NEW RECORDS OF *MIMILAMBRUS WILEYI* WILLIAMS, 1979 (CRUSTACEA: DECAPODA: BRACHYURA), WITH NOTES ON THE SYSTEMATICS OF THE MIMILAMBRIDAE WILLIAMS, 1979, AND PARTHENOPIDAE MACLEAY, 1838, SENSU GUINOT, 1978

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Abstract.—The family Mimilambridae was established by Williams (1979) to receive his new species *Mimilambrus wileyi*. The species is herein reported from several localities in Venezuela. The characters of *Mimilambrus* fit well within the definition of the subfamily Parthenopinae, family Parthenopidae MacLeay, 1838 (sensu Balss 1957) (equivalent to Guinot's (1978) Parthenopoidea). There is agreement in many morphological details, such as in the ventral spines, fingers and dentition of the chelipeds, and the form of the second male pleopod. Some characters like the ischio-meral articulation of the chelipeds and the articulation of segments 3 to 5 of the male abdomen, show a primitive condition. A comparison of the structures associated with respiration shows that the peculiar arrangement of afferent and efferent channels in *Mimilambrus* is merely a continuation of a trend already found in the more typical parthenopids. Placing this genus in a family of its own is thus unwarranted, and it should instead be included as a rather specialized genus with the rest of the parthenopids in the superfamily Parthenopoidea MacLeay, 1838, sensu Guinot, 1978.

Mimilambrus wileyi Williams, 1979, was described from two males and one female collected at Tobago, West Indies, and was placed by Williams in a new monotypic family, Mimilambridae, close to the family Parthenopidae MacLeay, 1838, sensu Balss, 1957. Guinot (1977a, 1978a, b, 1979), in her revision of Brachyuran classification, elevated the Parthenopidae to superfamily status. Bowman and Abele (1982) subsequently elevated the Mimilambridae to its own superfamily, Mimilambroidea, probably in accordance with the superfamilial method of classification proposed by Guinot (1977a, b, 1978a).

Williams (1979) suggested that his new family was intermediate between the traditional "oxyrhynchan" families Majidae and Parthenopidae (sensu Balss 1957), and

the traditional "oxystomatan" families Leucosiidae and Calappidae. The current evidence, however, suggests that both the Oxystomata and Oxyrhyncha, are in fact heterogeneous groups, and not 'good' taxa (Guinot 1977a, 1978a, b, 1979; Stevcić and Gore 1980). Within this context, a reexamination of the family Mimilambridae is of particular interest.

During the study of samples taken on the Venezuelan coast, several specimens of *Mimilambrus wileyi* were collected. Opportunity was taken to evaluate the characters used by Williams (1979) to differentiate his new family from the Parthenopidae sensu Balss, 1957. To this end, we have examined four American parthenopoids: *Parthenope agona* (Stimpson, 1871), *Platylambrus serratus* (H. Milne Edwards, 1834), *Leiolam-*

brus nitidus (Rathbun, 1901) and *Heterocrypta tomasii* da Costa, 1959; and five Indo-Pacific ones: *Daira perlata* (Herbst, 1790), *Daldorfia horrida* (Linnaeus, 1758), *Cryptopodia fornicata* (Fabricius, 1781), *Rhinolambrus longispinis* (Miers, 1879), and *Platylambrus echinatus* (Herbst, 1790). We have also used morphological data available in the literature whenever appropriate. The systematics of the Parthenopoidea sensu Guinot, 1978a, b, are also briefly discussed in relation to several other characters. The material cited is deposited in the reference collection of the Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, and the Zoological Reference Collection (ZRC) of the Department of Zoology, National University of Singapore.

Mimilambrus wileyi Williams, 1979

Mimilambrus wileyi Williams, 1979:400, Figs. 1–5.
Parthenope sp., Rodríguez, 1980:294, Fig. 70, Pl. 31A.

Material. — Punta Arenas de Pariche, Golfo de Cariaco, 10°32′N, 64°12′W, 12 Jul 1959; Luis R. Salazar: 1 male, cl. 26.3 mm, cb. 28.6 mm, exploratory fishing with shore net, shallow water (IVIC). — Between Margarita Island and the Venezuelan mainland, 8 km west of Isla Coche, 10°46′N, 62°50′W: 1 male, cl. 14.8 mm, cb. 16.2 mm, 9 fathoms (IVIC). — Paraguaná Península, north of Punto Fijo, 11°40′N, 70°10′W, 4 Mar 1982, G. Kremer & M. Bevilacqua: 1 male, cl. 29.7 mm, cb. 33.7 mm, 1 ovigerous, 1 spent female, cl. 25.6 and 30.5 mm, cb. 28.1 and 32.0 mm, respectively, between 10 and 17 fathoms (IVIC). (cb. measured at base of postero-lateral spines in all cases.)

Discussion

Our material agrees closely with Williams' (1979) original description. The eggs of our ovigerous female have a mean diameter of 0.32 mm (n = 15, largest 0.34, smallest 0.31 mm). The present records extend the range of the species to the north coast of South America and show that it is not an uncommon species.

The superfamily Parthenopoidea (essentially the Parthenopidae of Balss (1957) with the exclusion of the Eumedoninae Miers, 1879) has been subjected to considerable scrutiny recently. Their origins are poorly understood, and they appeared rather suddenly in the Middle Eocene (Glaessner 1969), some 45 million years ago. Most classifications have included them in the Oxyrhyncha, for they, like the majids and hymenosomatids, "have a general elongate-triangular, narrow fronted carapace and incomplete orbits which contrast strongly with the rest of the brachygnathous crabs" (Rice 1980:311). Acceptance of this systematic arrangement, however, is not unanimous. Flipse (1930) for instance, thought that the parthenopids were transitional between the Oxyrhyncha and the Cyclometopa. Guinot (1977a, b, 1978a, b), in her comprehensive review of Brachyuran systematics, dismantled the Oxyrhyncha, and elevated the Parthenopidae MacLeay, 1838, to their own superfamily, with the exclusion of the subfamily Eumendoninae Miers, 1879. Otherwise, they were essentially the Parthenopinae of Alcock (1895), Rathbun (1925), and Balss (1957). She recognized four groups within the Parthenopoidea: 1, With only the thoracic sternal sutures 4/5 and 5/6 interrupted and having the III B type of endophragmal skeleton (e.g., *Daldorfia* Rathbun, 1904). 2, With all the thoracic sternal sutures interrupted and having the III C type of endophragmal skeleton (e.g., *Parthenope* Weber, 1795). 3, Containing the genera *Daira* de Haan, 1833, and *Dairoides* Stebbing, 1920 (=*Asterolambrus* Sakai, 1938). 4, Containing the 'Parthénoxystomien' group (Guinot 1967a, 1978b), with the genera *Aethra* Leach, 1816, *Hepatus* Latreille, 1802, *Hepatella* Smith, 1869, *Osachila* Stimpson, 1871, and *Actaemorpha* Miers, 1878 (sensu Guinot 1967a, 1978b).

A new genus, *Sakaila* Manning & Holthuis, 1981, was subsequently included in Guinot's "Parthénoxystomien" group. Although she did not designate these groups as separate families, it may prove worthwhile to recognize each of these four groups as such, i.e., the families Daldorfidae, Parthenopidae s. s., Dairidae, and Aethridae respectively. All further references to these families in this paper will be used as defined above.

Guinot (1967b, 1977a, 1979) has also provided indications that the parthenopoids may have evolved from some xanthoid-like stock. In fact, the genera *Daira* and *Dairoides* are almost perfect intermediates for linking the xanthoids with the Daldorfidae and Parthenopidae s. s. The larval characters also suggest that the parthenopoids evolved from some xanthoid stock via the more primitive portunoid families (sensu Guinot 1978a, b) (Rice 1980, 1983) or that both the parthenopoids and portunoids evolved from the same xanthoid stock (Ng 1983).

The subfamily Eumedoninae Miers, 1879, formerly placed in the family Parthenopidae sensu Balss, 1957, is almost certainly not closely affiliated with the true parthenopoids, but is probably closer to the Xanthoidea (Serène, Tran, and Nguyen 1958), and may be related to (Serène 1968) or part of the Pilumnidae Samuelle, 1819, sensu Guinot, 1978 (Ng 1983). Recent work on the larvae of the eumedonine *Echinoechus pentagonus* (A. Milne Edwards, 1878) lends support to Ng's (1983) suggestion that the Eumedoninae be removed from the Parthenopoidea and affiliated with the Pilumnidae instead.

The family Parthenopidae s. s. forms a sharply defined and presumably monophyletic group, well characterized by the shape of the carapace and chelipeds. *Mimilambrus wileyi* shares with this family the following characters: heterotrematous gonopore arrangement (Guinot 1977a, b, 1978b, 1979; Saint Laurent 1980), carapace with frontal region narrow (the general outline is semicircular in *Mimilambrus* and several other genera, but more usually triangularly elongate or pentagonal), orbits distinct and complete, cardiac and gastric regions so deeply marked off as to make the dorsal surface of the carapace trilobed, pseudorostrum (sensu Stevcić and Gore 1980) simple (obscurely trilobed in *Mimilambrus* and some other species), second article of antennae small, short, not fused with the epistome or front, palp of the third maxilliped articulated at the antero-internal angle of the merus, chelipeds vastly longer and more massive than the ambulatory legs, and the second male pleopods relatively short.

Several characters that have been regarded as characteristic of the Mimilambridae are also not as definitive as they may initially appear. Williams (1979) gives diagnostic generic value to the articulation of segments 3 to 5 of the male abdomen. These segments do show a rather primitive condition in *Mimilambrus* since the articulation, although ankylosed, is still present as a thin line. In all parthenopoids, segments 3 to 5 are ankylosed (Flipse 1930; Ng 1983), but there is some variability as to whether the sutures are still distinct or not. In *Parthenope agona,* the sutures are still visible near the midline of the abdomen, while in *Platylambrus serratus,* they are completely absent. In the supposedly primitive *Daira* and *Dairoides,* the sutures are still relatively distinct. Whether the segments 3 to 5 are ankylosed or free is itself an important clue to the cohesiveness of the taxa, and also provides valuable information about their affinities. The ankylosed segments in all the members of the Parthenopoidea as recognized by Guinot (1978a, b) (including *Mimilambrus*) not only lends support to the exclusion of the Eumedoninae, in which all the segments are free, but also suggests that the parthenopoids have close phylogenetic links with the Portunoidea (sensu Guinot 1978a, b), as well as the more primitive xanthoids, like the Carpiliidae Ortmann,

1893. This relationship has in fact, already been suggested through the studies of their larvae (Rice 1980, 1983; Ng 1983). Williams (1979) also regards the first male pleopod as characteristic, but although it is certainly unusual, it could have been easily derived from ancestral parthenopid structures. In fact, *Cryptopodia concava* Stimpson, 1871 (Gore and Scotto 1979) and *Pseudolambrus triangula* (Stimpson, 1860) (Garth 1958) have very similar appendages, but their long subterminal spines are less well developed and the lateral hairs are still abundant.

The most important character that differentiates *Mimilambrus wileyi* from most Parthenopidae is probably the position and structure of the afferent channels which are located inside the buccal cavity, and the efferent channels, which are fused and discharge at the anteromedial part of the endostome. As a consequence of the reorganization of these respiratory channels, the exognath of the third maxilliped is completely concealed behind the endognath, and the anterior part of the carapace is narrow and spoutlike, implanted at a sharper angle in relation to the upper surface of the carapace. In this respect it resembles the frontal areas of some Leucosiidae which have similarly structured respiratory channels. The structure of the mouthparts is clearly an adaptation to a fossorial or semifossorial mode of life.

Burrowing activities differ greatly in various groups of crabs. The majids usually do not burrow into the substrate, whereas many catometopans tend to form permanent burrows in the sand. In contrast, many species of the traditional oxystomatan families Leucosiidae and Calappidae and many cyclometopans which inhabit sandy or gravelly substrata have burrowing habits. Their burrows, however, are never permanent channels in the sand but merely temporary excavations. Each of these different habits is associated with different morphological traits. In parthenopids, the crab is actually embedded in the sand (Schäfer 1950). The chelipeds are flexed to the underside of the anterolateral regions, with the fingers, which are flat and bend downwards and inwards, fitting closely at each side of the buccal cavity. The internal surfaces of the chelipeds are channeled and glossy. There is thus produced on each side of the crab, between the chelipeds and carapace, a ventral channel which communicates with the afferent aperture located at the base of the chelipeds. Since the back of the crab is covered with sand, the teeth on the internal margins of the merus of the cheliped, and those of the anterior part of the carapace, act as a coarse sieve placed at the orifice of these accessory channels.

In the most generalized condition, only these "exostegal channels" (Garstang 1897a, b) exist, and there are no accessory ridges or other structures on the pterygostomial regions to act as afferent channels. This condition is found in the genus *Cryptopodia* H. Milne Edwards, 1834 (A. Milne Edwards 1878, pl. 29, fig. 1a, 2a). In many parthenopids, there are usually ridges that delimit the afferent channels. In *Platylambrus serratus* for instance, there is a sinuous, crenulate ridge that runs transversely across the pterygostomial and distal subbranchial regions. In its distal part this ridge is provided with long hairs, which together with similar hairs on the anterior border of the coxa, basis and ischiomerus and third maxilliped, form a funnel-like entrance to the afferent aperture at the base of the cheliped. In *Heterocrypta,* there is a submarginal ridge that, starting at the suborbital region, runs parallel to the margin, and forms with it a channel that is lined with hairs. This channel is joined by a second channel that runs perpendicularly to the first, and ends at the base of the chelipeds. In *Heterocrypta tommasii,* the channels communicate with the upper surfaces of the carapace through an hepatic notch located at the junction of the two channels.

In *Solenolambrus* Stimpson, 1871 (Rath-

bun 1925), *Mesorhoea* Stimpson, 1871 (A. Milne Edwards 1878, pl. 29, fig. 5a, 6a) and *Aulacolambrus* Paulson, 1875 (Flipse 1930), there is on each pterygostomial region, a sharp, elevated and crenulate crest that runs from the antero-external angle of the buccal area to the base of the chelipeds, separating the concave pterygostomial region from the subhepatic region, which is also concave and channellike. When retracted, the extremity of the hands of the chelipeds covers the pterygostomial regions, forming the afferent passages. In the very rare genus *Tutankhamen* Rathbun, 1925, there are ridges similar to those of *Solenolambrus,* which extend from the antero-external angle of the buccal area to the base of the chelipeds, but the structure is more complex because the channels are shorter and deeper, bordered by a laminar expansion of the hepatic and anterior branchial margin above, and by a parallel lamina having an emargination near the beginning of the branchial region below (A. Milne Edwards 1878).

In *Leiolambrus* A. Milne Edwards, 1878, the exognath of the third maxilliped is partly concealed behind the endognath; the merus and ischium of the endognath are bordered by long, arched hairs which form with the hairs on the pterygostomial region, a ventral covering to the afferent channels. *Mimilambrus* has a similar arrangement, but the exognath is completely concealed beneath the endognath, and the pterygostomial ridge is more prominent, particularly in its distal part.

The efferent channels show a similar tendency towards a rearrangement within the buccal cavity. In *Aethra* Leach, 1816 (Guinot 1967a) and some parthenopids, the efferent channels are located on each side of the buccal frame, forming with the margin of the first maxilliped two separate sinuses. In *Parthenope agona, Platylambrus serratus, Leiolambrus nitidus,* and *Heterocrypta tommasii,* the anterior endostomial crests are sinuous, forming two adjacent openings

that are separated by a medial endostomial septum, but in fact discharging near the midline of the concave epistome. A last step in what Guinot (1966:747) has called "la tendence des Parthenopidae vers le type oxystomien" is seen in *Mesorhoea,* with "the two efferent channels meeting at the middle of the endostome, which has there a triangular projection, and a deep notch in its vertical, laminiform wall" (Rathbun 1925: 546). In *Mimilambrus,* a similar arrangement is found. The efferent respiratory channels empty through a common anterior median opening, into the concave epistome, which also has a ciliated notch.

Williams (1979) has noted that the last pair of ambulatory legs of *Mimilambrus* is similar in shape to that of the calappid *Acanthocarpus alexandri* Stimpson, 1871, and its structure suggests that *Mimilambrus* is probably a more active burrower than most of the other parthenopids (with the possible exception of *Mesorhoea).* Its more fossorial habits could easily explain why its mouthparts have evolved convergently with the leucosiids and calappids, which spend their daylight hours almost completely buried in sand or silt.

Stevcić and Gore (1980), in summarizing the known characters of the Parthenopidae and Mimilambridae, also noted that whereas the Parthenopidae have antennules folding slightly obliquely, *Mimilambrus* has them folding almost vertically. The folding of the antennule, however, appears to be a very variable character in the Parthenopidae, and appears to be dependent on the width of the pseudorostrum. In *Parthenope agona,* they are distinctly oblique, whereas in *Leiolambrus nitidus,* they are almost vertical. The presence of small antennae, with the peduncles in the orbital hiatus can also be found in many Parthenopidae.

In our comparative studies of the Parthenopoidea with the Mimilambridae, we also examined several other characters that are common to both. Of the genera dealt
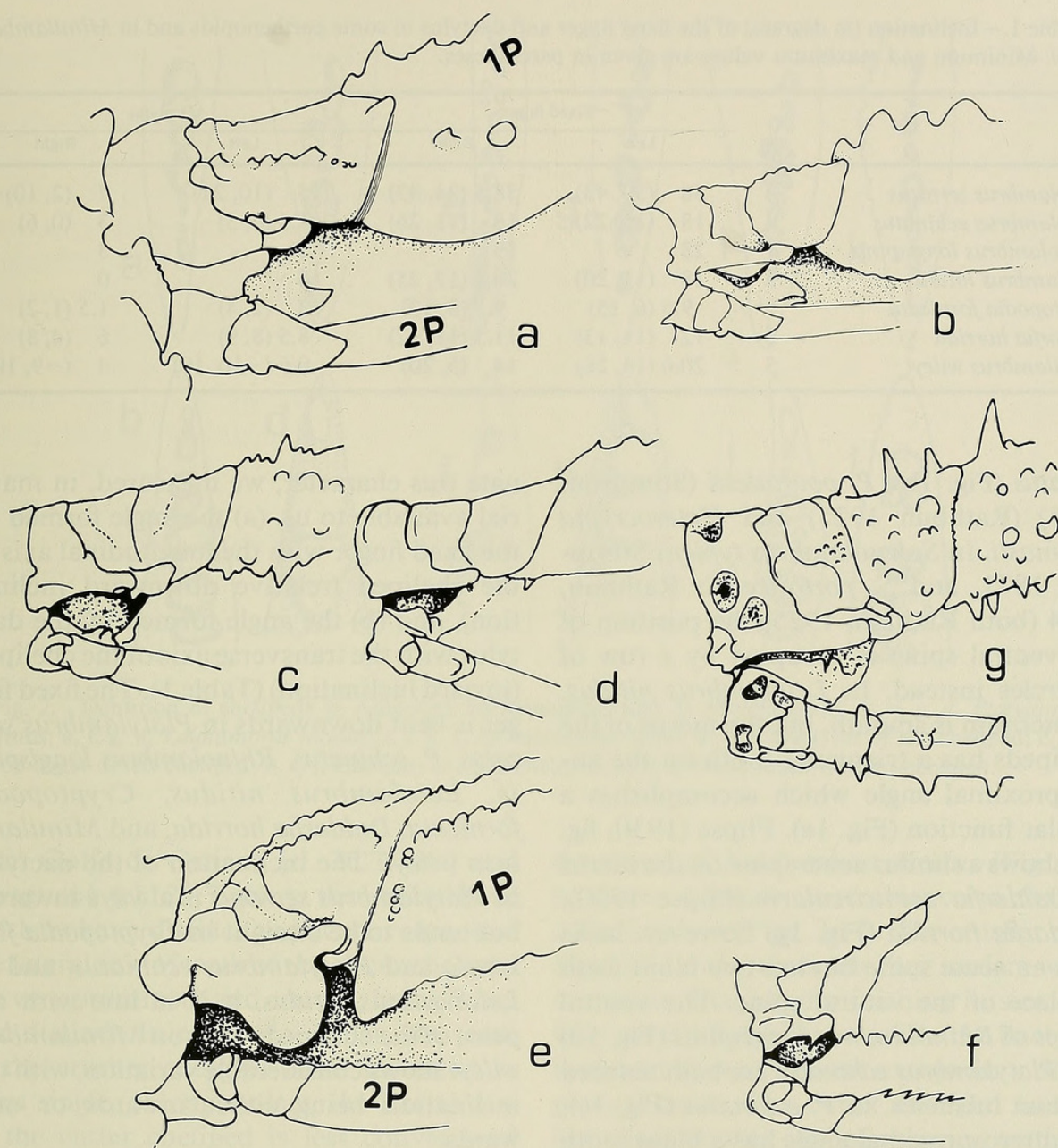
Fig. 1.   Ventral view of Parthenopidae and *Mimilambrus,* showing locking mechanism of chelipeds: a, *Mimilambrus wileyi;* b, *Platylambrus serratus;* c, *Platylambrus echinatus;* d, *Rhinolambrus longispinis;* e, *Leiolambrus nitidus;* f, *Cryptopodia fornicata;* g, *Daldorfia horrida.* 1P, Left cheliped; 2P, Second pereopod.

with, the only daldorfid is *Daldorfia; Daira* and *Dairoides* are dairids, *Aethra* the only aethrid, all the others being parthenopids. These characters will now be discussed systematically.

1. *Ventral spines.*—These spines are located at each side of the sternum, near the bases of the chelipeds. When the chelipeds are moved backwards, the respective spine locks against the ischio-meral articulation and prevents any further displacement backwards of the appendage (Fig. 1).

These spines have the same position in *Mimilambrus* (Fig. 1a) and *Parthenope agona, P. hyponca* (Stimpson, 1871), *P. ornatus* (Flipse, 1930, Fig. 24), *Platylambrus*

Table 1.—Inclination (in degrees) of the fixed finger and dactylus in some parthenopids and in *Mimilambrus wileyi*. Minimum and maximum values are given in parentheses.

	n	Fixed finger		Dactylus	
		Left	Right	Left	Right
Platylambrus serratus	4	38 (30, 43)	38.5 (34, 43)	15 (10, 21)	7 (2, 10)
Platylambrus echinatus	4	18 (16, 22)	18 (11, 26)	1.5 (0, 5)	3 (0, 6)
Rhinolambrus longispinis	1	28	19	8	3
Leiolambrus nitidus	5	18 (17, 20)	20.6 (17, 25)	0	0
Cryptopodia fornicata	5	9.5 (6, 15)	9.5 (8, 13)	3 (2, 4)	1.5 (1, 2)
Daldorfia horrida	2	12 (11, 13)	11.5 (11, 12)	8.5 (8, 9)	6 (4, 8)
Mimilambrus wileyi	5	20.6 (14, 26)	14 (5, 20)	0.6 (−10, 10)	4 (−9, 10)

serratus (Fig. 1b), *P. pourtalesii* (Stimpson, 1871) (Rathbun 1925) and *Heterocrypta tommasii*. In *Solenolambrus typicus* Stimpson, 1871, and *S. portoricensis* Rathbun, 1924 (both Rathbun 1925) the position of the ventral spine is occupied by a row of tubercles instead. In *Leiolambrus nitidus,* the sternum is smooth, but the merus of the chelipeds has a triangular tooth on the anteroproximal angle which accomplishes a similar function (Fig. 1e). Flipse (1930, fig. 40) shows a similar acute spine on the merus of *Daldorfia semicircularis* (Flipse 1930). *Daldorfia horrida* (Fig. 1g) however, lacks such an acute spine but has two blunt teeth in place of the ventral spine. The ventral spines of *Rhinolambrus longispinis* (Fig. 1d) and *Platylambrus echinatus* are both reduced to blunt tubercles. In *P. echinatus* (Fig. 1c), the antero-proximal angle has a blunt tooth which opposes the ventral tubercle. This tooth is absent in *R. longispinis*. The ventral spine of *Cryptopodia fornicata* (Fig. 1f) is quite well developed and opposes another sharp spine on the antero-distal angle of the coxa. The chelipeds are consequently much less mobile when compared to the other parthenopids and daldorfids. The chelipeds of *Daira* are extremely mobile, with only a very small tubercle located far back behind the sternum, and no opposing spine or tubercle on any part of the cheliped.

2. *Fingers of chelipeds.*—In most parthenopoids, the fingers of the chelipeds are bent downwards, and the dactylus bent inwards in a very characteristic way. To eval-uate this character, we measured, in material available to us, (a) the angle formed by the fixed finger with the longitudinal axis of the cheliped (relative downward inclination), and (b) the angle formed by the dactylus with the transverse axis of the cheliped (inward inclination) (Table 1). The fixed finger is bent downwards in *Platylambrus serratus*, *P. echinatus*, *Rhinolambrus longispinis*, *Leiolambrus nitidus*, *Cryptopodia fornicata*, *Daldorfia horrida*, and *Mimilambrus wileyi*. The inclination of the dactylus in *Platylambrus serratus* is always inwards, but tends to be straight in *Cryptopodia fornicata* and *Platylambrus echinatus*, and in *Leiolambrus nitidus*, it is in line with the palm of the cheliped. That on *Mimilambrus wileyi* shows considerable variation, with the inclination being either inwards or outwards.

3. *Dentition of the chelipeds.*—*Mimilambrus wileyi* shows dimorphic asymmetry in the dentition of the chelipeds (Fig. 2i–l); the occlusive surface of the cheliped on one side (the crusher) has a double row of teeth that coalesce side-by-side to form molariform crushers (Fig. 2j, l). The cheliped of the other side (the cutter) has two rows of broad, thin shearing teeth over the occlusive surface of the dactylus, and a row of similar teeth on the occlusive surface of the fixed finger (Fig. 2i, k). Additionally, the fixed finger has a lateral row, arched dorsally in the middle, bearing eight triangular teeth. Some variability is displayed in our material of *Mimilambrus*. In the male specimen
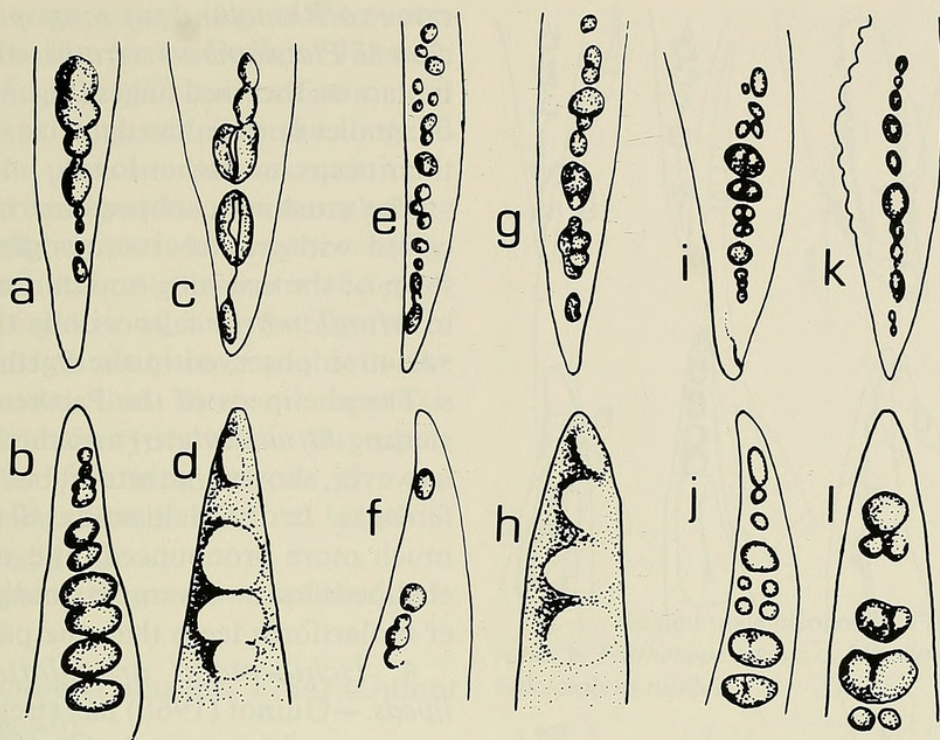
Fig. 2. Dentition of chelipeds in American Parthenopidae and in *Mimilambrus*: a, b, c, d, *Platylambrus serratus*; e, f, g, h, *Leiolambrus nitidus*; i, j, k, l, *Mimilambrus wileyi*. a, e, i, Dactylus of left cheliped; c, g, k, Fixed finger of left cheliped; b, f, j, Dactylus of right cheliped; d, h, l, Fixed finger of right cheliped.

from Golfo de Cariaco (cl. 26.3 mm) and Paraguaná (cl. 29.7 mm), the molariform crushers have distinct and acute cusps, and the lateral row of teeth of the cutter cheliped are very prominent and convex, being sharp and distinct. In other specimens, the teeth of the crusher cheliped have coalesced to form single, oblong molars, the lateral row of the cutter cheliped is less convex and prominent, with smaller teeth.

A similar dimorphic asymmetry is found in the members of the Parthenopidae. In *Parthenope agona* and *Platylambrus serratus* (Fig. 2a–d), there are two molar crushers on the fixed finger, but the cusps of the proximal one still have the cups discernible, and the cutter cheliped has a row of shearing teeth on both fingers and an additional oblique row of tubercles on the lateral surface of the fixed finger. *Heterocrypta tommasii* has three molars with indiscernible cusps on the fixed finger of the crusher cheliped, with crenulations on the dactylus, and there is no lateral row of tubercles on the fixed finger of the cutter cheliped. The chelar

dentition of *Leiolambrus nitidus* (Fig. 2e–h) shows a greater resemblance to that of *Mimilambrus* (Figs. 2e, i). The crusher cheliped of *Leiolambrus* has four molars without distinct cusps, diminishing in size distally on the fixed finger, while the dactylus is almost devoid of teeth except for a distal protuberance. The cutter cheliped has an indistinct double row of shearing teeth on the dactylus, some of which are fused to form molars. The lateral row of tubercles over the fixed finger is weak, with only minute granules.

The parthenopoids from the Indo-Pacific, *Cryptopodia fornicata* (Fig. 3m–p), *Rhinolambrus longispinis* (Fig. 3i–l), *Platylambrus echinatus* (Fig. 3e–h), and *Daldorfia horrida* (Fig. 3a–d) also show heterochely, with a distinct crusher and cutter cheliped. The crusher cheliped of *Daldorfia* is almost twice the size of the cutter, and the fixed finger has one very massive molar running through most of its length, without cusps, and slightly depressed medially (Fig. 3c). The dactylus bears a row of three strong,
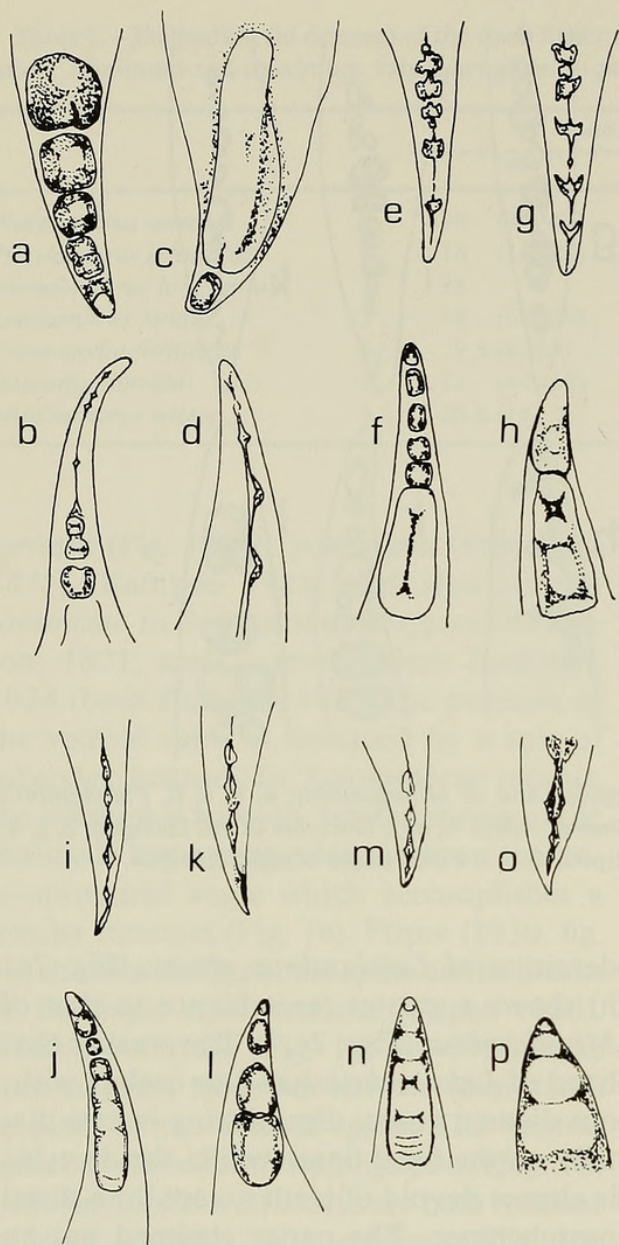
Fig. 3.   Dentition of chelipeds in Indo-Pacific Parthenopoidea: a, b, c, d, *Daldorfia horrida*; e, f, g, h, *Platylambrus echinatus*; i, j, k, l. *Rhinolambrus longispinis*; m, n, o, p, *Cryptopodia fornicata*. a, e, i, m, Dactylus of left cheliped; c, g, k, o, Fixed finger of left cheliped; b, f, j, n, Dactylus of right cheliped; d, h, l, p, Fixed finger of right cheliped.

ratus of *Rhinolambrus longispinis* is quite close to *Platylambrus serratus,* with two large molars on the fixed finger (Fig. 3l) and a row of smaller ones on the dactylus (Fig. 3j), but their cusps are rather lower.

The crushing chelipeds are clearly associated with molluscivorous diets, and the form of the crushing and cutting chelipeds of *Mimilambrus* falls within the range of variation observed in the Parthenopidae s. s. The chelipeds of the Parthenopidae (including *Mimilambrus*) and the Daldorfidae however, show some minor, but distinct differences. In the daldorfids, heterochely is much more pronounced, and the crushing chelipeds have very much stronger and larger molariform teeth than the parthenopids.

4. *Ischio-meral articulation of chelipeds.* — Guinot (1968) has stressed the importance of this articulation in the phylogeny of the Brachyura. In *Mimilambrus wileyi,* the ischio-meral articulation is still mobile, and the two articles are joined together by an arthrodial membrane. This character is commmonly found in the family Majidae (sensu Guinot 1978), and has been regarded by Guinot (1968) as primitive. In the Daldorfidae and Parthenopidae s. s., this character is rather variable, with a tendency towards ankylosis and total disappearance of the articulation and the arthrodial membrane. In *Platylambrus serratus, P. echinatus, Rhinolambrus longispinis,* and *Cryptopodia fornicata,* no arthrodial membrane is present, and movement of the two articles is at best very slight. In the genus *Mesorhoea* Stimpson, 1871, *Daldorfia horrida, Leiolambrus nitidus,* and *Parthenope agona,* there is a thin arthrodial membrane, but movement of the articles is still very restricted. In *Daira,* the arthrodial membrane is present, but it is thin, and the two main articles remain, for all purposes, immobile.

5. *Second male pleopod (P2).* — The P2 of all very primitive crabs (Dromiidae, Dynomenidae, and Homolidae) are long and whiplike, the cup is absent, and the basal portion of the flagellum cannot be differ-

coniform molars (Fig. 3a). The crusher cheliped of *Cryptopodia* is slightly less well developed than that of *Daldorfia,* but the molars on both fingers appear confluent (Fig. 3n–p). *Platylambrus echinatus* has two, almost confluent molars on the fixed finger of the crusher cheliped which have low cusps (Fig. 3h) that occlude on a larger molar on the dactylus (Fig. 3f). The crushing appa-

entiated. In some groups, e.g. in the super-family Xanthoidea (sensu Guinot 1978a, b), both long and short P2s can be found, and Ng (1983) has suggested that the long P2 represents the plesiomorphous condition.

In the Parthenopoidea, the morphology of the P2 is slightly more homogeneous (Fig. 4). An examination of the material deposited in our collections, and the figures of these appendages that are available in the literature reveal that there are approximately three main types within the superfamily. In the following list, we give the ratio of the flagellum to the total length of the appendage (f/a).

(A) Flagellum long and whiplike f/a > 0.4.

Aethra scruposa (Linnaeus, 1764) (Guinot 1967a, fig. 40).
Daldorfia horrida (Linnaeus, 1758).
Daira perlata (Herbst, 1790).
Dairoides margaritatus (Stebbing, 1920) (Guinot 1967b, fig. 14).

(B) Flagellum short, in the form of a spike, sometimes with basal cup, ratio f/a between 0.2 and 0.4.

Parthenope macrochelos (Herbst, 1790) (Monod 1956, fig. 861).
P. agona (Stimpson, 1871).
Platylambrus pourtalesii (Stimpson, 1871) (Williams 1965, fig. 252C).
P. fraterculus (Stimpson, 1871) (Williams 1965, fig. 252D).
P. echinatus (Herbst, 1790).
Rhinolambrus longispinis Miers, 1879.
R. massena (Roux, 1830) (Monod 1956, fig. 856).
Cryptopodia fornicata (Fabricius, 1781).
C. concava Stimpson, 1871 (Gore and Scotto 1979, fig. 5I).
Leiolambrus nitidus (Rathbun, 1901).
Solenolambrus typicus Stimpson, 1871 (Gore and Scotto 1979, fig. 9C).

(C) Flagellum very short, forming a cup-like structure, ratio f/a < 0.2.

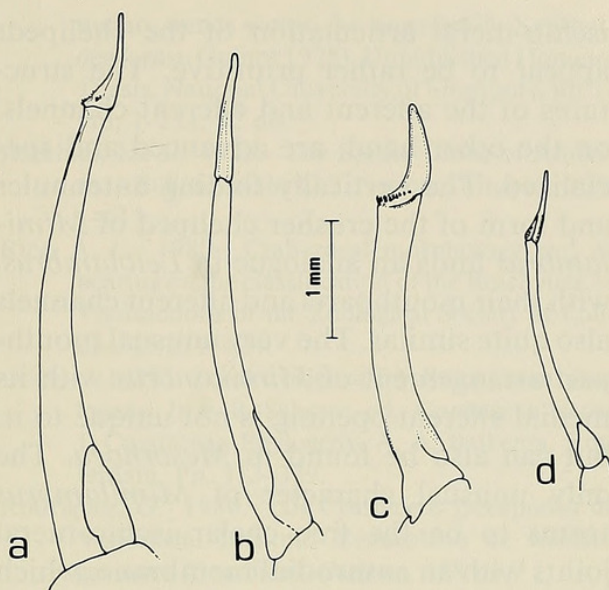*Platylambrus serratus* (H. Milne Edwards, 1834).

Fig. 4. Second male pleopod: a, *Platylambrus serratus*; b, *Parthenope agona*; c, *Mimilambrus wileyi*; d, *Leiolambrus nitidus*.

Heterocrypta maltzami Miers, 1881 (Monod 1956, fig. 867).
H. granulata (Gibbs, 1850) (Williams 1965, fig. 252E).
Thyrolambrus erosus (Miers, 1879) (Guinot 1967a, fig. 37).

All the genera with an f/a > 0.4 belong to the families Dairidae, Aethridae, and Daldorfidae, whereas genera with f/a < 0.4 constitute the Parthenopidae s. s. *Mimilambrus wileyi* belongs to the second group of P2 type, since its f/a is 0.22 with the flagellum relatively short, spikelike, with a fairly well developed basal cup, i.e., the Parthenopidae group.

Also, as mentioned earlier, the genera *Daira* and *Dairoides* or their allies probably gave rise to the main line of the parthenopids, and their male abdominal segments 3 to 5 are ankylosed, with the sutures still present, and their P2s are of the first group, i.e., with the flagellum long and whiplike. There is thus a very good chance that the evolutionary trend of the P2 observed in the Xanthoidea (Ng 1983) is also true for the Parthenopoidea.

In summary, some of the characters of *Mimilambrus*, such as the articulation of the male abdominal segments 3 to 5, and the

ischio-meral articulation of the chelipeds appear to be rather primitive. The structures of the afferent and efferent channels, on the other hand, are advanced and specialized. The vertically folding antennules and form of the crusher cheliped of *Mimilambrus* finds an analogue in *Leiolambrus*, with their mouthparts and afferent channels also quite similar. The very unusual mouthpart arrangement of *Mimilambrus* with its medial efferent opening is not unique to it, but can also be found in *Mesorhoea*. The only unusual character of *Mimilambrus* seems to be the free chelar ischio-meral joints with an anthrodial membrane, which appears to be a plesiomorphous condition. In the more primitive parthenopoids like *Daira,* these joints are tightly appressed, but still distinct. The genera *Mesorhoea* and *Leiolambrus* also have the two joints distinct, but basically immobile. The condition of the ischio-merus in *Mimilambrus* suggests that it may be a fairly primitive and specialized species. Presumably, the genus represents an early offshoot of the main parthenopoid stock. The respiratory adaptations could be explained by convergent evolution, and are unlikely to have been derived from similarly advanced structures like those on *Leiolambrus* and *Mesorhoea.* Placing *Mimilambrus* in a family (and superfamily) of its own is, therefore, unwarranted since it shares far too many common characters with the Parthenopidae s. s., and should instead be regarded merely as a rather specialized genus in the family.

Acknowledgments

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