

Review Paper

Are the Oxyrhyncha a natural group?

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The Oxyrhyncha (Crustacea Decapoda Brachyura) was established by Latreille 1803 and considered until now as a natural group (taxon) by the majority of carcinologists. However, the number of families composing this group varied during this period of time. According to present comprehension the Oxyrhyncha embrace the families Majidae, Parthenopidae, Hymenosomatidae, and perhaps also the newly described family Mimilambridae. A critical re-examination of morphological similarities shows that the previously held characters-in-common are not numerous, being more the consequence of convergent evolution than of common origin. Differences exist in a majority of features, especially in developmental and ecological ones. Therefore, the Oxyrhyncha have to be abandoned as a taxon and consequently families mentioned above should change their systematic status and position in the system of the brachyuran crabs.

INTRODUCTION

Brachyuran crabs in the section Oxyrhyncha have long been considered as a natural group by various carcinologists, and one in which the members are easily assignable to one of the three families, Majidae, Parthenopidae, or Hymenosomatidae, based on general morphological appearances. A fourth family, Mimilambridae, recently established by Williams¹ for an unusual parthenopid-like crab from the lower eastern Caribbean Sea, also appears to have affinities to the Oxyrhyncha. The general morphological characters that typify oxyrhynchous crabs were perhaps best summarized in a key provided by Rathbun² in which the couplet leading to Oxyrhyncha states that the forepart of the body is narrow, usually forming a distinct rostrum, the body is more or less triangular, and the orbits are generally incomplete. From this point the majid crabs were generally distinguished from the parthenopid, hymenosomatid and now also the mimilambrid crabs by having especially mobile chelipeds with straight or bent fingers, orbits more or less complete, hooked hairs on the carapace almost always present, and male openings coxal. The parthenopids have long, relatively mobile chelipeds in which the fingers are bent downward and inward, the orbits are complete, they lack in nearly every instance hooked hairs on the carapace, and (as with the majids and mimilambrids) the male openings are coxal. The mimilambrids are similar to the parthenopids, but the fingers of the chelipeds are distinctly horizontal. The hymenosomatid crabs differ from the other three families in having a thin, flat carapace, short and relatively mobile chelipeds, with fingers more or less horizontal, and male

openings sternal instead of coxal. So easily observable and generally unambiguous are these characters that it requires but little experience before a student can recognize that a crab before him is either majid, parthenopid, mimilambrid, or hymenosomatid. This grouping, as such, is certainly functional in this respect; whether it is a natural grouping (as originally espoused by H. Milne Edwards³, Stimpson⁴, Miers⁵, and others) is another question.

Before considering this point further, a brief historical resume on the Oxyrhyncha will help illustrate our contention: namely, that the Oxyrhyncha are not a natural grouping and, although functional as a means to indicate strictly morphological similarities, should not be construed as indicating phylogenetic relationships. To support this, we will provide in this report as far as possible morphological, taxonomic, physiological, and developmental data on the families Majidae, Parthenopidae, Mimilambridae, and Hymenosomatidae, in order to re-evaluate their taxonomic status, and to assign an alternative grouping based on a re-assessment of present knowledge in these four taxa.

HISTORICAL RESUME

The Oxyrhyncha, when established in 1803 by Latreille⁶ as the Oxyrhynchi, were at first a more broadly encompassing and interpreted taxon than recognized today. Latreille not only included oxyrhynchous crabs of the presently accepted sense, but other decapods as well, such as oxystomatous and anomuran crabs that exhibited morphological (but not necessarily phylogenetic) similarities among each other. It was not long before subsequent authors modified the systematic position and status of many of the groups comprising the originally delineated Oxyrhynchi.

H. Milne Edwards³, in establishing the Oxyrhynques, proposed three tribes, viz. Maiens, Macropodiens, and Parthenopiens, based on easily observable morphological characters. MacLeay⁷ erected five tribes, of which the Tetragonostoma and the Trigonostoma were equivalent to the Brachyura. He further arranged the brachyurous decapods into 10 stirpes in order to show, as he most prophetically wrote, »those analogies which by Milne Edwards and others have too often been taken for affinities«. Within the Tetragonostoma, the stirpes Inachina (»Triangular crabs«) and Parthenopina (»Rocky crabs«) were equivalent to Milne Edwards' Oxyrhynques, with size and the fusion of the basal segment of the antenna to the frontal region used as a delineating character. MacLeay also noted the intermediate position of the majid genus *Eurynome* to those of the parthenopid group, and the parthenopid genus *Aethra* with those in the cancrid grouping. This same author established the family Hymenosomidae (= Hymenosomatidae) to contain *Hymenosoma*, and placed this family within his stirpes Pinnotherina.

De Haan⁸ retained the name Majacea for the oxyrhynchous crabs, giving it a systematic rank more or less equivalent to family. In his synopsis, he included 5 genera, viz. *Parthenope*, *Maja* (sic), *Pisa*, *Doclea*, and *Inachus*. The genus *Parthenope* was further subdivided into subgenera containing *Cryptopodia*, *Oethra*, *Parthenope* and *Lambrus*. Similarly, each of the »majid« genera were subdivided, the genus *Maja* into 10, the genus *Pisa* into 9 (with 5 additional subgenera questionably appended), the genus *Doclea* into 4 (with 2 questionably added subgenera), and the genus *Inachus* into 9 subgenera. All of De Haan's »genera« have subsequently, at one time or another, been elevated to subfamilial rank, with the exception of *Doclea*. Moreover, most of his »sub-

genera« are presently ranked as genera, although not necessarily *sensu stricto* De Haan. Because De Haan placed rather great emphasis on mouthpart, branchial, antennular and gonopore morphologies, the differences in many of his taxa and those presently held today are differences more in degree than in kind. De Haan also addressed the problem of relationship of the hymenosomatid crabs to the majid crabs. After a comparison of several morphological characters, including gill number and position, formation of the »sella turcica«, and the position and form of sexual openings, De Haan considered *Hymenosma* and *Elamena*, at least, to be more closely allied to *Ocypoda*.

Dana⁹ established the subtribe Crustacea Maiioidea, or Oxyrhyncha, delineating three subgroups therein, termed legions; viz. Maiinea, Parthenopinea, and Oncininea. The latter legion contained the curious, monotypic genus *Oncinopus*, small crabs showing relationships to both majid and hymenosomatid crabs. The genus was subsequently placed in the family Inachidae by Miers⁵. Dana placed the hymenosomatid genera under the subtribe Crustacea Grapsoidea, and in the family Pinnotheridae, thereby agreeing in part with MacLeay's placement.

Miers⁵ stated that: »The oxyrhyncha, as defined by H. Milne Edwards, constitute as a whole a natural group; but no single character can be mentioned which will serve to distinguish them universally from the other brachyura«. In his classification, Miers retained only two of Dana's legions, the Maiinea and Parthenopinea, noting that the latter were »... very distinct as a group from the rest of the Oxyrhyncha«. In his later work on the Challenger Brachyura¹⁰, with the exception of the majids and parthenopids as noted above, this author adhered generally to the system proposed by Dana⁹, even to the ranking of the hymenosomatid crabs as a subfamily Hymenosominae under the family Pinnotheridae.

Ortmann¹¹ suggested another classification and divided the Majoidea into Majoidea Corystoidea and Majoidea typica. The latter group included Majidae, Hymenosomidae, Inachidae, and Periceridae. Ortmann also removed the Parthenopidae from the Oxyrhyncha entirely, placing the family instead under Cancroidea Cyclometopa, as the subgroup Parthenopini, consisting of the families Parthenopidae, Eumedonidae, Trichiidae, and Cheiragonidae.

Alcock¹² considered Ortmann's arrangement »... a more natural classification of the Cyclometopa« than that of Miers¹⁰ Challenger Report system, but could not agree with that author on the placement of the Parthenopidae. Earlier, he subdivided the tribe Oxyrhyncha or Maiioidea into just two families¹³, the Maiidae (containing all of the families of Miers and Ortmann except the Hymenosomidae), and the Parthenopidae. In this, he followed Claus¹⁴. Alcock placed the Hymenosomidae into the Catometopa.

Doflein¹⁵ followed along these same lines, retaining the Majidae in the Oxyrhyncha, but removing the Parthenopidae and the hymenosomid crabs to the Cyclometopa, along with the Atelecyclidae and Portunidae.

Borradaile¹⁶ soon reinstated the two families Parthenopidae and Hymenosomidae, with the Majidae, in his definition of Oxyrhyncha. The majority of authors since then have accepted this arrangement, with only a few (*e. g.*, Bouvier¹⁷, Monod¹⁸, Yang¹⁹, Števčić²⁰) expressing doubt that the Oxyrhyncha were a natural group. Garth²¹ gave an excellent historical review of the Oxyrhyncha, emphasizing especially the tangled history of the majids, but retained Borradaile's grouping in his classificatory scheme. Griffin²² in a review of Australian spider crabs, pointed out that the term Majoidea of Dana

and Miers is partially synonymous with Oxyrhyncha, and not with the taxon Majidae. Griffin also noted that even though de Haan⁸ had included the Hymenosomatidae in the majoids, the latter family was not generally accepted therein until after Rathbun's² monograph on the America spider crabs.

Balss²³ critically considered the family Majidae, and made additional brief mention of the Hymenosomatidae, but omitted reference to the Parthenopidae. His paper thus has little bearing on the problem we are considering.

In last years the question of the natural relationships among the Oxyrhyncha has been revived. Guinot²⁴⁻²⁹ in a series of papers suggested that the Oxyrhyncha be abandoned altogether, and the Majidae, Parthenopidae, and Hymenosomatidae be raised to the status of superfamilies. This followed closely along the lines of her original studies³⁰ which showed a »parthenoxystomienne« line for several genera exhibiting transitional character states between parthenopid and oxystomatous crabs. At about the same time, Števíć²⁹ reduced the Oxyrhyncha to only the Majidae, relegating the latter taxon to a somewhat isolated position among the Brachyura and showing uncertain relationships to either the Parthenopidae or the Hymenosomatidae. Recently Rice³¹, after a general re-examination of all known brachyuran larvae, concluded that »The zoeal evidence also supports the total separation of the three "oxyrhynch" groups« (p. 351). Furthermore, he pointed out that »there is justification for the recognition of an oxyrhynchous group distinct from the remaining Brachygnatha, but containing only the spider crabs« (p. 352).

It is apparent from the brief historical review just presented that the status and position of the Oxyrhyncha (*sensu lato*) remains in considerable confusion, much of this confusion dependent on the concepts employed by the carcinologists revising the group at the time, but also much of it a consequence of the increased attention directed toward revisionary work and positioning of many newly discovered species²¹.

THE OXYRHYNCHA

Analysis of the diagnostic characters delineating the Oxyrhyncha allows some judgement to be made as to their adequacy in a taxonomic sense, as well as to whether the Oxyrhyncha can be considered as a natural group. Homologous and/or synapomorphic characters would support the latter contention, on which (in turn) any judgement of adequacy depends. The Oxyrhyncha are usually defined as follows: Carapace narrowed anteriorly, terminated by a rostrum, broadened posteriorly, with well-developed branchial regions; orbits incomplete or absent; antennules infolded longitudinally or slightly obliquely; basal antennal article fused with front or epistome; latter usually large; buccal cavern quadrangular; male sexual openings coxal or sternal (summarised from Ortmann¹¹, Alcock¹³, Balss³², Glaessner³³). As Guinot²⁷ has noted, this subgroup within the Brachygnatha rests almost entirely on the form of the body and the presence of a rostrum, in which the four families show more or less overall similarity.

Analysis of characters

1. *Carapace narrowed anteriorly.* — This property by itself is not very useful, being neither specific for the four families, nor constant in all representatives in any of them. For example, the carapace in some members of the majid genus *Mithrax* ranges from distinctly narrowed (*M. acuticornis*) to ob-

lately oval (*M. coryphe*), while in some hymenosomatid crabs it is suboval, subcircular, or subpolygonal. Moreover, these same features are seen in many non-oxyrhynchous families, including the Raninidae (*Lyreidus*), Leucosiidae (Eballiinae), Corystidae, Pirimelidae, and Latreilliidae.

2. *Terminated anteriorly by a rostrum.* — Disregarding the fact that a true rostrum does not exist in brachyuran crabs¹⁸, the projecting (*i. e.*, »rostral«) part of the frontal region seen in the oxyrhynchous families is seen in one form or another in several other brachyuran families as well. This »pseudo-rostrum« (if it may be termed such), is often formed of prominent median teeth and can be recognized in the Raninidae, Corystidae, Pirimelidae, Atelecyclidae, and to a greater or lesser extent in several other families. This character otherwise provides insufficient support for showing presumed relationships among the four oxyrhynchous families in any supposedly natural classification.

3. *Broadened posteriorly with well-developed branchial regions.* — This property, which apparently has arisen independently within various lineages, is another feature of limited value in supporting the relationships of the four oxyrhynchous families. Broadly expanded carapaces, with well-developed branchial regions also occur in the Leucosiidae, Dorippidae, Gecarcinidae, some Grapsidae, Portunidae, Potamidae, and in the newly discovered family Bythograeidae³⁴ from Galapagoan submarine thermal vents.

4. *Orbits incomplete or absent.* — Orbits are usually incomplete in the Majidae (rarely complete or rarely absent), complete but small in the Parthenopidae and Mimilambridae, and absent in the Hymenosomatidae. Consequently this character not only does not support the unity of the Oxyrhyncha, it argues instead for the opposite conclusion.

5. *Antennules folding longitudinally or slightly obliquely.* — This character is shared by several non-oxyrhynchous families of decapods, and is insufficient to characterize any taxonomic grouping. Within the Oxyrhyncha the antennules fold longitudinally (= almost »vertical«)¹ in the Mimilambridae, and slightly obliquely in the Parthenopidae. The direction of antennular folding was used by Rathbun³⁵ in her key separating the families Atelecyclidae and Cancridae from the Xanthidae and Goneplacidae. The degree of antennular folding appears to be an ancestral property retained by several decapod crab lineages, and thus provides scant evidence for unity among the Oxyrhyncha.

6. *Basal antennal article fused with front or epistome.* — The position of the basal antennal article among the four families is completely different. In the Majidae it is fused with the epistome, and is also often fused with the front; in the Parthenopidae and Mimilambridae it is small, short, not fused with either the front or the epistome; in the Hymenosomatidae it is fused only with the epistome. With such a wide range of differences this character offers little support for close relationships among these families.

7. *Epistome usually large.* — The epistome is indeed large in all the families presently united in the Oxyrhyncha, but it remains a poor distinguishing character because it is not restricted to this group. In the majority of brachyuran groups which do not bury themselves in the substratum, the epistome is more or less distinct, whereas in many of those species which do bury in the substratum the epistome is greatly reduced or absent. The epistomial form

thus seems to be more of an adaptation to a mode of life than to exhibition of any phylogenetic affinities among groupings (see also below).

8. *Buccal cavern quadrangular*. — In the majority of the Brachyura genera the buccal cavern or mouthfield is quadrangular. It is mainly in those groups which bury (e. g., Calappidae, Parthenopidae, and perhaps Mimilambidae, but not the Portunidae) that the buccal cavern and its accompanying mouthparts is anteriorly narrowed. This last feature is noticeable in some parthenopid crabs (e. g., *Mesorhoea* spp.), and appears to be another property resulting from adaptation to a mode of life, rather than demonstrating phylogenetic affinities.

9. *Male sexual openings coxal or sternal*. — This character seems of little value defining the Oxyrhyncha, especially in light of Guinot's²⁶⁻²⁹ studies on gonopod and gonopore position. In the Majidae, Parthenopidae, and Mimilambidae (and in many other brachyuran crab families as well) the male opening is coxal. On the other hand, in the Hymenosomatidae (and still other families) the opening is sternal, so that there is no consistency among these families as members of the Oxyrhyncha. Nevertheless, it remains very important in the classification of brachyuran crabs because of its connection to several internal structures. It has also been shown to be of value in separating the higher crabs into the two principal groups, Catometopa and Cyclometopa. Both Guinot²⁶⁻²⁹ and Saint Laurent³⁶⁻³⁷ have used the position of the female openings, in conjunction with male openings, to re-define brachyuran classification.

It is seen, then, that the diagnostic characters previously used to define the Oxyrhyncha do not precisely delimit this group taxonomically. Moreover, the similarities that do exist among the four included families cannot be ruled out as being a result of convergent or parallel evolution. These same characters further indicate that the Oxyrhyncha cannot be considered a monophyletic taxon because the affinities of the four families contained therein are only superficial, and are not a consequence of phylogenetically derived states. There is other evidence based on larval development and maturational ecdysis which denies any natural relationships among these four families. Such evidence is considered below, and a synopsis of characters for each family is presented. Data for the following section come from numerous authors, and from unpublished studies or observations by the second author. Cheliped terminology is that of Brown *et al.*³⁸, Schäfer³⁹; gonopore terminology follows Hartnoll⁴⁰; data on the thoracic endophragmal system are from Guinot^{24, 29}; summaries of larval characters are from numerous sources in the recent literature (see, e. g., Rice³¹), and from studies conducted by the second author.

Majidae

The carapace is triangular or subtriangular, often pyriform, with a well-defined pseudorostrum. Orbits are incomplete or lacking, rarely complete. The antennules fold longitudinally. The basal article of the antenna is well-developed, fused with the epistome, and in some genera (e. g., *Macrocoeloma*) fused with the front; urinary openings are placed far from the basal article. The buccal cavern is quadrate, more rarely trapezoidal, incompletely covered by the third maxilliped; the palp of the latter is articulated at the anteromedial angle of the merus, and is not concealed. Chelipeds are usually long, often massive, but seldom longer than the pereopods. They are usually monomor-

phic, homiochelic, symmetrical (*i. e.*, equal in size and structure), usually adontic (with some exceptions, *e. g.*, in the genus *Mithrax*), extremely mobile, with the articulation between basis-ischion and merus always very mobile (cf. Guinot⁴¹), not held pressed against the anterolateral margin of the cephalothorax, and able to reach almost every point on the carapace. Hooked hairs almost always present on the latter. The thoracic endophragmal system is at level IIIC. The sternum is broad, but all sutures are incomplete, being interrupted medially. Sternites are arranged in radial. A sterno-abdominal cavity is present, as is a functional retaining mechanism of the abdomen. Male openings are coxal, the first pleopod usually having a complex apex, the second being short and relatively simple. Female openings are sternal, the gonopore is of the concave type.

The larvae differ from all of other Oxyrhyncha in both morphology and number of stages. Rostral and dorsal spines, only dorsal spines, or rostral, dorsal, and lateral carapace spines may be present. Zoeal stages are relatively large compared to parthenopid and hymenosomatid larvae; a posterolateral hair series may be present on the carapace. Antenna is type A or B of Aikawa⁴², the endopodite bud appears in the first stage, and the exopodite usually carries well-developed subterminal spines. The mandibular palp appears in the second (*i. e.*, last) zoeal stage. The maxillary endopodite bears 4–6 setae, usually grouped terminally, or has a subterminal group very close to the endopodal apex; four endites are present, the coxal endite is well-developed, and spinose; the scaphognathite carries more than 6 marginal setae in Zoa I, these setae are not split into two marginal groups in either stage. Five abdominal somites are seen in the first zoeal stage, five or six (depending on genera) in the second stage. Pleopod buds usually are present as primordia in stage I, as buds in stage II. The telson is lunate to truncately trapezoidal, bearing elongate furcae; lateral, or dorsal spinules, or both, may be present. Although Rathbun⁴³ noted abbreviated development in the Australian majid *Paranoxia serpulifera* (Guerin), two zoeal stages, plus a megalopal stage are most usual.

Majidae differ from all other brachyuran crabs in an important physiological aspect. The pubertal molt, with the concomitant onset of sexual maturity, is the terminal molt⁴⁴. Chaix *et al.*⁴⁵ presented data which indicate that the arresting of further molts is a result of degeneration in the Y-organ and its subsequent disappearance very soon after the pubertal molt.

The majid (spider) crabs occur on a variety of bottom types, and many species are adapted to climbing on, or clinging to, various types of substrata, including algae, sponges, bryozoans, corals, and other sessile or colonial forms. None are known to bury. By using the greatly mobile chelipeds, many species are able to camouflage themselves using bits and pieces of foreign matter, or to cut living algae and other epiphytes and attach the shreds of material to the hooked hairs which usually occur in great abundance on the carapace^{46, 47}. The radially arranged sternites allow locomotion in all directions, and most species, although not excessively fast-moving, are nevertheless quite agile. Majid species are exclusively marine or estuarine, none are known to penetrate fresh or slightly brackish waters. They occur from intertidal zone to the continental slope and rise. Some shallow-water forms, and many of the deeper-living species (*e. g.*, *Chionoecetes*, *Macrocheira*, *Mithrax*, *Leptomithrax*) often attain extremely large size. The family is found in all the world oceans,

although maximum diversity is attained in tropical seas. The fossil record extends from the Eocene to the Recent with an unverifiable record from the upper Cretaceous²³.

The Majidae, as a consequence of the oxyrhynchine diagnosis, are the most typical of Oxyrhyncha, a fact noted by Guinot^{24, 26}. The family as presently constituted consists of a large variety of diverse groups, previously relegated familial status but now assigned subfamilial rank. Garth²¹ and Griffin²² summarized the historical classification within the family, pointing out the inadequacies of some previously used morphological characters as majid criteria. The espousal by Garth (and subsequently by Griffin) of the male first pleopod as a taxonomic character of great value, coupled with the form of the orbits, has brought relative stability to most of the family (see Griffin²², for a complete discussion).

Parthenopidae

The parthenopid crabs are characterized as having a cephalothorax usually equilaterally triangular, sometimes subpentagonal, or ovately pentagonal. The pseudorostrum is simple or obscurely trilobed. Orbits are complete but small. The antennules fold slightly obliquely. The basal article of the antenna is not fused with either the epistome or the front; the urinary opening is near the basal article. The buccal cavern is usually quadrangular, narrowed somewhat in front in some genera, and completely covered by the third maxilliped; the palp of the latter is reduced and lies partially concealed in the groove of the merus. The chelipeds are vastly longer and more massive than the walking legs, and distinctly longer than the carapace, their fingers shorter than the palm, and curving abruptly downward. While the chelipeds may be held transversely in front of the carapace, they are not pressed against its anterolateral margin; they are mostly monomorphic, but in some genera may be heteromorphic (heterochelic), but in none are the especially mobile. The thoracic endophragmal system in the majority of subtaxa is on the IIIC level^{24, 29}, but in *Daldorfia* and allied genera is on the IIIB level. The sternum is usually large, and in most genera the sutures are incomplete; in *Daldorfia* and some allied genera the last 2 sternites are complete (*i. e.*, sutures are not interrupted). A sterno-abdominal cavity is present with a functional abdominal retaining mechanism. Sternites of the walking legs are arranged in parallel. Male openings are coxal, the first pleopod is long, strong, and possesses a complex tip; the second is distinctly shorter, with a simple flagellum-like tip. Female gonopores are sternal, and of the concave type.

The larvae of parthenopid crabs differ from those of other oxyrhynchous crabs in both form and number of zoeal stages^{10, 48-50}, (Gore, unpublished). Zoeal stages are exceedingly small, often less than 0.2 mm in carapace length¹⁰ (Gore, unpublished). Larval stages possess rostral, dorsal, and lateral carapacial spines, but there is apparently no posterolateral hair series on the carapace. Antenna is type B of Aikawa, the antennal endopodite bud appears in stage III, and the exopodite lacks long, subterminal spines. The mandibles are without palp until the last zoeal stage. The maxillary endopodite has setae placed stepwise in 3 groups, usually 2, 2, 3, or 2, 3, 3, progressing distally; four endites are present, the coxal endite being well-developed and spinose; scaphognathite carries 4 marginal setae and an apical process in stage I, and in stage II the marginal setation is split into an apical and basal group. There

are 5 abdominal somites in the first two zoeal stages, 6 somites thereafter. Pleopod buds appear in stage IV, developing further in later stages. The telson is lunate and bears a dorsal spinule on each furca. The number of zoeal stages is 5—6, and a megalopal stage is present.

Some parthenopids exhibit allometric growth of male gonopods, and the width of the female abdominal terga, in relation to carapace width prior to the pubertal molt. Molting continues after the pubertal ecdysis (at which time sexual maturity is attained) with reduced allometry or even isometric growth occurring in some species (Gore, unpublished). Whether a terminal molt takes place has not been ascertained. There are no published data on molting or growth in parthenopid crabs.

The Parthenopidae (calthrop crabs, rocky crabs, pebble crabs, pentagon crabs) are exclusively marine crustaceans, but may sometimes occur in highly saline estuarine conditions³⁷. The species inhabit various types of sea bottom, including sand, coral, rock, shell hash, mud, and mixtures of these. While not actually burrow-forming, the species are known to be semi-burrowing, cryptic forms. The tuberculations and prominences on the carapace provide excellent camouflage, allowing these crabs to blend completely into the background of shell hash and rock rubble which forms their primary habitat. None are known to actively camouflage themselves, although some species may, as a consequence of digging into the substratum, become covered with mud and debris among the spines and tuberculations of the body⁴⁶. The relative immobility of the greatly elongated claws precludes attaching algal camouflage, as does the almost complete absence of hooked hairs. Some species of parthenopids share with the Oxystomata (another heterogeneous group) a mouth region modified with grooves and ridges to allow respiratory water currents to be drawn over the gills while they lie concealed⁵⁷. The family is distributed in all the world oceans except polar seas, occurring from the shallow intertidal to the lower continental shelf and upper slope, with some unverified records being even deeper⁵⁷. The palaeontological range extends from the middle Eocene³³.

The family was previously divided into two subfamilies, the Parthenopinae and the Eumedoninae. Present relationships remain unclear, and Guinot^{27, 30} excluded the Eumedoninae (a very aberrant group of small tropical crabs living commensally with echinoderms) from the family. The majority of species, however, are placed in the subfamily Parthenopinae.

The Parthenopidae, although a fairly large and diverse group, are thus not particularly uniform in a taxonomic sense. The inclusion of some genera (*e. g.*, *Aethra*, *Mesorhoea*, *Cryptopodia*, *Daira*, *Dairoides*) within the family has often been questioned (see Guinot^{30, 24, 27}, for discussion), and other genera show a disconcerting resemblance to majid crabs, resulting in further confusion as to both their taxonomic relationships and position⁴⁰. As presently conceived, parthenopids show relationships to both oxystome and cancrid crabs in several important characters, a fact originally emphasized by Miers⁵. Moreover, Guinot³⁰ cited several authorities (among them Drach) who have shown that the parthenopids differ from the majids in such ecological, behavioral, and physiological characters as the ability to bury themselves, the inability to attach camouflage to the carapace, and the attainment of the pubertal molt well

before the terminal molt. In regard to larval characters, Lebour⁴⁸ had already pointed out that parthenopid zoeae did not agree with majid zoeae in many respects, and were a general exception to oxyrhynchous zoeae, so far as they were known at the time. Yang¹⁹ admirably summarized the known data on larval development and concluded that larval characters strongly suggested that the Parthenopidae were more closely related to the Brachyrhyncha than the Oxyrhyncha. Whatever the true affiliation, brachyrhynch or oxystome, or both, it seems apparent that the Parthenopidae can no longer be considered members of the Oxyrhyncha, however that taxon is defined, and should therefore be removed.

Mimilambridae

This monotypic family was established by Williams¹ for a West Indian crab which superficially resembles crabs in the subfamily Parthenopinae. The only species, *Mimilambrus wileyi*, is known from Tobago. Although the sole member of this family shows resemblances to both the Leucosiidae (Oxystomata) on the one hand, and the Parthenopidae on the other, Williams considered its relationships more parthenopid than calappoid, and placed the family with some hesitation into the Oxyrhyncha.

The carapace is subcircular or roughly octagonal, with a pointed pseudo-rostrum. Orbits are complete and well-developed. The antennules fold nearly longitudinally (= nearly »vertical«). The basal segment of the antenna is not fused with the epistome or the front. The buccal cavern is truncately triangular, almost completely covered by the third maxilliped, but with a definite medial hiatus; the palp of this appendage is exposed. The chelipeds are approximately homoiochelid, with dentate cutting edges, much longer and heavier than the walking legs, distinctly longer than the carapace, and with fingers shorter than the palms and directed horizontally. Although held transversely in front of the carapace, the chelipeds are not appressed to its anterolateral margins; mobility appears limited. The thoracic endophragmal system is uninvestigated. The sternum is large, with sutures incomplete; a sterno-abdominal cavity is present with a functional retaining abdominal retaining mechanism. Sternites of walking legs are arranged radially. Male openings are coxal, the first pleopod is long, strong, with a spiny tip; second pleopod is considerably shorter, simple. Female gonopores open sternally, and are of the concave type.

The larval development is unknown.

The collection data for the type series indicated that *Mimilambrus wileyi* occurs in sand. This, plus the superficial parthenopine resemblance, and the similarity of the last pair of walking legs to the calappid species *Acanthocarpus alexandri* (Stimpson), suggests that this crab buries itself in a manner similar to that seen in members of the Parthenopidae.

Williams¹ provided a complete summary of the features which the new family both shared and did not share with the families Calappidae, Leucosiidae, and Parthenopidae. *Mimilambrus wileyi* is unusual exhibiting superficial resemblances in mouthpart, sensory appendage, and abdominal somite morphology to these named families. The Mimilambridae may prove to be transitional between the oxystomatous crabs on the one hand, and the parthenopids (including, perhaps, the »parthenoxystomienne line« of Guinot) on the other. No fossils are known.

Hymenosomatidae

The hymenosomatid crabs (crown crabs, false spider crabs) are a very unusual group. The members of this family are characterized by a flattened, subcircular, subtriangular, suboval, or polygonal cephalothorax made of thin, poorly calcified cuticle, which is commonly encircled by a raised rim. Hooked hairs, if present, are not used for attaching camouflage as in the Majidae. The pseudorostrum is variable in length and shape, being either tridentate (trilobular), or if simple, triangular and tapering to a rounded or broadly truncate tip. There are no, or very incomplete, orbits. The antennular fossae are shallow and ill-defined, with the antennules folding longitudinally. The basal antennal article is slender and fused only with the epistome, not the front. In some genera the third pair of maxillipeds completely cover the quadrangular buccal cavity and mouthparts, while in others a large space appears between the maxillipeds. Chelipeds are not held pressed against the anterolateral margin of the carapace, and, judging from the pictures provided by Melrose⁵², are monomorphic, chiefly homiochelic not very long (although often quite large) in relation to the carapace, only little longer than the walking legs, and the fingers are not bent downward; they are relatively immobile. The thoracic endophragmal system is on the IIID level. The thoracic sternum is very large, all sutures are incomplete and very short, and the sternites are radially arranged. A sterno-abdominal cavity is present and very well-developed. The retaining system for the abdomen, although present and functional, is atypical. The male first pleopod is expanded at the base, often twisted distally about 90°, and of varying length; the second pleopod is short. The female gonopore is sternal and of the concave type^{24, 25, 29}.

The larval stages differ in both number (0 or 3) and in morphology from those of the Parthenopidae and Majidae^{19, 53-58}, but show some similarities to larvae of some pinnotherid and leucosiid species^{5, 31, 54, 57, 58}. Although a rostral spine is always present, hymenosomatid larvae may lack both dorsal and lateral carapacial spines; there is no series of hairs on the posterolateral carapace margin; the antenna is aberrant (modified type D?); the antennal exopods are without setae or spines; the mandibles lack a palp bud in all zoeal stages; the endopodal setae on the maxilla are placed 2, 3, subterminally and terminally; the endites are undivided (*i. e.*, only 2 lobes), the coxal endite is reduced, and usually carries but a single seta; the scaphognathite (in the first zoeal stage) bears 3 marginal seta and an apical process; but the setal groups are split in the subsequent stages; there are only 5 abdominal somites, and pleopods are absent in all stages; the telson is elongate and truncate, lacking dorsal and lateral spinules. More notable, the Hymenosomatidae lack a megalopal stage, and development proceeds from the last zoea directly to the reftant first crab stage, without pleopod development or swimming taking place.

Information provided by Broekhuysen⁵⁹, Hill and Forbes⁶⁰, and Lucas⁵⁸, indicate that *Hymenosoma orbiculare* Desmarest and *Elamenopsis lineata* continue to molt the pubertal ecdysis, but how many other genera do so remains unknown. *Amarinus* and *Halicarcinus*, for example, have a common pubertal-terminal molt⁵⁸. The problem is complicated by the fact that immature males in some species may be sexually mature and active prior to the pubertal molt which confers mature morphological characters.

The 62 species in the family exhibit considerable ecological diversity^{52, 58}, and occur on various types of substrata in algae, under stones, from the intertidal to 494 m in the deep sea. They are considered to be primarily shallow sublittoral crabs⁵⁸. Although the majority of species are marine, several are estaurine, and some species enter brackish or fresh waters^{58, 60} and apparently live there permanently. The various species are cryptically colored⁶¹, but do not seem to attach camouflage materials, even though hooked hairs are present in some cases. The inability of the chelipeds to reach far over the back of the carapace may partially explain this lack. Several species of crabs, by virtue of carapacial hairs, become covered with detritus; others may support large numbers of epizooites. Some species have been observed to bury themselves, or in exceptional cases, to swim⁵² (Kensley, personal communication). The family is known only from the Recent, and is principally distributed in warm tropical waters of the Indo-Pacific region centered around Australia and New Zealand, and in temperature waters of Chile and Argentina (cf. Coelho⁶²), Africa⁶³, with at least one marine form occurring in a freshwater lake in South Africa⁶⁰. Another species has apparently been introduced by man to Pacific Panama⁶⁴ and 3 species occur in the Southern Atlantic Ocean.

The systematic position of this family has long been an enigma. The genus *Hymenosoma*, one of 10 presently recognized⁵⁸ was originally placed with the Pinnotheridae by H. Milne Edwards³, but only Dana⁹ accepted this classification. De Haan⁸ assigned the genus to the »Majacea« (*i. e.*, Majidae), although MacLeay⁷ had previously erected the family Hymenosomidae, under stirpes Pinnotherina, to contain this group. Many subsequent authors either ignored, or were unaware of, this taxonomic assessment. Others^{10, 65} thought the family better placed in the Catometopa, and Alcock regarded them to be closely related to the Mictyridae (soldier crabs). After Borradaile's¹⁶ reclassification of the Decapoda, the family was placed again in the Oxyrhyncha and there they have remained until the present^{52, 58}.

The adult and larval morphological characters just presented indicate that the Hymenosomatidae are better considered as an isolated family in the Brachyura, showing little if any affinity to other recent taxa with the possible exception of the Pinnotheridae, and perhaps the Hexapodidae or Hapalocarcinidae. Further studies on both adult and larval stages in these families may provide a basis for a sounder classification. Guinot^{24, 25} has already proposed placing the hymenosomatids in their own superfamily Hymenosomatoidea. Rice³¹ gives cogent reasons (based on larval studies by Lucas⁵⁷, and others) why the family is more closely allied with advanced catometopan crabs such as the Pinnotheridae and Leucosiidae, rather than with the Majidae. We concur with both these authors, that the taxon should be separated from the Oxyrhyncha and replaced in the Catometopa, thereby following earlier suggestions of Miers¹⁰ and Alcock⁶⁵.

DISCUSSION

With the removal of the parthenopid, mimilambrid, and hymenosomatid crabs from the section Oxyrhyncha, only the Majidae remain. It thus seems hardly necessary to retain the taxon Oxyrhyncha solely for the Majidae, unless it be thought desirable to distinguish crabs in this group from the Brachyrhyncha. Even the derivation of the nomenclatural term Oxyrhyncha (»sharp-nosed«) loses its value, because as pointed out earlier, other brachyuran decapods can also be considered »sharp nosed«. We can only conclude, therefore, that

the similarities among the four families previously placed under this taxon are secondarily derived, and have arisen either through convergent or parallel evolution, and not as a consequence of any phylogenetic relationships. Indeed, larval evidence suggests that the oxyrhynchous crabs arose independently and that the Oxyrhyncha are thus a polyphyletic group. Because this grouping is not a natural one we suggest its abandonment.

What then will be the systematic status of the four families? Earlier authors (*e. g.*, MacLeay, Dana, Miers, Ortmann, cited herein) incorporated the Majidae and Parthenopidae under taxa equivalent more or less to superfamilial rank (*e. g.*, Parthenopina, Parthenopini, Maiinea, Majoidea). Nomenclaturally, the erection, or re-establishment, of the superfamilies Hymenosomatoidea, Majoidea and Parthenopoidea by Guinot^{24, 25} seems justified, and provides a solution as to how to treat three of the families. Whether a fourth superfamily, Mimilambroidea, should be established, for the monotypic Mimilambroidea cannot be decided until its relationship with other brachyuran decapods, is clarified. What is certain is that by relying on Guinot's^{24, 25} revision of the Brachyura at the infra-ordinal level, the Majoidea, Parthenopoidea (and the Mimilambroidea, if that group is established) would all become members of her Section Heterotremata, and the Hymenosomatoidea would be placed in the Section Thoracotremata*. Considering the groups in this way also emphasizes the gonopodal and gonoporal characters within the superfamilies, characters with the studies of which Garth²¹ and others have shown they will assume increasing importance in future classifications of the Brachyura.

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IZVOD

Da li su Oxyrhyncha prirodna skupina?

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Oxyrhyncha (Crustacea Decapoda Brachyura) opisani su po Latreilleu 1803. godine i većina karcinologa smatrala ih je do sada prirodnom skupinom — svojtom. Međutim, broj porodica koje su je sačinjavale kolebao je tijekom vremena. Prema današnjem shvaćanju obuhvaćaju slijedeće porodice: Majidae, Parthenopidae, Hymenosomatidae, a među njih bi se trebala uvrstiti i novoopisana porodica Mimi-lambridae. Kritičko preispitivanje sličnosti pokazuje da im zajednička svojstva nisu brojna i da su ova više posljedica konvergentne evolucije nego zajedničkog podrijetla. Razlike postoje u većini svojstava, osobito ekoloških. Dosljedno tome, Oxyrhyncha nisu prirodna skupina, a četiri spomenute porodice trebaju promijeniti svoj status i položaj u sistemu kratkorepih rakova (Decapoda Brachyura).