its relatives.

DISCUSSION. Ambler (1980) synonymized M. geveri with M. subsquamosa Henderson 1885, noting that Mayo (1974) had previously suggested that such a course of action might be required when more material became available. However, the original description provided by Henderson (1885) and the expanded description and illustration given by the same author (1888) shows that the specimens from the Atlantic cannot be assigned to Henderson's taxon for the following reasons. The carapace is not "sparingly pubescent," none of the very distinct rugae ("scale-like tubercles") terminate in short stout spines near the rostral base, the gastric region bears only 2, not "several" spines, the cardiac area is quite distinct, rather than "indistinctly mapped out," the rostrum is clearly upswept and approximately  $0.4 \times$  the carapace length, and not "nearly horizontal," the lateral spine at the postcervical groove is directed obliquely, not "almost horisontal in direction," and the small, intraocular plate is more pentagonal, then rectangular in form. These differences are sufficiently distinct to warrant continued separation of M. subsquamosa from M. geyeri.

The relationships of M. geyeri and Muni-

Character	Munidopsis geyeri	Munidopsis pallida	Munidopsis subsquamosa
Carapace shape	Rectangular	Subrectangular	Subrectangular
Antennal spine	Less oblique	More oblique	Absent
carina	Continued imaginary line leaves carapace ahead of epibranchial spine	Continued imaginary line leaves carapace behind epibranchial spine	Character not applicable
Gastric spines	2	2	More than 2
Intra- and post- spinular squamae	In regular increasing rows; 1,1,2,3,3,4,6	In irregular increasing rows; not evenly spaced	Numerous and irregularly contiguous, not separated in rows
Ophthalmic spine	hthalmic spine Long, sharp Short, acute		Short, acute
Antennular spine	Upper about ¾ length of lower	Upper less than <sup>1</sup> /3 length of lower	No data available
Rostral spine	Distinctly upswept	Moderately to slightly curved	Nearly horizontal
Cardiac region	Distinctly delineated	Distinctly delineated	Indistinctly delineated

TABLE 2. Comparison of characters in 3 species of Munidopsis.

dopsis (Orophorhynchus) subsquamosa var. pallida Alcock 1894, and Munidopsis subsquamosa of Faxon (1895) are closer. All 3 taxa have 2 gastric spines (instead of several as in M. subsquamosa sensu stricto), and all have more clearly outlined cardiac regions than does Henderson's species. When Alcock and Anderson's (1895, pl. 13, fig. 7) illustration is examined, at first glance there seems to be little difference between Alcock's (1894) species and M. geveri. Even more interesting are Faxon's (1895) description and discussion of an eastern Pacific species attributed to M. subsquamosa, because they suggest that Alcock's Bay of Bengal form and the eastern Pacific form are the same. However, neither is assignable to M. subsquamosa Henderson, nor is M. geyeri synonymous with either.

A reassessment of Alcock's description and illustration of *M. subsquamosa* var. *pallida* shows that the differences delineated by Alcock are sufficiently distinct to raise his infraspecific taxon to full species; viz. *Munidopsis pallida* Alcock 1894. Benedict (1902) had already raised Alcock's variety to full specific status but he was not followed by other authors (e.g. Doflein and Balss 1913, p. 155).

Moreover, in comparing, the descriptions and illustrations of Alcock's and Faxon's material to M. geyeri it is easily seen that the former 2 species agree with each other in 2 important features, while jointly disagreeing in these same features with M. geyeri; namely, the number and arrangement of the squamae on the gastric region between and posterior to the gastric spines, and the presence and direction of the antennal spine carina on the anterior carapace margin. These and other differences are listed in Table 2.

I examined the holotype of *M. geyeri* Pequegnat and Pequegnat 1970 (USNM 128811), one of the specimens of *M. subsquamosa* of Faxon (USNM 21314), from the Gulf of Panama, and *M. subsquamosa* of Ambler (1980, USNM 171348; and see also below). This material was compared to *M. subsquamosa* Henderson (pl. 17, fig. 4) and concomitant description, and with Alcock's (1894, 1901) description, as well as to Alcock and Anderson's (1895) illustration (pl. 13, fig. 7). In M. geyeri, the squamae between the gastric spines progressing posteriad increase in a regular manner (1, 1, 2, 3, 3, 4, 6; the antennal spine carina is directed only slightly obliquely away from the carapace anterior margin, and an imaginary line continuing this carina posteriorly passes off the carapace ahead of the large epibranchial spine. In Faxon's specimen the squamae between the gastric spines form an irregular row progressing posteriad, the antennal spine carina is more obliquely directed with the imaginary line continuing this carina passing off the carapace behind the epibranchial spine. Alcock and Anderson's illustration shows M. pallida to also have irregularly increasing rows of squamae behind the gastric spines, and a clearly indicated antennal spine carina that passes (in an imaginary line) behind the epibranchial spine. Contrarily, in M. subsquamosa Henderson the squamae are all united, not separated into increasingly wider rows as seen in either M. geveri, M. pallida, or Faxon's species, and no antennal spine carina extends from the anterior margin of the carapace. Additional differences between the Pacific and Atlantic species are listed in Table 2.

Thus, Faxon's specimen seems identical to Alcock's M. pallida, but in no case can either form be identical to M. subsquamosa Henderson or M. geyeri Pequegnat and Pequegnat. Nor can M. geveri be synonymized with *M. subsquamosa* either sensu stricto or sensu lato. Instead, the conservative course of action that I take here is to synonymize Faxon's M. subsquamosa with Alcock's M. pallida, and thus to consider the latter to have a wide distributional range extending from the Bay of Bengal to the Bay of Panama. However, if eventual comparison of Alcock's material with Faxon's shows the American form to be distinct, then Faxon's specimen (and Ambler's material previously assigned to M. subsquamosa, but excluding *M. geyeri*) would need a new name, either as a subspecies of Alcock's taxon, or as a new species.

Finally, it is necessary to correct an error in assignment of type material made by Ambler (1980). Although she presented morphometric evidence that M. geveri (and by inference *M. pallida* Alcock?) were synonymous with M. subsquamosa Henderson, the alleged "holotype" of the latter species that she used for comparison is not Henderson's material or species. Instead, this is material considered by Faxon in his 1895 report (USNM 21314, 20 mm cl female, ALBATROSS Stn 3361, 6°10.0'N, 83°6.0'W, in the eastern Pacific between Mariato Point and Cocos Island, 1471 fm [2692 m]; fide Faxon 1895: 257). Henderson's material, on the other hand, was a male and 'the softened remains of another male,' 29 mm cl or 39 mm Rcl, HMS CHALLENGER Stn 237, off Yokohama, Japan, 1875 fm (3431 m). The described male was deposited in the British Museum and was designated as lectotype by Gordon in 1955. Thus, the only possible synonymization that could arise from Ambler's comparison is that of M. geveri to M. pallida Alcock, a course of action already discounted earlier. If, on the other hand, Faxon's M. subsquamosa proves to be a separate and new species as suggested above, it would undoubtedly be the eastern Pacific analog of *M. geveri* Pequegnat and Pequegnat,

PARASITISM. The female from Stn 88 was parasitized in the right branchial cavity by a large bopyrid isopod.

COLOR. A lustrous, almost alabaster white in living specimens, with golden eyes lacking dark corneal pigment; setae and fine hairs on the carapace and pereopods yellow-gold, especially prominent on the carapacial rugae.

ECOLOGY. Mayo (1974) listed the benthos off Haiti where some of her material was taken as consisting of yellow clay mud, with vegetable debris and rotten logs. The

BARTLETT material was taken only on hemipelagic sediment, with abundant sponge and holothurians present. The species appears to be quite rare in the area of the Venezuela Basin investigated by USNS BARTLETT, and is not common anywhere, with only 10 specimens now known in collections. Owing to the scarcity of material no gut contents analyses were made on either individual.

DEPTH AND DISTRIBUTION. Gulf of Mexico in approximately 3000 m (1600–1640 fm), upper Caribbean Sea off Jamaica and Haiti, near the Mexican Basin from about 2600– 3500 m, the Venezuela Basin in about 3500 m, and the Colombia Basin in 4151 m.

# FAMILY DORIPPIDAE MACLEAY 1838

## Genus Ethusina Smith 1884

### Ethusina abyssicola Smith 1884

- Ethusina abyssicola Smith 1884: 349, pl. 2, fig. 1, 1a; 1886: 606, 635 [listed]. Faxon 1895: 36, 37 [discussion]. Rathbun 1898: 615 [listed]; 1937: 91, fig. 21, pl. 26, fig. 1, pl. 27, fig. 1. A. Milne Edwards and Bouvier 1900: pl. 1, fig. 6 [figure in outline, not color]; ibid.: 30 et seq. [discussion]. Pequegnat and Pequegnat 1970b: 175, fig. 6-2. Manning and Holthuis 1981: 42 et seq. [discussion and partial synonymy].
- *Ethusa (Ethusina) abyssicola:* Doflein 1904a: 31; 1904b, pl. 13, figs. 1–2.
- *Ethusina abyssicola typica* Ihle 1916a: 360; 1916b: 147, 148 [listed and discussion].

Ethusina abyssicola dofleini Ihle 1916b: 147.

Not *Ethusina abyssicola:* Bouvier 1896: 66 [listed]; 1922: 53, 91, pl. 2, fig. 1. A. Milne Edwards and Bouvier 1899: 18, 19 [listed and discussion]; 1900: 29 [coloration of specimen in pl. 1, fig. 6, not outline]. Monod 1956: 85 [references in part] [= *Ethusina alba* (Filhol, 1884)].

MATERIAL EXAMINED. Stn 36, 19, 12.9 × 12.6 mm, NOR $\vec{D}$ A; Stn 38, 1 $\delta$ , 16.2 × 13.5 mm, USNM 204596; Stn 40, 19, 16.2 × 15.5 mm, ANSP CA4533; Stn 60, 299 (1 ovig), 15.5 × 14.8, 16.1 × 15.0 mm (ovig), BMNH 1983-356, RMNH D00000,' respectively; Stn 91, 1 $\delta$ , 17.1 × 14.2 mm, AHF 2492-02.

REMARKS. Smith (1884) described this species from 8 specimens, and since that time it has been sparingly collected, un-

doubtedly because of the great depths that it inhabits. The BARTLETT material agreed in most respects with Smith's original description, with only slight variation noted. However, the type of variation seen was consistent with that recorded by other authors, and was related to the prominence of the frontal region, and the development and angle of the outer orbital spinules. The frontal margin was, for the most part, characterized as truncated, but this truncation was more pronounced in some specimens than in others. More important, perhaps, was the fact that the outer orbital spines in every BARTLETT specimen were quite small (in some cases appearing as if eroded or broken), and all pointed directly, or nearly directly forward and not obliquely outward as noted in the specimens originally described by Smith.

DISCUSSION. It is precisely this type of variation, noted by A. Milne Edwards and Bouvier (1900), and Pequegnat and Pequegnat (1970b) that raises the possibility of a second species occurring within the range of E. abyssicola, or alternatively, that E. abyssicola is a variable form over a very wide distributional range. In reading the descriptions of closely related species such as E. faxoni Rathbun 1933, or E. challengeri Miers 1886, one is struck by the apparently wide range of variability in certain morphological features, notably in the frontal margin and orbital spination. Other authors have noted such variation as can be seen in the synonymies for such species (e.g. that of Garth and Haig 1971). Of equal importance, however, is the possibility that the genus *Ethusina*, as presently characterized, may overlap into the genus *Ethusa*. Presently, the major character separating the two genera seems to be whether the eyes are immovable (*Ethusina*) or movable (*Ethusa*), and Garth and Haig comment on this overlap. In another example, A. Milne Edwards and Bouvier (1900) pointed out that if E. challengeri is merely a simple variety of E.

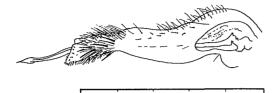


FIG. 3. *Ethusina abyssicola* Smith. Left gonopod of male, USNS BARTLETT Stn 38. Scale line equals 5 mm.

abyssicola, then the latter would have nearly world wide distribution. On the other hand, Pequegnat and Pequegnat (1970b) demonstrated that the most "typical" E. abyssicola in the R/V ALAMINOS material came from depths shallower than 2100 fms (3843 m), whereas specimens approaching E. faxoni in morphology were taken only at the latter depth. It is interesting to note that of all the 5 stations at which the BARTLETT material was collected, Stn 91 (3459-3507 m) was the shallowest, and the male specimen from here resembled "typical" E. abyssicola, while at Stn 36 (3952-4044 m) the female showed a close resemblance to E. faxoni. At the deepest station (Stn 60, 5046 m) the 2 females had nonprominent frontal regions and outer orbital spines reduced to a nub or completely absent. Whether or not these differences are significant is unknown. Certainly, no decision can be made as to their validity without a reassessment of all available specimens of Ethusina. Manning and Holthuis (1981), for example, have shown by use of gonopod characters and geographical records that many of the eastern Atlantic citations of E. abyssicola refer instead to E. alba (Filhol), and they provide a complete discussion of this synonymy. A gonopod from the male collected at Stn 38 is illustrated (Fig. 3) and was compared with that from a male in Smith's syntypic series (USNM 7119) and found to be identical. Rathbun's (1937) description of this appendage is quite accurate.

PARASITISM. The female from Stn 36 was

parasitized with a large rhizocephalan barnacle on the abdomen. The ovigerous female from Stn 61 carried several small eggs which were not noticeably developed, and this and all other specimens showed no noticeable parsitism. Pequegnat and Pequegnat (1970) made no mention of parasitism in their material. These authors did note a female from 765 fm (1400 m) carrying "a few advanced embryos." Perhaps egg size and number will prove of some aid in determining the taxonomic status and relationships of species within this very interesting genus.

COLOR. The specimens were all dirty creamy white when brought on board. Most were still at least partially covered with sediment. This contrasts with the color notes given by A. Milne Edwards and Bouvier (1900) of bluish with violet tint, legs and abdomen yellowish white, dactyls rose, now shown by Manning and Holthuis (1981) to be applicable to *E. alba* (Filhol) from the eastern Atlantic.

ECOLOGY. The BARTLETT specimens were collected from all 3 sediment types sampled in the Venezuela Basin. Smith (1884) recorded the benthos as being globigerina ooze, and A. Milne Edwards and Bouvier listed specimens from gray or soft white mud.

GUT CONTENTS. The female from Stn 36 (NORDA) had a gut packed with flocculent dark brown material interspersed with foraminiferans, radiolarians, and sponge spicules. Most of this material was broken but recognizable. The cheliped fingers are long thin and scissors-like but the maxillipeds are well-developed, suggesting that if detrital feeding is the main nutritional mode the latter appendages are probably more important than the chelipeds, which seem best adapated for cutting, not scooping.

DEPTH AND DISTRIBUTION. As noted by Faxon (1895), Milne Edwards and Bouvier (1900), and others, *Ethusina abyssicola* is the deepst living known brachyuran crab.

The TALISMAN specimens reported from 4060 m by Milne Edwards and Bouvier (1900) were the deepest previously known, but the 2 females from USNS BARTLETT Stn 61 at 5046 m extend the depth range nearly 1000 m deeper.

Following Rathbun (1937) and treating the various subspecies established by Ihle (1916a, b) merely as variants of a single, widely dispersed taxon, *Ethusina abyssicola* is known from the vicinity of Nantucket Shoals off New England southward to North Carolina, throughout the Gulf of Mexico except for the southeastern quadrant (Pequegnat and Pequegnat 1970b), now for the first time in the Caribbean Sea proper, and off Cape Frio, Brazil.

In establishing Filhol's *Ethusina alba*, Manning and Holthuis have restricted its distribution to the eastern Atlantic from north of the Azores to the Cape Verde Islands. This range encompasses records from A. Milne Edwards and Bouvier (1899, 1900) previously assigned to *E. abyssicola*. However, Doflein (1904a) listed a specimen from off Zanzibar and believed that *E. challengeri* specimens attributed to that species by Faxon (1895) were simply variants of *E. abyssicola*. If so, the distribution of the species would be western Atlantic, eastern Pacific, and the Indo-Pacific Ocean and the Sea of Japan (see also Ihle 1916b).

## ZOOGEOGRAPHICAL CONSIDERATIONS

The question of deep basin endemicity among the galatheidean and brachyuran species collected by USNS BARTLETT remains unresolved. All of the species in this report have wide distributional ranges, but mostly within their respective ocean (i.e. the Atlantic, and disregarding for the moment the possible cosmopolitan range of *Ethusina abyssicola*). It is apparent from the literature records, and an examination of the limited amount of BARTLETT material, that the 4 galatheid species are not restricted to any major ocean basin. The rarest species, *Munidopsis geyeri*, for example, has been recorded from basins in the Gulf of Mexico (Pequegnat and Pequegnat 1970a), and in adjacent basins in the Caribbean Sea (Mayo 1974, and this study). Similarly, the distributions of *Munidopsis crassa*, *M. bermudezi*, and *M. aries* also extend from basins in the eastern to the western Atlantic Ocean.

It is, however, interesting to note the close morphological relationships of those closely related species from the eastern Pacific that are presently separated by the presumably impassable Central American isthmus barrier (viz. M. tuftsi, M. cascadia, and perhaps M. pallida, assuming that Faxon's specimen remains synonymous with the latter), with their Atlantic counterparts. The eastern Pacific forms also show a relatively wide latitudinal distribution, occurring from off of Oregon southward to off Central America and beyond. The data available for both groups suggest that ecological conditions do not seem to be limiting or isolating because the Pacific-Atlantic analogues occupy relatively similar depth ranges and bottom substrata.

The primary isolating mechanism for speciation in these species-groups would seem to be geological and chronological. Such isolation may have begun to be important after the closing of the Caribbean-Eastern Pacific seaway some 3 million yr bp, but one cannot discount as an alternative (or perhaps corollary) hypothesis the possibility that such isolation may have already begun prior to the final closure. The very close morphological similarities seen in Eastern Pacific and Atlantic-Caribbean species further suggests that such isolating factors which were present have either been operational for only a relatively short time, or that speciation in deep sea populations of anomuran galatheids takes place relatively quickly once such mechanisms come into play.

It is hard to specify just how much gene

flow, if any, occurred or presently occurs between galatheid populations occupying adjacent basins (e.g. Colombia and Venezuela, or Venezuela and Mexican). Even harder to determine is how much exchange occurs between more widely separated populations (e.g. Caribbean basin species and those from the Azores region). It might be, given the relatively similar and constant conditions found in abyssal areas, that populations are under little pressure to diverge greatly, and what variation that does occur may be more in response to genetic drift and perhaps of little selective import. On the other hand, the clear divergence in morphological characters exhibited by the Eastern Pacific galatheids from the Atlantic-Caribbean relatives, implies that some significant factors are operating. But just what these are can only be speculative at present.

One means of providing gene dispersal, of course, is via larvae. Those specimens in the BARTLETT material which were ovigerous carried relatively large (greater than 1 mm) eggs. But as pointed out by Rabalais and Gore (in press) large egg size is not necessarily an exclusionary argument for advanced larval development, or even short developmental time. Yet if such larvae do hatch in an advanced state and undergo relatively brief developmental time, then they would probably not disperse far from the parental populations as long as they stayed close to the bottom, owing to the slow dispersive quality of deep sea currents. And if the species is barophilic to the extent that it cannot enter more shallow areas on the upper continental slope and shelf (as seems to be the case for the deep-sea genus Munidopsis as a whole, with only a few exceptions; see Mayo 1974), then each population may indeed be basin restricted both as adults and as larvae.

The observations made by numerous authors of noticeable, but heretofore considered "relatively minor" variation implies some degree of morphotypic plasticity in the species. As noted by these authors (Chace 1942; Mayo 1974; and others) the heterogeneity of the genus *Munidopsis* is bewildering and exasperating. The *Munidopsis subsquamosa* problem addressed earlier illustrates this situation.

What we may be observing, however, is not so much a series of fixed species-types occupying a variety of genera or subgenera, but perhaps more a situation of continuing incipient speciation and concomitant "subgenerization or generization" in these crabs, partly as a consequence of selection pressures on adults and larvae, and partly owing to ecological conditions (however minor the variant) within their respective basins. To this extent it would be extremely interesting to examine the various speciescomplexes electrophoretically to determine whether such variation is correlatable with geographical, geological, ecological, or some other factor, within each basin. Such deep sea basins may well function as abyssal "islands" with zoological boundaries delimited by conditions of increasingly shallow depths at the perimeters, increasingly warmer temperatures and even increasingly higher illumination. Barophilic, psychrophilic, photophobic animals such as Munidopsis may thus be effectively caged within their respective basins as adults, with larvae providing the only option to ride over the barriers.

Finally, in regard to the larval development of the various species, it would be of some importance (but not altogether surprising) to find that larval morphology varied between the individuals of the species of one basin population and the next. If such variation did occur it would support the concept of adult morphoplasticity noted above, and explain in some measure the variation noted in the adults, as well as indicate the extent of influence such variation might have in the process of species or subspecies (or even varietal) formation in the genus *Munidopsis* sensu lato. There is no denying that the genus today is characterized more by a morphospecies concept than by any other. This is a necessary but regrettable consequence of the limited material presently available for study.

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#### LITERATURE CITED

- ALCOCK, A. 1894. XXXV. Natural history notes from H.M. Indian Marine Survey Steamer 'Investigator,' commander R. F. Hoskyn, R.N., late commanding. Annals and Magazine of Natural History, series 6, 13: 321-334.
- . 1901. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala in the Indian Museum, being a revised account of the deep-sea species collected by the Royal Marine Survey Ship 'Investigator.' Trustees of the Indian Museum, Calcutta. iv + 286 pp.
- AND A. R. S. ANDERSON. 1895. Illustrations of the zoology of the Royal Indian Marine Surveying Steamer Investigator, under the command of Commander A. Carpenter, R.N., D.S.O., or the late Commander R. F. Hoskyn, R.N., and of Commander C. F. Oldham, R.N. Crustacea, Part III, plates IX-XV. (Calcutta)
- AMBLER, J. W. 1980. Species of Munidopsis (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters. Fishery Bulletin, U.S. Fish and Wildlife Service 78(1): 13–34.
- BENEDICT, J. E. 1902. Description of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of the known marine species. Proceedings of the United States National Museum 26(1311): 243–334.
- BOUVIER, E-L. 1896. Sur la classification, les origines et la distribution des crabes de la famille des Dorippidés. Bulletin de la Société Philomathique de Paris, 8<sup>me</sup> séries, 9: 54–70.
- ———. 1922. Observations complémentaires sur les Crustacés décapodes (abstraction faite des Carides, provenant des Campagnes de S.A.S. le Prince de Monaco). Résultats Campagnes de Sciences de Monaco 62: 3–106.
- CHACE, F. A., JR. 1939. Reports on the scientific results of the first Atlantis expedition to the West Indies under the joint auspices of the University of Havana and Harvard University. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 13(1): 31-54.
- 1942. Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The Anomuran Crustacea. I. Galatheidea. Torreia (11): 1–105.
- DOFLEIN, F. 1904a. Brachyura. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899, Bd. 6: xii + 314 pp.
- 1904b. Atlas. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899. Pls. 1–58.

--- AND H. BALSS. 1913. Die Galatheiden der Deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899, Bd. 20, lief. 3: 1–184.

- FAXON, W. 1895. The Stalk-eyed Crustacea. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapago Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut.-Commander Z. L. Tanner, U.S.N., commanding. XV. Memoirs of the Museum of Comparative Zoology at Harvard College 18: 1– 292.
- Fowler, H. W. 1912. The Crustacea of New Jersey. Annual Report of the New Jersey State Museum, 1911, part 2: 29–650.
- GARTH, J. S. AND J. HAIG. 1971. Decapod Crustacea (Anomura and Brachyura) of the Peru-Chile trench. Anton Bruun Report (6). Scientific results of the southeast Pacific Expedition (6): 6.3–6.20.
- GORDON, I. 1955. Crustacea Decapoda. Reports of the Swedish Deep-Sea Expedition, 2, Zoology (19): 239–245.
- HENDERSON, J. R. 1885. Diagnoses of the new species of Galatheidea collected during the 'Challenger' Expedition. Annals and Magazine of Natural History, series 5, 96: 407–421.
- . 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873–76. Report on the scientific results of the voyage of H.M.S. Challenger. Zoology 27(1): xi + 221 pp.
- IHLE, J. E. W. 1916a. Über einige von der Siboga-Expedition gesammelte Tiefsee-Brachyuren aus der Familie der Dorippidae und ihre geographische Verbreitung. Zoologische Anzeiger 46: 359–363.
  — . 1916b. Die Decapoda Brachyura der Siboga-Expedition. II. Oxystomata, Dorippidae. Siboga-Expeditie 39<sup>b</sup> 1: 97–158.
- KENSLEY, B. F. 1968. Deep sea decapod Crustacea from west of Cape Point, South Africa. Annals of the South African Museum 50(12): 283–323.
- LAIRD, C. E., E. G. LEWIS AND P. A. HAEFNER, JR. 1976. Occurrence of two galatheid crustaceans, *Munida forceps* and *Munidopsis bermudezi*, in the Chesapeake Bight of the western North Atlantic Ocean. Fishery Bulletin, U.S. Fish and Wildlife Service 74(2): 462–463.
- MANNING, R. B. AND L. B. HOLTHUIS. 1981. West African brachyuran crabs (Crustacea: Decapoda). Smithsonian Contributions to Zoology No. 306: xii, 1–379.
- MAYO, B. S. 1974. The systematics and distribution of the deep-sea genus *Munidopsis* (Crustacea, Galatheidae) in the western Atlantic Ocean. Unpubl. dissertation, Univ. Miami. xii + 432 pp.

- MIERS, E. J. 1886. Report on the Brachyura collected by H.M.S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of H.M.S. Challenger, Zoology 17: xlix + 362 pp.
- MILNE EDWARDS, A. 1880. Reports on the results of dredging under the supervision of Alexander Agassiz in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the United States coast survey Steamer "Blake," Lieut.-Commander C. D. Sigsbee, U.S.N., Commanding. VIII. Études préliminaires sur les Crustacés. Bulletin of the Museum of Comparative Zoology at Harvard College 8(1): 1–67.

— AND E-L. BOUVIER. 1894. Considérations générales sur la famille des Galathéidés. Annales des Sciences Naturelles, Zoologie et Paléontologie 16: 191–327.

- AND ———. 1897. Reports on the results of dredging under the supervision of Alexander Agassiz in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the United States coast survey steamer "Blake," Lieut-Commander C. D. Sigsbee, U.S.N., Commanding. XXXV. Description des Crustacés de la famille des Galathéidés recueillis pendant l'Expédition. Memoirs of the Museum of Comparative Zoology at Harvard College 19(2): 1–141.
- AND 1899. Crustacés Décapodes provenant des campagnes de l'Hirondelle (supplément) et de la Princesse-Alice (1891–1897). Résultats des campagnes scientifiques accompliés sur son yacht par Albert I<sup>er</sup> Prince Souverain de Monaco, Fasc. XIII, Brachyures et Anomoures: 1– 106.
- AND ———. 1900. Crustacés Décapodes. Première partie. Brachyures et Anomoures. Expéditions scientifiques du Travailleur et du Talisman pendant les années 1880, 1881, 1882, 1883: 396 pp.
- MIYAKE, S. AND K. BABA. 1970. The Crustacea Galatheidae from the tropical-subtropical region of West Africa, with a list of known species. Atlantide Report 11: 1–97.
- MURRAY J. AND J. HJORT. 1912. The depths of the ocean. Macmillan and Company, Ltd., London. xx + 821 pp.
- NOBRE, A. 1931. Crustaceos Decapodes e Stomatopodes marinhos de Portugal. Instituto de Zoologie, Universidad de Porto. iv + 307 pp.
- . 1936. Crustaceos Decapodes e Stomatopodes marinhos de Portugal. Fauna marinha de Portugal 4: 1–213.
- PEQUEGNAT, W. AND L. H. PEQUEGNAT. 1970a. Deepsea anomurans of superfamily Galtheoidea with descriptions of three new species. *In* W. E. Pequegnat and F. A. Chace, Jr. (eds). Contributions

on the biology of the Gulf of Mexico. Vol. 1, chap. 5, pp. 125–170. Texas A&M University Oceanographic Studies, Gulf Publishing Co., Houston.

AND — . 1970b. Deep-water brachyuran crabs. In W. E. Pequegnat and F. A. Chace, Jr. (eds). Contributions on the biology of the Gulf of Mexico. Vol. 1, chap. 6, pp. 171–204. Texas A&M University Oceanographic Studies, Gulf Publishing Co., Houston.

- AND ———. 1971. New species and new records of *Munidopsis* (Decapoda: Galatheidae) from the Gulf of Mexico and Caribbean Sea. Texas A&M Oceanographic Studies, supplement to volume 1. Contributions on the biology of the Gulf of Mexico. Gulf Publishing Co., Houston. 24 pp.
- AND . 1973. *Munidopsis albatrossae*, a new species of deep-sea Galatheidae (Decapoda. Anomura) from the eastern Pacific Ocean. Crustaceana 24(2): 163–168.
- RABALAIS, N. N. AND R. H. GORE. Abbreviated development in decapod larvae. *In* A. M. Wenner (ed). Crustacean growth. A. A. Balkema, Publ., Rotterdam (in press).
- RATHBUN, M. J. 1898. The Brachyura collected by the U.S. Fish Commission steamer Albatross on the voyage from Norfolk, Virginia to San Francisco, California, 1887–1888. Proceedings of the United States National Museum 21(1162): 567– 615.
  - 1933. Brachyuran crabs of Porto Rico and the Virgin Islands. Scientific Survey of Porto Rico and the Virgin Islands. New York Academy of Sciences 15(1): 1–121.

- 1937. The oxystomatous and allied crabs of America. Bulletin of the United States National Museum 166: vi + 278 pp.
- SIVERTSEN, E. AND L. B. HOLTHUIS. 1956. Crustacea Decapoda (The Penaeidea and Stenopodidea excepted). Reports of the scientific results of the "Michael Sars" North Atlantic Deep-sea Expedition, 1910, 5(12): 1–54.
- SMITH, S. I. 1884. Report on the decapod Crustacea of the Albatross dredgings off the east coast of the United States in 1883. Report of the Commission on Fish and Fisheries 10: 345–426.
- ———. 1885. On some new or little known decapod Crustacea, from recent Fish Commission dredgings off the east coast of the United States. Proceedings of the U.S. National Museum 7(31–32): 493–511.
- . 1886. Report on the decapod Crustacea of the Albatross dredgings off the east coast of the United States during the summer and autumn of 1884. Report of the U.S. Fish Commission 13: 605-706.
- TÜRKAY, M. 1975. Decapoda Reptantia aus dem Iberischen Tiefseebecken Auswertung der Fahrten 3 (1966) und 15 (1968) von F.S. "Meteor." "Meteor" Forschungs-Ergebnisse, Reihe D (20): 66– 70.
- ZARIQUIEY ALVAREZ, R. 1968. Crustaceos Decapodos Ibericos. Investigation Pesquera, Barcelona 32: xv + 510 pp.