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PRELIMINARY REVISION OF THE GENERA
PSEUDOSQUILLA AND *LYSIOSQUILLA*
 WITH DESCRIPTIONS OF SIX NEW GENERA
 (CRUSTACEA: STOMATOPODA)¹

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ABSTRACT

Two of the eleven currently recognized genera of stomatopod crustaceans, *Pseudosquilla* Dana, 1852 and *Lysiosquilla* Dana, 1852, are shown to be catchalls of unrelated species. Seven genera are recognized in the *Pseudosquilla* complex, including two new genera, *Eurysquilla* and *Eurysquilloides*. Other genera considered to be related to *Pseudosquilla* are *Pseudosquillopsis* Serène, 1962, *Parasquilla* Manning, 1961, *Manningia* Serène, 1962, and *Coronidopsis* Hansen, 1926. Six genera are recognized in the *Lysiosquilla* complex, of which three, *Nannosquilla*, *Acanthosquilla*, and *Heterosquilla*, are described as new. *Coronis* Desmarest, 1823, is recognized, and *Coronida* Brooks, 1886, is believed to be related to *Lysiosquilla*, which is restricted to *L. maculata* and similar species. *Bathysquilla* is described and is shown to be unrelated to the *Lysiosquilla* complex. Diagnoses are given for each of these 14 genera, and all described species in each of the genera are listed.

INTRODUCTION

The generic classification of the stomatopod crustaceans has remained relatively stable since the publication of Kemp's monograph of the Indo-Pacific species in 1913. This is due in part to Kemp's influence and his thorough coverage, and in part to our lack of knowledge. Kemp (1913) recognized six genera: *Gonodactylus* Latreille, 1825, *Odontodactylus* Bigelow, 1893, *Pseudosquilla* Dana, 1852, *Lysiosquilla* Dana, 1852, *Coronida* Brooks, 1886, and *Squilla* Fabricius, 1787. He overlooked *Hemisquilla* Hansen, 1895, but subsequently recognized it (Kemp and Chopra, 1921). *Coronidopsis*, supposedly related to *Coronida*, was described by Hansen (1926). Manning (1961) erected *Parasquilla* for the aberrant *Squilla ferussaci* Roux and an American species. Serène (1962) separated *Pseudosquillopsis* and *Manningia* from the heterogenous *Pseudosquilla*. By 1962, a total of 11 genera were recognized.

The present effort to achieve a more satisfactory and natural classification within the Stomatopoda is the result of studies on American species, supplemented by material from the Indo-Pacific region. As a fair percentage of the known species of *Pseudosquilla* and *Lysiosquilla* are American, this work is restricted to a revision of those genera and related forms described in other genera. Publication of these conclusions was prompted in part

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by Serène's revision of *Pseudosquilla*, published in 1962, which did not come to my attention until most of the ideas presented here were formulated.

It is hoped that the preliminary nature of this paper will not detract from its value. Some of the ideas concerning relationships presented herein will undoubtedly be considered unconventional, and comments on this scheme from other carcinologists will be welcome. The diagnoses and discussion presented herein will be enlarged and accompanied by complete definitions, synonymies, and illustrations in a monograph of northwestern Atlantic stomatopods now in preparation.

In the list of species under each genus, an asterisk (*) preceding the name indicates that I have examined material of that species.

I must express my thanks to Raoul Serène for agreeing to allow me to publish my ideas before he completes the revisionary studies alluded to in his review of *Pseudosquilla*.

I would also like to thank G. L. Voss and F. M. Bayer, Institute of Marine Science, for reviewing the manuscript; F. A. Chace, Jr., U.S. National Museum, for his comments and encouragement throughout the course of my work on stomatopods; L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden, for his comments and technical advice; and W. D. Field, U.S. National Museum, for supplying information on the date of publication of *Coronis* Huebner. I would also like to thank the National Science Foundation for its support under Grant GB-389; this paper constitutes a technical report to that organization.

PSEUDOSQUILLA AND ALLIES

Three groups of species recently have been separated from this genus. Manning (1961) established *Parasquilla* for *Squilla ferussaci* Roux (also placed in *Pseudosquilla*) and another species, *meridionalis*. Serène (1962) recognized the distinctness of *Pseudosquilla cerisii* and its allies from *Pseudosquilla ciliata* and its relatives, and proposed for it the genus *Pseudosquillopsis* (type species, *Squilla cerisii* Roux, 1828). He included the following species in the nominate subgenus *Pseudosquillopsis*: *Squilla cerisii* Roux, 1828; *Squilla lessonii* Guérin, 1830; and *Pseudosquilla dofleini* Balss, 1910. In the monotypic subgenus *Faughnia*, Serène included *Pseudosquilla haani* Holthuis, 1959 (substitute name for *Squilla empusa* de Haan, 1844). Serène also erected *Manningia* for *Pseudosquilla pilaensis* de Man, 1888, Serène deferred changing the status of the following species currently included in *Pseudosquilla*: *P. veleronis* Schmitt, 1940; *Lysiosquilla maiaguesensis* Bigelow, 1901; *L. plumata* Bigelow, 1901. He noted that revision of these species should wait until analogous species in *Lysiosquilla* (especially *L. sewelli* Chopra, 1939) were revised.

Serène's account is very good in many ways. He pointed out the

importance of several characters, especially the shape of the eye, not previously stressed. He was correct in recognizing the fundamental differences between *P. cerisii* and its allies and *P. ciliata* and its allies, and in stressing the distinctness of *P. pilaensis* de Man.

Serène was aware that *S. lessonii* has been chosen as the type of *Pseudosquilla* Dana and that recognition of *cerisii* and allies would necessitate the erection of a new genus for *ciliata* and related species. This would cause great confusion, for it is the well-known *P. ciliata* which has been commonly associated with the generic name. As Serène (p. 11) noted, *ciliata* has appeared in the literature more than 100 times. Unfortunately, Serène did not recognize Dana's (1852) validation of the name *Pseudosquilla*. Instead, he referred to the account of the genus given by Eydoux and Souleyet (1841) in which (p. 263) they refer to a subgenus ("Pseudosquille") which Guérin apparently had intended to separate from *Squilla*. The name "Pseudosquille," however, was published in the vernacular and, under the present Code, cannot be used. Since Rathbun (1926, p. 137) designated *lessonii* as the type-species of *Pseudosquilla* Dana, 1852, *Pseudosquillopsis* Serène, 1962, is a subjective synonym.

The problem is further complicated by the fact that two names originally proposed for larval forms, *Pseuderichthus* Brooks, 1886, p. 16 [type species, by present selection, *Pseudosquilla ciliata* (Fabricius 1787)], and *Alimerichthus* Guérin-Méneville, 1857, p. lxiv [type species, by present selection, *Alimerichthus cylindricus* Guérin-Méneville, 1857], are available for the genus which includes *Squilla ciliata* and its allies. Hansen (1895) identified his *Pseuderichthus communis* as the pelagic larva of *Pseudosquilla ciliata*, and Gurney (1946) identified *A. cylindricus* with *P. communis*. Thus, if *Pseudosquilla* is retained for *P. lessonii*, the name *Alimerichthus* must be used for *ciliata* and its allies.

I must agree with Serène that changing the generic name of the well-known *ciliata* will cause a great deal of confusion. Moreover, the next nomenclaturally available name for it, *Alimerichthus*, is now in current use as a category name for a particular type of stomatopod larva.

This problem could be settled easily by setting aside Rathbun's type designation in favor of *Squilla ciliata* Fabricius, 1787, as the type species of *Pseudosquilla* Dana, 1852. Thus, both *Alimerichthus* Guérin-Méneville, 1857, and *Pseuderichthus* Brooks, 1886, would become subjective junior synonyms of *Pseudosquilla* Dana, 1852. A petition to the International Commission on Zoological Nomenclature for the use of its Plenary Powers to suppress *S. lessonii* in favor of *S. ciliata* as the type species of *Pseudosquilla* is being prepared. Until this petition is acted upon, *Pseudosquilla* will be used by me in the restricted sense employed by Serène (1962). *Pseudosquillopsis* (*Pseudosquillopsis*) Serène, 1962, proposed for *S. cerisii*, *S. lessonii*, and *P. dofeini*, would be validated by this action and will be used by me until the Commission has taken action.

The subgenus *Faughnia* Serène, 1962, of *Pseudosquilla* is here transferred to *Parasquilla*. Two new genera, one including *Lysiosquilla plumata* Bigelow, 1901, and related species, and one including only *Squilla sibogae* Hansen, 1926, are described below. In my opinion, none of the genera listed below are related to any of the groups of species now included in *Lysiosquilla sensu lato*.

Pseudosquilla Dana, 1852

"Pseudosquille" Eydoux and Souleyet, 1841, p. 263.

Pseudosquilla Dana, 1852, p. 615.

Alimerichthus Guérin-Méneville, 1857, p. lxiv.

Pseuderichthus Brooks, 1886, p. 16.

Diagnosis.—Body compact, compressed, smooth; cornea of eye cylindrical or expanded, rarely bilobed; rostral plate usually ovate; antennal protopod with a prominent, channeled dorsal process; carapace without cervical groove or carinae; raptorial claw slender, dactylus armed with three teeth, propodus pectinate proximally only; abdomen without sharp carinae on first five somites; telson slender, with sharp median crest and three or four pairs of longitudinal carinae; submedian denticles absent; submedian teeth with bases appressed; basal prolongation of uropod produced into two spines.

Remarks.—*Pseudosquilla* contains the following species:

1. **Squilla ciliata* Fabricius, 1787 (Atlantic; Indo-Pacific)
2. **Squilla oculata* Brullé, 1836-44 (Atlantic; Indo-Pacific)
3. **Pseudosquilla ornata* Miers, 1880 (Indo-Pacific)
4. **Pseudosquilla megalopthalma* Bigelow, 1893 (Indo-Pacific)
5. **Pseudosquilla oxyrhyncha* Borradaile, 1898 (Indo-Pacific)
6. **Pseudosquilla oculata*, Schmitt, 1940 (=n. sp.) (East Pacific)

The channeled dorsal process on the antennal protopod is a unique feature of this genus.

Type-species.—*Squilla ciliata* Fabricius, 1787, designated by Serène, 1962, p. 11 (in accordance with a petition being prepared for the ICZN).

Pseudosquillopsis Serène, 1962

Pseudosquillopsis (*Pseudosquillopsis*) Serène, 1962, p. 12 [non *P. (Faughnia)* Serène, 1962].

Diagnosis.—Body compact, compressed, smooth; cornea of eye bilobed, outer margin of eye longer than inner; rostral plate triangular, with long apical spine; carapace without cervical groove but with marginal carina, not recurved, on posterior portion of lateral plates; raptorial claw short, stout, dactylus armed with three teeth; propodus fully pectinate; abdomen without sharp carinae on first five somites; telson slender, with sharp crest and five

pairs of carinae; submedian teeth with bases appressed; basal prolongation of uropod with outer spine the longer, two smaller spines on inner margin.

Remarks.—This genus includes the following species:

1. **Squilla cerisii* Roux, 1828 (Mediterranean)
2. **Squilla lessonii* Guérin, 1830 (East Pacific)
3. *Pseudosquilla dofleini* Balss, 1910 (Indo-Pacific)

Pseudosquillopsis agrees with *Pseudosquilla* in that the body is smooth, compact, with the abdomen strongly compressed and not carinate anteriorly; the raptorial dactylus is armed with three teeth; submedian denticles are absent and the bases of the submedian teeth are appressed. *Pseudosquillopsis* differs from *Pseudosquilla* as follows: there is no channeled dorsal process on the antennal protopod; the cornea of the eye is strongly bilobed, and set differently on the stalk; marginal carinae are present on the carapace; the raptorial claw is stout and the propodus is fully pectinate; the basal prolongation of the uropod terminates in a long outer spine with two smaller spines on its inner margin.

Type-species.—*Squilla cerisii* Roux, 1828, designated by Serène, 1962, p. 16.

Parasquilla Manning, 1961

Parasquilla Manning, 1961, p. 7.

Pseudosquillopsis (Faughnia) Serène, 1962, p. 17.

Diagnosis.—Body compact, depressed, minutely pitted; cornea of eye bilobed, outer margin of eye longer than inner; rostral plate pentagonal, without apical spine; carapace with cervical groove, marginal carinae present on posterior portion of lateral plates; raptorial claw short, stout, dactylus armed with three teeth, propodus fully pectinate; abdomen with sharp carinae on first five somites; telson slender, with sharp crest and at most one pair of dorsal carinae; submedian denticles present; submedian teeth with bases separate; uropod with outer spine the longer and with two smaller spines on inner margin.

Remarks.—The original generic diagnosis is here expanded to include *Pseudosquillopsis (Faughnia)* Serène, 1962. The monotypic *Faughnia*, proposed for *Pseudosquilla haani* Holthuis, 1959, differs from the nominate subgenus in two features: the marginal carinae of the carapace are not recurved and the submedian abdominal carinae are absent. *Parasquilla* now contains the following species:

1. **Squilla ferussaci* Roux, 1828 (East Atlantic)
2. **Pseudosquilla haani* Holthuis, 1959 (Indo-Pacific)
3. **Parasquilla meridionalis* Manning, 1961 (West Atlantic)
4. **Parasquilla coccinea* Manning, 1962 (West Atlantic)

Parasquilla agrees with both *Pseudosquilla* and *Pseudosquillopsis* in having the raptorial dactylus armed with three teeth and in the overall slender shape of the telson. It differs from both in the rugose body, pentagonal rostral plate, carinate abdomen, presence of submedian denticles, and separation of submedian teeth of the telson. It further agrees with *Pseudosquillopsis* in eye shape, pectination of raptorial propodus, and structure of uropod.

Type-species.—*Parasquilla meridionalis* Manning, 1961, by original designation.

Manningia Serène, 1962

Manningia Serène, 1962, p. 20.

Diagnosis.—Body compact, depressed, smooth; cornea of eye bilobed, outer margin of eye longer than inner; rostral plate pentagonal, without apical spine; carapace without cervical groove, marginal carinae present on posterior portion of lateral plates; raptorial claw short, stout, dactylus armed with four teeth; propodus fully pectinate; first five abdominal somites without carinae; telson broad, with crest and five pairs of carinae; submedian denticles absent; bases of submedian teeth appressed; basal prolongation of uropod produced into two spines, inner longer, with a row of slender spinules on inner margin.

Remarks.—This genus includes only one species:

1. **Pseudosquilla pilaensis* de Man, 1888 (Indo-Pacific)

Manningia differs from *Pseudosquilla*, *Pseudosquillopsis*, and *Parasquilla* in that the raptorial claw is armed with four teeth, the telson is broader, and the basal prolongation of the uropod has the inner spine much the longer. It further differs from *Pseudosquilla* in the following features: bilobed cornea and shape of eye; pentagonal rostral plate; marginal carina on the carapace; raptorial propodus fully pectinate; and body depressed. It differs from *Parasquilla* in lacking submedian denticles and abdominal carinae. It agrees with *Pseudosquillopsis* and *Parasquilla* in eye shape and in propodal pectination, and differs from *Pseudosquillopsis* but agrees with *Parasquilla* in having a pentagonal rostral plate.

Type-species.—*Pseudosquilla pilaensis* de Man, 1888, by monotypy.

Coronidopsis Hansen, 1926

Coronidopsis Hansen, 1926, p. 19.

Diagnosis.—Body depressed, smooth; cornea of eye bilobed; rostral plate with two anterior spines; carapace without cervical groove, marginal carinae present on posterior portion of lateral plates; raptorial claw short, stout, dactylus armed with four teeth, propodus fully pectinate; first four ab-

dominal somites without carinae; telson broad, with sharp median crest, remainder of dorsal surface ornamented with spinules; submedian denticles absent, bases of submedian teeth appressed; basal prolongation of uropod produced into two spines, inner longer, with a row of slender spinules on inner margin.

Remarks.—This genus includes only one species:

1. *Coronidopsis bicuspis* Hansen, 1926 (Indo-Malaya)

Coronidopsis, based on a single specimen, differs from all other genera in having the rostral plate armed with two anterior spines; if this feature proves to be abnormal, there will be little reason for maintaining *Manningia* as a distinct genus. *Coronidopsis* appears to be closely related to *Manningia*, sharing the following features with it: cornea bilobed; cervical groove absent, short marginal carinae present; raptorial claw armed with four teeth, propodus fully pectinate; telson broad, lacking submedian denticles; intermediate denticles represented by two lobes, outer with a ventral spinule, and lateral denticles with a ventral spinule; basal prolongation of uropod with inner spine longer and a row of spinules on inner margin.

Hansen (1926) stated that *Coronidopsis* was allied to *Squilla* and *Coronida*. In my opinion it is related to neither of these but to *Manningia* and the new genus described below.

Type-species.—*Coronidopsis bicuspis* Hansen, 1926, by monotypy.

Eurysquilla, new genus

Diagnosis.—Body smooth, depressed, loosely articulated; cornea of eyes variable, rounded or bilobed; rostral plate triangular; carapace without cervical groove, marginal carina present on posterior portion of lateral plates; raptorial claw slender, dactylus with more than seven teeth, propodus fully pectinate; abdomen without sharp carinae on first three somites; occasionally carinate on fourth and fifth somite; sixth somite with submedian carinae poorly indicated or absent; six posterior spines present; telson broad, with a sharp crest and one or more pairs of longitudinal carinae; submedian teeth with movable apices, bases appressed; submedian denticles absent; basal prolongation of uropod produced into two spines, inner longer; inner margin of basal prolongation with a row of slender spinules, a single spine or lobe, or unarmed.

Remarks.—This genus contains four species:

1. **Lysiosquilla plumata* Bigelow, 1901 (West Atlantic)
2. **Lysiosquilla maiaguesensis* Bigelow, 1901 (West Atlantic)
3. *Lysiosquilla sewelli* Chopra, 1939 (Gulf of Aden)
4. **Pseudosquilla veleronis* Schmitt, 1940 (East Pacific)

Eurysquilla differs from *Pseudosquilla*, *Pseudosquillopsis*, and *Para-*

squilla in having a broad telson and in the shape of the basal prolongation of the uropod; in these two features *Eurysquilla* agrees with *Coronidopsis* and *Manningia*. *Eurysquilla* further differs from all these genera in that the raptorial dactylus is slender, armed with seven or more teeth.

Type-species.—*Lysiosquilla plumata* Bigelow, 1901.

Gender.—Feminine.

Etymology.—The generic name is derived from the Greek, *eurys*, meaning broad, and the generic name *Squilla*.

***Eurysquilloides*, new genus**

Diagnosis.—Body smooth, depressed; cornea of eye expanded but not bilobed; rostral plate rounded; carapace narrowed anteriorly, without cervical groove or carinae (?); raptorial claw slender, dactylus with eight or nine teeth, propodus pectinate proximally only; first five abdominal somites with carinae, submedians absent; telson with a sharp crest and one pair of dorsal carinae; submedian denticles present; submedian teeth with bases separated; basal prolongation of uropod produced into two spines, inner longer.

Remarks.—*Eurysquilloides* includes only one species:

1. *Squilla sibogae* Hansen, 1926 (Indo Malaya)

In my opinion this genus shows close resemblance to *Eurysquilla*, but differs in the following features: raptorial propodus not fully pectinate; carapace without marginal carina; abdomen partially carinate; submedian carinae well defined on sixth abdominal somite; submedian denticles present; submedian teeth with bases separated. It agrees with *Eurysquilla*, *Manningia* and *Coronidopsis* in shape of telson and structure of uropod. Finally, it differs from all these genera in the extreme elongation of the antennular somite.

Type-species.—*Squilla sibogae* Hansen, 1926.

Gender.—Masculine.

Etymology.—The generic name is derived from the Greek, *oides*, meaning like, and the generic name *Eurysquilla*.

DISCUSSION OF THE *PSEUDOSQUILLA* COMPLEX

The following distinct features link together the seven genera discussed above:

1. The propodi of the third and fourth maxillipeds are slender.
2. The telson has a sharp median crest.
3. The posterior armature of the telson consists of three pairs of teeth,

submedians, intermediates, and laterals, and the submedians always have movable apices.

4. There are no more than two intermediate denticles and one lateral denticle. The intermediate denticles may be present in the following forms: (a) two sharp spinules; (b) two rounded spinules, each with or without an apical spine; (c) two rounded or truncate lobes, outer with a ventral spinule. The lateral denticle may be rounded or truncate, with or without an apical or ventral spinule.

These features not only link all of these genera but also separate them from *Lysiosquilla sensu lato* and *Coronida*, which have broad propodi on the third and fourth maxillipeds and lack a sharp crest on the telson, and from *Squilla*, which typically has more than four intermediate denticles. Further, these features link the seven genera of the *Pseudosquilla* complex with *Gonodactylus*, *Odontodactylus*, and *Hemisquilla*.

This realignment of genera also brings out another feature. Body carination or lack of it cannot be regarded as proof of common descent. The abdominal carination of *Parasquilla* and *Eurysquilloides* does not any more link them to *Squilla* than the depressed body of *Eurysquilla* links it to *Lysiosquilla*. Whether or not body carination is an old feature, retained in some genera and lost in others, or is a new feature present in only a few genera, cannot be determined at the present time.

Although I realize that segmentation of the inner branch of the walking legs is a character of importance in *Pseudosquilla* and allies, this character has not been described for all species and it is not stressed in the present account.

LYSIOSQUILLA AND ALLIES

The genus *Lysiosquilla* was erected by Dana in 1852 for four species: *Squilla maculata* Fabricius, 1793; *Squilla vittata* H. Milne-Edwards, 1837 (now *L. glabriuscula*); *S. scabricauda* Lamarck, 1818; and a new species, *L. inornata*, a synonym of *scabricauda*. In 1913, Kemp included 28 named species and "varieties," of which 13 were Indo-Pacific, three East Atlantic, and the remainder American; one American species, *L. platensis* Berg, 1900, was omitted from Kemp's list. Up to the present time, some 44 species and "varieties" have been included in the genus (excluding species included in *Eurysquilla*, above). Chace (1958) recorded eight western Atlantic species, and, at the present time (1963), 16 species have been recorded from that area.

This large increase in number of described species has provided an opportunity to evaluate various characters in the different groups of species in the genus. In his key to the species, Kemp (1913, p. 110) separated the genus into two groups of species, based on the presence or absence of dorsal spines on the telson. Chace (1958), who also commented on the

heterogeneity of the genus, used a similar subdivision in his key. The present subdivision of the genus is based primarily on this feature.

Two characters, position and number of antennal papillae and shape of the inner branch of the walking legs, are not stressed here, primarily because they have not always been recorded in species accounts. In *Lysiosquilla*, s.s. and *Coronida*, the inner branch of the walking legs is elongate; in most of the other genera the inner branch is ovate, broader on the first two legs than on the last. *Lysiosquilla* s.s. has three antennal papillae; these are absent or variable in number in the other genera.

In my opinion, the following characters are important in the recognition of genera in the *Lysiosquilla* complex: shape and size of eye; shape and size of rostral plate; structure and posterior armature of telson; and structure of uropod. The mandibular palp is apparently totally absent in one of the genera recognized below, present or variable in the other genera.

Lysiosquilla Dana, 1852

Lysiosquilla Dana, 1852, p. 616.

Diagnosis.—Body depressed, smooth; eyes large, bilobed; rostral plate cordiform or subtriangular; carapace without trace of carinae, spines, cervical groove on dorsum; antennal protopod with three papillae, one dorsal, two ventral; raptorial claw large, dactylus armed with five or more teeth, propodus pectinate throughout its length; propodi of third and fourth maxillipeds as broad as or broader than long; mandibular palp and five epipods present; thoracic and abdominal somites without longitudinal carinae; telson broad, without sharp crest, movable submedian marginal spines, or well-defined dorsal teeth; basal prolongation of uropod composed of two slender trefoil spines, inner much the longer. Size large, adults in excess of 90 mm TL, exceeding 300 mm in some cases.

Remarks.—*Lysiosquilla* is here restricted to the following species:

1. **Squilla maculata* Fabricius, 1793 (Indo-Pacific)
2. **Squilla labriuscula* Lamarck, 1818 (West Atlantic)
3. **Squilla scabricauda* Lamarck, 1818 (Atlantic)
4. *Squilla desaussurei* Stimpson, 1857 (East Pacific)
5. *Lysiosquilla capensis* Hansen, 1895 (South Africa)
6. **Lysiosquilla sulcirostris* Kemp, 1913 (Indo-Pacific)
7. *Lysiosquilla maculata tredecimdentata* Holthuis, 1941 (Gulf of Aden)
8. *Lysiosquilla aulacorhynchus* Cadenat, 1957 (West Africa)
9. **Lysiosquilla campechiensis* Manning, 1962 (West Atlantic)

The large size (reaching TL 300 mm or more as adults) and telson lacking a sharp crest and either fixed dorsal or movable submedian marginal spines separate this genus from all others.

Type-species.—*Lysiosquilla inornata* Dana, 1852 [=*L. scabricauda* (Lamarck, 1818)], Fowler, 1912, p. 539.

Coronis Desmarest, 1823

Coronis Desmarest, 1823, p. 345 [published September, 1823; see Sherborn, 1922, p. xliv].

Not *Coronis* Huebner, 1823, p. 265 [Lepidoptera; published on or before 21 December 1823].

Diagnosis.—Eyes small, cornea subglobular; rostral plate cordiform, with apical spine; carapace without trace of cervical groove, carinae, or spines; antennal protopod with one ventral and one mesial papilla; raptorial dactylus armed with 13-15 teeth; propodus pectinate throughout its length; propodi of third and fourth maxillipeds as broad as or broader than long; mandibular palp and five epipods present; abdomen very flattened, thoracic and abdominal somites without longitudinal carinae; telson broader than long, with smooth, unspined dorsal median projection, and two pairs of marginal projections, inner obtuse, unarmed; posterior armature reduced, consisting of, on either side of midline, a row of slender, fixed denticles, a movable submedian tooth, and a fixed lateral tooth on lateral projection; spines of basal prolongation of uropod flattened, outer much the larger. Size moderate, TL 80 mm or less.

Remarks.—*Coronis* contains but two species:

1. **Coronis scolopendra* Latreille, 1825 (West Atlantic)
2. **Lysiosquilla excavatrix* Brooks, 1886 (West Atlantic)

The genus superficially resembles *Nannosquilla*, with which it agrees in many features. However, in *Coronis* there is no false eave on the telson and only submedian denticles are present; the antennal protopod is provided with papillae; the mandibular palp and five epipods are present, and the spines of the basal prolongation are noticeably flattened.

Type-species.—*Coronis scolopendra* Latreille, 1825, by subsequent monotypy.

Gender.—Feminine.

Nannosquilla, new genus

Diagnosis.—Body depressed, smooth; eyes small, cornea rarely bilobed; rostral plate subrectangular; carapace without trace of cervical groove on dorsum, carinae, or spines; antennal protopod without papillae; raptorial claw small, dactylus armed with seven or more teeth; upper margin of propodus pectinate throughout its length; propodi of third and fourth maxillipeds as broad as or broader than long; mandibular palp absent; four epipods present; thoracic and abdominal somites without longitudinal carinae; telson broad, without sharp crest, posterior margin produced into false eave

medially under which originates true marginal armature, consisting of, on either side of midline, a row of submedian denticles, a movable submedian tooth, and three or four fixed lateral teeth, usually with an intervening denticle; basal prolongation of uropods produced into two slender spines of variable length; size small, adults TL 40 mm or less.

Remarks.—The genus includes the following species:

1. **Lysiosquilla decemspinosa* Rathbun, 1910 (East Pacific)
2. *Lysiosquilla occulta* Giesbrecht, 1910 (Mediterranean)
3. *Lysiosquilla varicosa* Komai and Tung, 1930 (Japan)
4. *Lysiosquilla chilensis* Dahl, 1954 (East Pacific)
5. *Lysiosquilla hystricotelson* Barnard, 1958 (Indian Ocean)
6. **Lysiosquilla grayi* Chace, 1958 (West Atlantic)
7. **Lysiosquilla californiensis* Manning, 1961 (East Pacific)
8. **Lysiosquilla antillensis* Manning, 1961 (West Atlantic)
9. **Lysiosquilla hancocki* Manning, 1961 (West Atlantic)
10. **Lysiosquilla schmitti* Manning, 1962 (West Atlantic)

L. occulta, *L. varicosa* and *L. hystricotelson* are placed here provisionally as all three are of small size and have a false eave on the telson. *L. hystricotelson*, at least, lacks the mandibular palp; this feature should be checked in the other two species. *L. varicosa* differs from all of the other species placed here in that the cornea of the eye is bilobed.

The absence of papillae on the antennal protopod and of the mandibular palp, the reduction in epipods, the configuration of the telson with a false eave and ventral armature, and the diminutive size separate this genus from all others in the *Lysiosquilla* complex.

L. perpasta Hale, 1924 has a similar configuration of the telson but the body is more compact than any of the species placed here. Further, the antennal protopod is provided with papillae.

Type-species.—*Lysiosquilla grayi* Chace, 1958.

Gender.—Feminine.

Etymology.—The name is from the Greek, *nannos*, a dwarf, and the generic name *Squilla*.

***Acanthosquilla*, new genus**

Diagnosis.—Eyes small, cornea globular or subglobular; rostral plate subquadrate with apical spine, anterolateral spines present or absent; carapace without trace of cervical groove, carinae or spines; antennal protopod with one ventral papilla, mesial papilla present or absent; raptorial claw small, dactylus armed with five or more teeth; propodus pectinate throughout its length; propodi of third and fourth maxillipeds as broad as or broader than long; mandibular palp present or absent (usually present);

five epipods present; thoracic and abdominal somites without longitudinal carinae; telson broad, without sharp crest, but with a fan-shaped series of five or more dorsal teeth above posterior armature, which consists of, on either side of midline, a row of slender, fixed denticles, a movable submedian tooth, and either three or four fixed lateral teeth, with one or more denticles between each tooth; basal prolongation of uropod produced into two slender spines, inner the longer. Size moderate to small, TL 70 mm or less.

Remarks.—*Acanthosquilla* includes the following species:

1. **Lysiosquilla acanthocarpus* Miers, 1880 (Indo-Pacific)
2. **Lysiosquilla septemspinosa* Miers, 1881 (East Atlantic)
3. **Lysiosquilla biminiensis* Bigelow, 1893 (West Atlantic)
4. **Lysiosquilla multifasciata* Wood-Mason, 1895 (Indo-Pacific)
5. *Lysiosquilla tigrina* Nobili, 1903 (Indo-Pacific)
6. *Lysiosquilla vicina* Nobili, 1904 (Indo-Pacific)
7. **Lysiosquilla digueti* Coutiere, 1905 (East Pacific)
8. **Lysiosquilla floridensis* Manning, 1962 (West Atlantic)

Although *L. spinosa* (Wood-Mason) approaches these species in that the dorsal surface of the telson is armed with spines, the broad shape of the basal prolongation of the uropod, with the outer spine much larger than the inner, excludes it from this genus. In all of the species of *Acanthosquilla* the spines of the basal prolongation are slender, inner spine the longer.

The species included here fall into two groups, with either three (*acanthocarpus*, *biminiensis*, *multifasciata*, *septemspinosa*) or four (*digueti*, *floridensis*, *tigrina*, *vicina*) primary marginal teeth on the telson.

Acanthosquilla can be distinguished from all other genera by the series of five or more dorsal spines on the telson, arranged in a semicircle. The median spine is not sharply carinate anteriorly nor is it situated on a broad median projection.

Type-species.—*Lysiosquilla multifasciata* Wood-Mason, 1895.

Gender.—Feminine.

Etymology.—The name is from the Latin, *acanthus*, a thorn, in combination with the generic name *Squilla*.

Heterosquilla, new genus

Diagnosis.—Eyes small, cornea usually bilobed or expanded, rarely globular; rostral plate usually cordiform, with apical spine, occasionally truncate; carapace without trace of cervical groove, carinae, or spines; antennal protopod with one or more mesial or ventral papillae; raptorial dactylus armed with four or more teeth; propodus fully pectinate; propodi

of third and fourth maxillipeds as broad as or broader than long; mandibular palp present or absent; four or five epipods present; abdomen depressed but compact, thoracic and abdominal somites without longitudinal carinae; telson broad, with a smooth, elevated median dorsal projection, spined or lobed posteriorly (occasionally only a single blunt spine), lateral projections or carinae also present on dorsal surface; posterior armature consisting of, on either side of midline, a row of small fixed denticles, a movable submedian tooth, occasionally flanked by a fixed tooth, and either two or three large fixed teeth, with one or more intervening denticles; basal prolongation of uropod produced into two spines, length variable. Size moderate, TL 100 mm or less.

Remarks.—The following species are included in this genus:

1. **Squilla eusebia* Risso, 1816 (Mediterranean)
2. **Squilla latifrons* de Haan, 1844 (Indo-Pacific)
3. *Coronis spinosa* Wood-Mason, 1875 (Indo-Pacific)
4. **Lysiosquilla armata* Smith, 1881 (West Atlantic)
5. **Lysiosquilla polydactyla* von Martens, 1881 (West Atlantic)
6. **Lysiosquilla platensis* Berg, 1900 (West Atlantic)
7. *Lysiosquilla insignis* Kemp, 1911 (Indo-Pacific)
8. *Lysiosquilla osculans* Hale, 1924 (Australia)
9. **Lysiosquilla perpasta* Hale, 1924 (Australia)
10. *Lysiosquilla vercoi* Hale, 1924 (Australia)
11. **Lysiosquilla mccullochae* Schmitt, 1940 (East Pacific)
12. **Lysiosquilla enodis* Manning, 1962 (West Atlantic)
13. **Lysiosquilla insolita* Manning, 1963 (West Atlantic)

As the name implies, this group of species is heterogeneous. The genus includes some of the least known stomatopods and further study is needed to clarify their position. Two of the species, *H. eusebia* and *H. enodis*, have the movable submedian tooth of the telson flanked by an adjacent fixed tooth and three other fixed lateral teeth. In the remainder of the species (possible exception, *H. perpasta*) there are but two fixed lateral teeth and no large tooth near the movable submedian. There is a large range in number of teeth on the dactyl of the raptorial claw, from four in *H. mccullochae* to 20 in *H. polydactyla*. The inner spine of the basal prolongation is the longer in most of the species, but in four the outer is longer, and in *H. spinosa* the inner is very much reduced. *H. spinosa* approaches *Acanthosquilla* in the dorsal armature of the telson but the uropod structure seems to exclude it from that genus. In shape of eye (subglobular) and configuration of telson, *H. spinosa* agrees with *H. vercoi* and *H. osculans*; the rostral plate of the latter, however, is truncate, not cordiform. *H. perpasta* approaches *Nannosquilla* in several features, including shape of rostral plate and eye, and configuration of telson, but the

body is very compact and the antennal protopod bears three papillae.

These species of doubtful position are intentionally lumped in *Heterosquilla*, which admittedly is a wastebasket. They cannot be included in *Lysiosquilla* as redefined above, for all have movable submedian teeth and dorsal sculpture on the telson. In my opinion, it is better at the present time to include all of these species in one small catchall than to include them in the otherwise well-defined groups discussed above. Further study might well clarify their positions and indicate the separation of one or more new genera or subgenera.

Type-species.—*Lysiosquilla platensis* Berg, 1900.

Gender.—*Feminine*.

Etymology.—The name is from the Greek, *heteros*, meaning different, in combination with the generic name *Squilla*.

Coronida Brooks, 1886

Coronida Brooks, 1886, p. 79.

Diagnosis.—Body depressed; eyes small, cornea bilobed; rostral plate rounded or subrectangular; carapace without trace of cervical groove dorsally, carinae or spines; raptorial claw small, dactylus inflated at base, armed with teeth on inner margin; propodus proximally pectinate, distally ridged; third and fourth maxillipeds as broad as or broader than long; mandibular palp present or absent; five epipods present; thoracic somites and first four abdominal somites without sharp carinae or spines, fifth abdominal somite occasionally spined on posterior margin; sixth somite and telson with dorsal spines, tubercles or ridges; telson broad, posterior armature poorly marked, movable submedian teeth present; basal prolongation of uropod with inner spine the longer. Size small, TL 50 mm or less.

Remarks.—The following species are included in *Coronida*:

1. **Squilla bradyi* A. Milne-Edwards, 1869 (Atlantic, East Pacific)
2. *Gonodactylus trachurus* von Martens, 1881 (Indo-Pacific)
3. *Squilla multituberculata* Borradaile, 1898 (Indo-Pacific)
4. *Coronida sinuosa* Edmondson, 1921 (Hawaii)

Brooks (1886) believed that *Coronida* was the link between his *Protosquilla* and the other stomatopod genera (see also below). Hansen (1895) pointed out the relation of *Coronida* to *Lysiosquilla*, with which I am in full agreement.

Type-species.—*Squilla bradyi* A. Milne-Edwards, 1869, designated by Balss, 1938, p. 130.

DISCUSSION OF THE *LYSIOSQUILLA* COMPLEX

The following characters link together all species now placed in

Lysiosquilla, *Heterosquilla*, *Coronis*, *Acanthosquilla*, *Nannosquilla*, and *Coronida*:

1. The flattened shape and loose articulation of the body.
2. The general absence of carination on the body.
3. The propodi of the fourth and fifth maxillipeds are broader than long. This was first pointed out by Hansen (1895) with reference to larval forms and the feature is apparently consistent in adults as well.
4. The telson is subquadrate to broadly rounded, usually broader than long, without a sharp median crest.
5. The submedian teeth of the telson are movable; these teeth are absent in *Lysiosquilla* s.s.

The absence of a sharp crest distinguishes all of these genera from *Squilla* as well as from *Pseudosquilla* and its allies, including the species of *Eurysquilla* which have a flattened, *Lysiosquilla*-like body.

It has proved difficult to arrive at conclusions on affinities of the genera in the *Lysiosquilla* complex, as all of the genera superficially resemble one another. In the *Pseudosquilla* complex, two groups of genera can be distinguished, but such groups, if they exist, are not easily seen in *Lysiosquilla*. The affinities of the genera recognized here will be difficult to determine until many of the species can be studied in greater detail. In particular, the species now placed in *Heterosquilla* need further study.

The following new genus is apparently unrelated to the *Lysiosquilla* complex and is here treated separately from that group of genera. Both species placed in the new genus have been placed in *Lysiosquilla* in the past.

Bathysquilla, new genus

Diagnosis.—Body depressed, smooth anteriorly, tuberculate posteriorly; cornea of eyes bilobed or subglobular; rostral plate subtriangular or trapezoidal, with apical spine; carapace without longitudinal carinae or spines, marginal carinae present on posterior portion of lateral plates; raptorial dactylus armed with 10 or more teeth, propodus with a row of long, fixed spines on inner face of upper margin; propodi of third and fourth maxillipeds slender; telson with four pairs of marginal teeth, all with movable apices.

Remarks.—*Bathysquilla* includes only two species:

1. *Lysiosquilla crassispinosa* Fukuda, 1910 (Indo-Pacific)
2. **Lysiosquilla microps* Manning, 1961 (West Atlantic)

The slender propodi of the last maxillipeds, striking armature of the raptorial claw, and peculiar structure of the telson, with a well defined crest and four pairs of marginal teeth, all with movable apices, separate this genus from all other stomatopod genera. The structure of the raptorial claw resembles that of *Squilla raphidea* (Fabricius) and its allies but the

forms are not similar in any other feature. At the present time I cannot relate *Bathysquilla* to any other known genus; in particular it cannot be considered related to *Lysiosquilla* and its allies.

Type-species.—*Lysiosquilla microps* Manning, 1961.

Gender.—Feminine.

Etymology.—The name is from the Greek, *bathys*, deep, combined with the generic name *Squilla*.

GENERAL DISCUSSION

Few attempts have been made to review the interrelationships of the various stomatopod genera. Brooks (1886) was apparently the first to propose a scheme linking together all of the known genera. He recognized the genus *Protosquilla*, which he separated from *Gonodactylus* on the basis of the partially fused articulation of the sixth abdominal somite with the telson. Brooks equated this condition to that found in larval forms, and apparently believed that the partial fusion was a primitive character. All stomatopod genera were derived by Brooks from a *Protosquilla*-like ancestor, which gave rise to *Gonodactylus*, *Pseudosquilla* and *Coronida*. *Coronida*, a name derived from *Coronis* and *Chlorida* (because of the flattened body of the former and the small eyes of the latter), led to *Squilla* through *Chlorida* on one hand and to *Lysiosquilla* through *Coronis* on the other.

Brooks was misled to considering *Protosquilla* (now *Gonodactylus* Group III of Kemp) to be primitive; Hansen (1895) has shown that the articulation of the telson to the abdomen is not comparable to the situation found in the larvae. Further, the restriction of all but one species in Group III to the Indo-Pacific region might indicate that it is a relatively recent group; species in *Gonodactylus* Group I, for example, are world-wide. There is little basis for any part of Brooks's scheme which was devised before many of the species known today had been described.

Hansen (1895, p. 71) showed that in the larval forms attributed to *Lysiosquilla* and *Coronida* the propodi of the third and fourth maxillipeds were broader than long and much broader than the propodus of the fifth maxillipeds. In the larvae attributed to *Pseudosquilla*, *Gonodactylus* and *Odontodactylus*, the propodi of the third and fourth maxillipeds are longer than broad and not much broader than that of the fifth.

Giesbrecht (1910, pp. 122, 148) divided the stomatopods into three groups on the basis of the type of development and type of larva, as follows:

1. Group *Lysiosquillinae*: *Lysiosquilla* and *Coronida*. First larva an antizoea (appendages of first five thoracic somites biramous; abdomen poorly segmented, without appendages), developing into an erichthus (one intermediate denticle on the telson).

2. Group Gonodactylinae: *Gonodactylus*, *Pseudosquilla*, and *Odontodactylus*. First larva a pseudozoea (first and second thoracic appendages uniramous, second raptorial) with five pairs of pleopods developing into an erichthus.

3. Group Squillinae: *Squilla*. First larva a pseudozoea with four pairs of pleopods, developing into an alima (telson with four or more intermediate denticles).

Giesbrecht's alignment is essentially the same as that of Hansen. Giesbrecht also definitely indicated these groups as of family or subfamily status (1910, p. 148).

The most prominent worker in the group, Kemp, said little about the relations of the different genera. He was of the opinion (1913, p. 17) that *Squilla* probably contained the most primitive species of the order, and, on p. 130, he indicated that *Coronida* was probably more closely related to *Squilla*, *Pseudosquilla* and *Lysiosquilla* rather than to *Odontodactylus* and *Gonodactylus*. In his key to genera (p. 16) he grouped *Gonodactylus* and *Odontodactylus* together and separated *Squilla* from the rest of the genera, but nowhere did he indicate that the key portrayed true relationships.

Foxon (1932) disagreed with Hansen's grouping of the larvae and tried to show that the larvae could be fitted into a scheme identical with that found in Kemp's key. Foxon apparently believed that the alignment of genera in that key was intended to approximate a natural grouping.

Previous ideas on classification of larvae were summarized by Gurney (1937), who criticized Foxon's approach. Foxon (1939) again attempted to show that the larval forms could be fitted into a scheme which not only linked larvae to adults but did this without "upsetting the main points of Kemp's classification" (1939, p. 254). In this scheme, advanced as a key, the genera were linked as follows: *Coronida* with *Lysiosquilla*, *Squilla* with *Pseudosquilla*, and *Gonodactylus* with *Odontodactylus*.

Gurney (1946) again summarized the literature from the point of view of larval studies and supported the ideas of Hansen and Giesbrecht.

Serène (1962, p. 4) pointed out that the recognition of several families within the Stomatopoda might clarify the position of the various genera, inasmuch as the single family, Squillidae, contained different forms and two basically different types of larvae.

It is rather unfortunate that a subdivision of the family has been made on the basis of characters of larval forms only. Not only do we know little about stomatopod larvae (Gurney, 1937, pointed out that only the larvae of *Squilla* and *Gonodactylus* have been hatched from the egg) but, at the present time, no student of the group is familiar enough with both larvae and adults to evaluate the situation satisfactorily.

The genera and groups of genera recognized above substantiate, by

and large, the ideas of Hansen and Giesbrecht. *Bathysquilla*, however, falls into none of the three groups delimited by those workers, and its larvae are unknown or at least have not been linked to the adult. I feel that, at the present time, we do not know enough about either the adults of the larvae even to speculate upon a natural classification above the generic level. Our knowledge of adults is advancing rapidly, and indications are that studies on larval forms are also progressing. Of particular interest in this latter regard is the work on rearing postlarvae through the juvenile to an identifiable stage by K. H. Alikunhi in India; his studies should give us some ideas on what types of larvae are associated with groups of species. Unfortunately most of his papers are unavailable to me, and I have not been able to study his results in detail.

Although I am not familiar with many of the Indo-Pacific species of stomatopods, I have examined various species now placed in *Gonodactylus* Groups I, II, and III. Lack of familiarity with many of the species precludes any attempt by me to revise this genus, but I am in accord with the view of Serène (1962, p. 4) that these distinct groups are worthy of generic recognition.

In future works describing new species of stomatopods, especially those of uncertain position, particular attention should be paid to the following features: presence, absence, number, and position of papillae on antennal protopod; presence or absence of mandibular palp; relative size of the propodi of the last three maxillipeds; pectination and spination of the propodus of the raptorial claw; number and relative size of epipods; and absence, presence and shape of median ventral keel or projection on eighth thoracic somite. This last feature has not generally been used, but it affords specific characters in *Squilla* and some other genera and may be of importance at the generic level.

SUMARIO

REVISION PRELIMINAR DEL GENERO *Pseudosquilla* Y *Lysiosquilla* CON DESCRIPCIONES DE SEIS NUEVOS GENEROS (CRUSTACEA: STOMATOPODA)

Dos de los once géneros de crustáceos estomatópodos corrientemente reconocidos: *Pseudosquilla* Dana, 1852 y *Lysiosquilla* Dana, 1852, son expuestos como receptores de especies sin relación. Se consideran siete géneros en el complejo *Pseudosquilla*, incluyendo dos nuevos géneros: *Eurysquilla* y *Eurysquilloides*. Otros géneros que se consideran relacionados con *Pseudosquilla* son: *Pseudosquillopsis* Serène, 1962, *Parasquilla* Manning, 1961, *Manningia* Serène, 1962 y *Coronidopsis* Hansen, 1926. Se consideran seis géneros en el complejo *Lysiosquilla*, de los cuales tres: *Nannosquilla*, *Acanthosquilla* y *Heterosquilla* se describen como nuevos. *Coronis* Desmarest, 1823, es reconocido y *Coronida* Brooks, 1886, se cree que está relacionado con *Lysiosquilla*, que es restringido a *L. maculata* y

especies similares. Se describe *Bathysquilla* y se demuestra que no está relacionado con el complejo *Lysiosquilla*. Se dan características de cada uno de estos 14 géneros y se relacionan todas las especies descritas en ellos.

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