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THE SUPERFAMILIES, FAMILIES, AND GENERA OF RECENT STOMATOPOD CRUSTACEA, WITH DIAGNOSES OF SIX NEW FAMILIES

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Abstract.—Four new superfamilies are recognized: Bathysquilloidea, Gonodactyloidea, Lysiosquilloidea, and Squilloidea. Six new families are recognized: Hemisquillidae, for *Hemisquilla*, formerly assigned to the Pseudosquillidae; Odontodactylidae, for *Odontodactylus*, and Protosquillidae, for *Protosquilla* and three other genera, all formerly assigned to the Gonodactylidae; Coronididae and Nannosquillidae, based on three and 10 genera, respectively, previously assigned to the Lysiosquillidae; and Harpiosquillidae, for *Harpiosquilla*, previously assigned to the Squillidae. The first four new families have raptorial claws adapted for smashing, the last two for spearing. Original citations for the six previously established families and all 66 currently recognized genera of Recent Stomatopoda are included.

A review of the classification of Recent Stomatopoda has been in preparation for several years. Its completion has been delayed unavoidably and regrettably will be delayed further. Accounts now in preparation of the results of several different studies will be more meaningful if the proposed classification, which is now in manuscript form, could be used in them. For this reason, this account of six new families, accompanied by a key to superfamilies and families as well as a list of genera belonging to them, is presented here.

The more detailed review takes into account recent findings in morphology, evidence from behavioral studies by colleagues, and other information, such as the determination that although species of some genera, such as *Gonodactylus* (see Manning and Provenzano, 1963) and *Squilla* (see Giesbrecht, 1910), carry their egg mass in an irregular ball, some members of at least one genus, *Nannosquilla*, attach their eggs singly to the sides of their burrow (Manning, 1979), demonstrating fundamental differences in brood care within the group.

Recent studies on agonistic behavior of stomatopods (Caldwell and Dingle, 1975) have revealed the functional significance of the two kinds of raptorial claw found in the group. One is a spearing appendage, with a slender dactylus armed with teeth on its opposable margin, adapted for preying on soft bodied organisms; it is found in squillids, eurysquillids, pseudosquillids, and most of the genera then assigned to the Lysiosquillidae. The other is a

smashing appendage, with the dactylus inflated proximally and usually unarmed, adapted for feeding on hard-bodied organisms such as mollusks and crustaceans: it is found in most genera hitherto assigned to the Gonodactylidae.

Three genera, *Coronida, Neocoronida,* and *Parvisquilla,* currently assigned to the Lysiosquillidae, differ from the remaining members of the family in that they possess a smashing claw (Manning, 1978a: figs. 7*b,* 8*c*). A second group of 10 genera, *Nannosquilla* and allies, that has been placed in the Lysiosquillidae, differ from other lysiosquillids in their smaller size, in the shape of the endopods of the walking legs, and in having a distinct proximal fold on the inner margin of the uropodal endopod (Manning, 1969b: 21, first couplet of key). Each of these two groups of genera are assigned to new families.

Members of one genus of the very diverse family Squillidae, *Harpiosquilla,* share the spearing claw with the other members of that family, but differ in size and in numerous morphological features, including the deep excavations of the posterolateral angles of the carapace, unique within the Stomatopoda, and the structure of the claw, with numerous long, erect spines replacing the usual pectinations on the opposable margin of the propodus (Manning, 1969c). *Harpiosquilla* is relegated to a new family.

The representatives of the genus *Hemisquilla,* until now recognized as belonging to the Pseudosquillidae, differ from those of other genera in the family in being much larger, in having a large, globular eye, and in having an unarmed smashing claw (Manning, 1969b: figs. 68, 69), rather than a slender spearing claw armed with three or more teeth. *Hemisquilla* is assigned to a new family.

Certain genera previously recognized as belonging to the Gonodactylidae are transferred to new families. One contains *Odontodactylus* which differs from gonodactylids in being much larger, in having a different kind of telson ornamentation, a rostral plate that lacks an apical spine, and in having the dactylus of the smashing claw provided with teeth; the ischiomeral articulation of the claw in *Odontodactylus* is subterminal, as however, it is in the Gonodactylidae *s.s.* (Manning, 1969b: figs. 80, 81). A second group of four genera, related to *Protosquilla,* agrees with almost all other Recent stomatopods and differs from the Gonodactylidae as restricted herein in having the articulation of the distal segment of the uropod terminal rather than subterminal (compare figures 6b and 7b, terminal articulation, with figures 1b and 3c, subterminal articulation, in Manning, 1969a); these four genera are assigned to a new family herein.

The Stomatopoda represent an old crustacean stock, the Hoplocarida (Schram, 1969, 1973), the Recent members of which in my opinion are far more diverse than suggested by past classifications. Many genera that are now recognized appear to be relicts, broadly distributed but containing few

species, each with relatively restricted ranges: *Pseudosquillopsis*, with one species in the East Atlantic, two in the East Pacific, and one in the Indo-West Pacific (Manning, 1977a: fig. 50), is a good example. Other genera, like *Gonodactylus* (35+ species), *Squilla* (30 species), and *Oratosquilla* (22 species), with larger numbers of species, each usually occupying relatively broad ranges, may well represent younger stock.

The proposed familial revision does not alter the concept that Recent Stomatopoda comprises four distinct lineages: 1, bathysquillid (Bathysquillidae); 2, squillid (Harpiosquillidae and Squillidae); 3, gonodactylid (Eurysquillidae, Gonodactylidae, Hemisquillidae, Odontodactylidae, Protosquillidae, and Pseudosquillidae); and 4, lysiosquillid (Coronididae, Lysiosquillidae, and Nannosquillidae). These four lineages are recognized herein as new superfamilies.

The Order Stomatopoda recently was divided into two suborders by Schram (1969). The Suborder Archaeostomatopoda Schram (1969:260) was established for the fossil family Tyrannophontidae Schram (1969:260), containing the single genus *Tyrannophontes* Schram (1969:260), represented by a single species from the Middle Pennsylvanian. The Suborder Opisterostomatopodea Schram (1969:266) was established to contain the fossil family Sculdidae Dames (1886:565), in which the uropodal exopod is one-segmented, and the four families of Recent Stomatopoda then recognized, Bathysquillidae, Gonodactylidae, Lysiosquillidae, and Squillidae, in which the uropodal exopod is two-segmented.

However, as pointed out by Holthuis and Manning (1969:R542), the subordinal category Unipeltata Latreille (1825:283) was recognized by that author for the Stomatopoda *sensu stricto*. Unipeltata Latreille has clear precedence over Opisterostomatopodea Schram.

It is clear that several morphological features, important at different levels of classification, have been retained or developed independently in different stomatopod lineages, including: body carination (Squillidae and Harpiosquillidae); smashing claws in the Coronididae and the Gonodactylidae, Hemisquillidae, Odontodactylidae, and Protosquillidae (armed with teeth in the Coronididae and Odontodactylidae), spearing claws in the other families; elongate antennular somite in *Parvisquilla* (Coronididae), *Eurysquilloides* (Eurysquillidae), and *Leptosquilla* and *Tulеariosquilla* (Squillidae); and spined rather than pectinate opposable margin of the propodus of the claw in Bathysquillidae and Harpiosquillidae.

These changes in the classification of Recent stomatopods have resulted largely from my own observations, some unpublished, stimulated and aided by discussions of problems in the group with Roy L. Caldwell, University of California, Berkeley, Hugh Dingle, University of Iowa, and Marjorie L. Reaka, University of Maryland, all of whom have freely shared field observations with me.

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Superfamilies, Families, and Genera of Recent Stomatopoda

Superfamily Bathysquilloidea Manning, 1967

Diagnosis.—Propodi of posterior 3 maxillipeds slender, not beaded or ribbed ventrally. Telson with distinct median carina. All marginal teeth of telson with movable apices.

Included families.—Bathysquillidae Manning, 1967.

Family Bathysquillidae Manning (1967:238)

Diagnosis.—Size large to very large. Body loosely articulated, depressed. Propodus of claw with erect spines, dactylus slender, opposable margin with teeth.

Included genera.—Two: *Bathysquilla* Manning (1963:323) and *Indosquilla* Ingle and Merrett (1971:193).

Superfamily Gonodactyloidea Giesbrecht, 1910

Diagnosis.—Propodi of posterior 3 maxillipeds slender, not beaded or ribbed ventrally. Telson with distinct median carina. At most submedian teeth of telson with movable apices. No more than 2 intermediate denticles present on telson.

Included families.—Eurysquillidae Manning, 1977, Gonodactylidae Giesbrecht, 1910, Hemisquillidae, new family, Odontodactylidae, new family, Protosquillidae, new family, and Pseudosquillidae Manning, 1967.

Family Eurysquillidae Manning (1977a:33)

Diagnosis.—Size very small to moderate. Body loosely articulated, depressed. Rostral plate unarmed or with up to 2 apical spines. Ischiomeral articulation of raptorial claw terminal. Dactylus of claw slender, not inflated basally, opposable margin armed with 4 or more teeth. Articulation of uropod segments terminal.

Included genera.—Five: *Coronidopsis* Hansen (1926:19), *Eurysquilla* Manning (1963:314), *Eurysquilloides* Manning (1963:315), *Manningia* Serène (1962:20), and *Sinosquilla* Liu and Yongliang (1978:89) [a senior synonym of *Eurysquillopsis* Makarov (1978:185)].

Family Gonodactylidae Giesbrecht (1910:148)

Diagnosis.—Size very small to moderate. Body compact, subcylindrical. Rostral plate with apical spine. Ischiomeral articulation of raptorial claw

subterminal. Dactylus of claw stout, inflated basally, opposable margin unarmed. Articulation of uropodal exopod segments subterminal.

Included genera.—Seven: *Gonodactylolus* Manning (1970:206), *Gonodactylopsis* Manning (1969a:149), *Gonodactylus* Berthold (1827:271), *Hoplosquilla* Holthuis (1964:141), *Hoplosquilloides* Manning (1978a:6), *Mesacturoides* Manning (1978b:1), and *Mesacturus* Miers (1880:124).

Hemisquillidae, new family

Diagnosis.—Size large. Body compact, depressed. Rostral plate triangular, lacking apical spine. Ischiomeral articulation of claw terminal, merus not projecting posteriorly. Dactylus of claw inflated basally, opposable margin unarmed. Articulation of uropodal exopod segments terminal.

Included genera.—One, the type-genus, *Hemisquilla* Hansen (1895:72).

Odontodactylidae, new family

Diagnosis.—Size moderate to large. Body compact, subcylindrical. Rostral plate unarmed. Ischiomeral articulation of claw subterminal. Dactylus of claw inflated basally, opposable margin with teeth. Articulation of uropod exopod segments terminal.

Included genera.—One, the type-genus, *Odontodactylus* Bigelow (1893:100).

Protosquillidae, new family

Diagnosis.—Size very small to moderate. Body compact, subcylindrical. Rostral plate trispinous. Ischiomeral articulation of claw subterminal. Dactylus of claw inflated basally, opposable margin unarmed. Articulation of uropod exopod segments terminal.

Included genera.—Four: the type-genus *Protosquilla* Brooks (1886:84), *Chorisquilla* Manning (1969a:157), *Echinosquilla* Manning (1969a:155), and *Haptosquilla* Manning (1969a:159).

Family Pseudosquillidae Manning (1977a:95)

Diagnosis.—Size small to moderate. Body compact, subcylindrical or depressed. Rostral plate unarmed or with apical spine. Ischiomeral articulation of claw terminal. Dactylus of claw slender, opposable margin with teeth. Articulation of uropodal exopod segments terminal.

Included genera.—Four: *Faughnia* Serène (1962:17) (see Manning and Makarov, 1978:517), *Parasquilla* Manning (1961:7), *Pseudosquilla* Dana (1852:615), and *Pseudosquillopsis* Serène (1962:12).

Superfamily Squilloidea Latreille, 1803

Diagnosis.—Propodi of posterior 3 maxillipeds slender, not beaded or ribbed ventrally. Telson with distinct median carina. At most submedian teeth of telson with movable apices. 4 or more intermediate denticles present on telson.

Included families.—Harpiosquillidae, new family, and Squillidae Latreille, 1803.

Harpiosquillidae, new family

Diagnosis.—Size large to very large. Body depressed, carinate. Carapace with posterolateral margin deeply excavate. Propodus of claw with erect spines on opposable margin.

Included genera.—One, the type-genus, *Harpiosquilla* Holthuis (1964:140).

Family Squillidae Latreille (1803:36)

Diagnosis.—Size small to large. Body depressed, carinate. Posterolateral margin of carapace without deep excavation. Propodus of claw pectinate on opposable margin.

Included genera.—24: *Alima* Leach (in Tuckey, 1817: unnumbered plate), *Alimopsis* Manning (1977b:421), *Anchisquilla* Manning (1968:127), *Anchisquilloides* Manning (1977b:421), *Areosquilla* Manning (1976b:2), *Busquilla* Manning (1978a:23), *Carinosquilla* Manning (1968:135), *Clorida* Eydoux and Souleyet (1842:264), *Cloridopsis* Manning (1968:128), *Distosquilla* Manning (1977b:421), *Dictyosquilla* Manning (1968:131), *Kempina* Manning (1978c:39), *Lenisquilla* Manning (1977b:422), *Levisquilla* Manning (1977b:422), *Leptosquilla* Miers (1880:12), *Lophosquilla* Manning (1968:133), *Meiosquilla* Manning (1968:125), *Natosquilla* Manning (1978c:40), *Oratosquilla* Manning (1968:133), *Pterygosquilla* Hilgendorf (1890:172), *Schmittius* Manning (1972:300), *Squilla* Fabricius (1787:333), *Squilloides* Manning (1968:131), and *Tulеariosquilla* Manning (1978a:30).

Superfamily Lysiosquilloidea Giesbrecht, 1910

Diagnosis.—Propodi of posterior 3 maxillipeds broad, usually beaded or ribbed ventrally. Telson lacking distinct median carina. At most submedian teeth of telson with movable apices.

Included families.—Coronididae, new family, Lysiosquillidae Giesbrecht, 1910, and Nannosquillidae, new family.

Coronididae, new family

Diagnosis.—Size very small to moderate. Body depressed, compact. Dactylus of claw inflated basally, with teeth on opposable margin. Endopods of

walking legs slender. Uropodal endopod lacking proximal fold on inner margin.

Included genera.—Three: *Coronida* Brooks (1886:84), the type-genus; *Neocoronida* Manning (1976a:222); and *Parvisquilla* Manning (1973:299).

Family Lysiosquillidae Giesbrecht (1910:148)

Diagnosis.—Size moderate to very large. Body loosely articulated, depressed. Dactylus of claw not inflated basally. Endopods of walking legs slender. Uropodal endopod lacking proximal fold on inner margin.

Included genera.—Four: *Heterosquilla* Manning (1963:320), *Heterosquilloides* Manning (1966:124) (until now considered to be a subgenus of *Heterosquilla*), *Lysiosquilla* Dana (1852:615), and *Lysiosquilloides* Manning (1977a:84).

Nannosquillidae, new family

Diagnosis.—Size very small to moderate. Body loosely articulated, depressed. Dactylus of claw not inflated basally. Endopods of anterior 2 walking legs ovate or subcircular. Uropodal endopod with strong proximal fold on outer margin.

Included genera.—Ten: *Acanthosquilla* Manning (1963:319); *Allosquilla* Manning (1977a:64); *Austrosquilla* Manning (1966:127); *Coronis* Desmarest (1823:345); *Hadrosquilla* Manning (1966:115); *Keppelius* Manning (1978a:9); *Nannosquilla* Manning (1963:318), the type-genus; *Nannosquilloides* Manning (1977a:89); *Platysquilla* Manning (1967:238); and *Pullosquilla* Manning (1978a:18).

Key to the Recent Superfamilies and Families of Stomatopoda

1. Propodi of third and fourth maxillipeds broad, usually beaded or ribbed ventrally. (Telson lacking sharp median carina) [Lysiosquilloidea] **2**
– Propodi of third and fourth maxillipeds slender, not beaded or ribbed ventrally (Telson with sharp median carina) **4**
2. Distal segment of endopod of anterior 2 walking legs broadly ovate or subcircular. Proximal portion of outer margin of uropodal endopod with strong fold ..... Nannosquillidae, new family
– Distal segment of endopod of anterior two walking legs strap-shaped, elongate. Proximal portion of outer margin of uropodal endopod lacking strong fold **3**
3. Dactylus of claw inflated basally. Propodus of claw pectinate proximally only. Rostral plate rounded or subrectangular .... Coronididae, new family

– Dactylus of claw not inflated basally. Propodus of claw fully pectinate. Rostral plate cordiform or triangular .. Lysiosquillidae Giesbrecht

4. All marginal teeth of telson with movable apices [Bathysquilloidea] ..... Bathysquillidae Manning

– At most submedian marginal teeth with movable apices **5**

5. Four or more intermediate denticles present on telson [Squilloidea] **6**

– No more than 2 intermediate denticles present on telson [Gonodactyloidea] **7**

6. Posterolateral angles of carapace deeply emarginate .... Harpiosquillidae, new family

– Posterolateral angles of carapace rounded. Propodus of claw pectinate, lacking erect spines ..... Squillidae Latreille

7. Ischiomeral articulation of claw subterminal, merus projecting posteriorly beyond articulation. Dactylus of claw inflated basally, with prominent, rounded projection on outer (extensor) margin **8**

– Ischiomeral articulation of claw terminal, merus not projecting posteriorly beyond articulation. Dactylus of claw not broadly inflated, lacking prominent projection on outer (extensor) margin **10**

8. Rostral plate lacking apical spine. Dactylus of claw with teeth on inner (flexor) margin ..... Odontodactylidae, new family

– Rostral plate with apical spine. Dactylus unarmed on inner margin **9**

9. Articulation of segments of uropodal exopod subterminal, proximal segment projecting posteriorly beyond articulation .... Gonodactylidae Giesbrecht

– Articulation of segments of uropodal exopod terminal, proximal segment not projecting posteriorly beyond articulation .... Protosquillidae, new family

10. Rostral plate triangular. Cornea globular. Dactylus of claw unarmed ..... Hemisquillidae, new family

– Rostral plate oval or pentagonal, not triangular. Cornea not globular. Dactylus of claw with teeth **11**

11. Body loosely articulated. Dactylus of claw with 4 or more teeth ..... Eurysquillidae Manning

– Body compact. Dactylus of claw with no more than 3 teeth .... Pseudosquillidae Manning

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