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Archaeosculda phoenicia n. gen., n. sp. (Crustacea, Stomatopoda, Pseudosculdidae) from the Upper Cretaceous (Cenomanian) of Lebanon

Abstract - The second species and genus of Pseudosculdidae is described from the Cenomanian of Lebanon. *Archaeosculda phoenicia* n. gen., n. sp. resembles *Pseudosculda laevis* in the subcylindrical body form and raptorial claw, but differs chiefly in the broad and subovate rather than elongate, triangular telson, presence of prominent instead of indistinct primary teeth lateral to the primary submedian teeth, and the broad instead of slender uropodal endopod. In addition, at about 75 mm in length, *Archaeosculda phoenicia* attains a considerably larger size than *Pseudosculda laevis*, which is known to reach 55 mm in length. The status of Pseudosculdidae is discussed and a list of the known fossil unipeltatans is given.

Key words: Crustacea, Stomatopoda, Pseudosculdidae, Upper Cretaceous, Lebanon.

Riassunto - *Archaeosculda phoenicia* n. gen., n. sp. (Crustacea, Stomatopoda, Pseudosculdidae) del Cretacico superiore (Cenomaniano) del Libano.

Vengono descritti il secondo genere e la seconda specie della famiglia Pseudosculdidae del Cenomaniano del Libano. *Archaeosculda phoenicia* n. gen., n. sp. ricorda *Pseudosculda laevis* nella forma subcilindrica del corpo e del chelipede, ma si differenzia soprattutto per il telson triangolare, ampio e subovale piuttosto che allungato, per i denti primari e submediani ben sviluppati piuttosto che indistinti e per l'endopodite degli uropodi ampio piuttosto che sottile. Inoltre, *Archaeosculda phoenicia* n. gen., n. sp. con una lunghezza totale pari a 75 mm raggiunge una considerevole dimensione rispetto a *Pseudosculda laevis* che non supera una lunghezza complessiva di 55 mm. Viene discusso lo status della famiglia Pseudosculdiae e viene fornita una lista delle forme fossili di unipeltati finora conosciuti.

Parole chiave: Crustacea, Stomatopoda, Pseudosculdidae, Cretacico superiore, Libano.

Introduction and geological setting

The mantis shrimps, order Stomatopoda, are best known for their powerful raptorial claws that resemble the forelimbs of the terrestrial preying mantis. Stomatopoda comprises two suborders, the Carboniferous Archaeostomatopodea, and the Unipeltata, to which all extant stomatopods belong. A characteristic feature

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of the unipeltatan suborder is the marked specialization of the maxillipeds. Whereas archaeostomatopodeans possessed approximately equal, moderately-sized sub-chelate maxillipeds, those of unipeltatans became strongly specialized. The second maxilliped is greatly enlarged as a raptorial claw and used for prey capture, in contrast to the other maxillipeds, which are much reduced in size and specialized for prey manipulation. The unipeltatan fossil record is poor, with only 29 named species known to date (Schram & Müller, 2004).

Prior to the present study, two species of stomatopod were known from the Upper Cretaceous of Lebanon: *Pseudosculda laevis* (Schlüter, 1872) (family Pseudosculdidae Dames, 1886) and *Sculda syriaca* Dames, 1886 (family Sculdidae Dames, 1886), studied by Schlüter (1872, 1874), Woodward (1879), Dames (1886), Roger (1946), and Teruzzi (1983). Pseudosculdidae and Sculdidae, with an Upper Cretaceous and Jurassic–Cretaceous range, respectively, are believed to represent stem-lineage unipeltatans (Hof, 1998b; Ahyong & Harling, 2000). In 2001, an unusual fossil stomatopod was discovered in the Upper Cretaceous lithographic limestone of Haqel quarry, northeastern Lebanon. Haqel, located about 12 km from the Mediterranean coast and 45 km from Beirut, is one of the richest fossil sites in Lebanon, yielding numerous invertebrate and vertebrate fossils (Hückel, 1969, 1970, 1974a, 1974b; Hemleben, 1977; Cappetta, 1980; Dal Sasso & Pinna, 1997; Garassino, 1994, 2001; Dalla Vecchia *et al*., 2001; Larghi, 2004; Rieppel & Head, 2004; Bracchi & Alessandrello, 2005; Garassino & Schweigert, 2006; Fuchs, 2006). The studied specimen, representing a new genus and species of Pseudosculdidae, is described below.

Preservation and material

The Haqel quarry is of lower–middle Cenomanian age (Hückel 1970, 1974a, 1974b) and the sedimentary layers are fine grained, well-laminated and yellow-cream coloured. The studied specimen is compressed and flattened on a bedding plane and its preparation was made easy by the softness of the surrounding rock. The specimen is deposited in the palaeontological collection of the Museo di Storia Naturale di Milano (Italy) (MSNM) and the comparative specimen of *Hemisquilla australiensis* Stephenson, 1967, is deposited in the invertebrate collection at the National Institute of Water and Atmospheric Research of Wellington (New Zealand) (NIWA).

The systematic arrangement used in this paper follows the classification proposed by Martin & Davis (2001).

Systematic Palaeontology

Order Stomatopoda Latreille, 1817
Suborder Unipeltata Latreille, 1825
Family Pseudosculdidae Dames, 1886

Diagnosis: second maxilliped well-developed as raptorial claw, massive, considerably larger than other maxillipeds; ischiomeral articulation terminal; merus with distinct dorsal saddle; dactylus robust, broadly curved, unarmed on occlusal margin; abdomen without dorsal carinae, subcylindrical in cross-section; telson with

distinct median carina; submedian primary teeth with moveable apices; uropodal protopod terminating in two primary spines; exopod unisegmental, outer margin lined with moveable spines.

Type genus: *Pseudosculda* Dames, 1886.

Generic composition: *Pseudosculda* Dames, 1886; *Archaeosculda* n. gen.

Stratigraphic range: Upper Cretaceous (Cenomanian).

Genus *Archaeosculda* nov.

Diagnosis: telson subovate, slightly broader than long, with distinct median carina and four pairs of primary marginal teeth, submedians with movable apices; uropodal endopod broad, subovate.

Type species: *Archaeosculda phoenicia* n. gen., n. sp., by present designation and monotypy.

Etymology: derived from the Greek, *arche*, old, beginning, in combination with the generic name *Sculda*. Gender: feminine.

Description: as for the type species.

Archaeosculda phoenicia n. gen., n. sp.
Figs. 1-4

Diagnosis: as for the genus.

Etymology: the trivial name alludes to the ancient name for Lebanon, Phoenicia; used as a noun in apposition.

Holotype: MSNM i26595.

Stratigraphic range: Upper Cretaceous (Cenomanian).

Type locality: Haqel (Lebanon).

Occurrence: one specimen in dorsoventral view, about 75 mm in length.

Fig. 1 - *Archaeosculda phoenicia* n. gen., n. sp., n. cat. MSNM i26595, holotype (olotipo) (x 1.3).

Description. Carapace and anterior appendages poorly preserved. Thoracic somites poorly preserved, shorter and narrower than abdominal somites. Abdominal somites I–V smooth dorsally, apparently subcylindrical in cross-section, not dorsoventrally flattened. Sternites with median knob or short carina. Abdominal somite VI with blunt posterolateral tooth; dorsolateral surface slightly wrinkled. Telson slightly wider than long, subovate. Dorsal surface irregularly wrinkled, with median carina. Accessory median and anterior submedian carina. Median carina with proximal notch. Accessory median carina low, uninterrupted, extending from distal end of telson to at least midlength of median carina. Anterior submedian carina low, curved, extending from base of submedian primary tooth almost to anterior margin of telson. Lateral margin of telson arcuate, with low marginal carina. Anterolateral margin of telson with low marginal thickening. Posterior margin with broad triangular sinus between base of each submedian tooth. Submedian primary teeth with moveable apices, flanked either side by smaller triangular tooth; with three pairs of fixed triangular primary teeth lateral to submedians, lateral margins slightly sinuous. Uropodal protopod with straight anterior margin, distally terminating in two primary teeth, inner longer, apices reaching beyond distal margin of endopod and exopod. Sinus between terminal spines of uropodal protopod reaching approximately one-third distance between apex of inner spine and articulation of endopod. Uropodal exopod unisegmental, about 3 ? times longer than wide, tapering distally. Outer margin of uropodal exopod armed with at least 11 straight, moveable spines. Uropodal endopod broad, subovate, inner margin concave; widest at about midlength; width exceeding half-length. Raptorial claw large, well-developed; merus distodorsal saddle distinct, outer inferodistal angle, rounded; carpus subtriangular; propodus length

Fig. 2 - *Archaeosculda phoenicia* n. gen., n. sp., n. cat. MSNM i26595, detail of the anterior part of the body (dettaglio della parte anteriore del corpo) (x 2.5).

about 4 times greatest height at midlength, occlusal margin apparently unarmed; dactylus slender, scythe-like, about as long as propodus, deepest at proximal sixth, outer margin broadly curved, with basal notch; occlusal margin unarmed. Maxillipeds III–V poorly preserved, traces visible adjacent to raptorial claw. Pereiopods ill-preserved, only traces visible adjacent to thoracic somites. Pleopods poorly preserved but outer margins of exopod partially visible.

Fig. 3 - *Archaeosculda phoenicia* n. gen., n. sp., n. cat. MSNM i26595, detail of the tail fan (dettaglio del ventaglio caudale) (x 3.3).

Remark. *Archaeosculda phoenicia* n. gen., n. sp. is the second genus and species to be recognised in the Pseudosculdidae, including to date *Pseudosculda laevis*, discovered in Sahel Alma and Haqel quarries. *Archaeosculda* is unique in the family for the broad telson with three pairs of prominent, fixed primary teeth (in addition to the moveable submedian teeth) and the broad, ovate, uropodal endopod. In contrast, the only other recognised pseudosculdid, *Pseudosculda laevis*, bears an elongate, triangular telson with small primary teeth that do not project much beyond the general telson outline, and a slender, elongate, uropodal endopod (Fig. 4). Moreover, at 75 mm total length, *Archaeosculda phoenicia* apparently reaches a larger size than *P. laevis*, known to reach only 55 mm total length (Holthuis & Manning, 1969). The dissimi-

larities between the telson of *Archaeosculda* and *Pseudosculda* are marked, but the four pairs of primary teeth can probably be homologized between the two genera. Homologizing the telson teeth of pseudosculdids and those of crown-group unipeltatans is more complicated, and requires further research.

Feldmann *et al.* (1999) reported a fragmentary fossil stomatopod from Cretaceous of Colombia that was tentatively assigned to *Sculda* on the basis of telson morphology whereby the length and width are approximately equal and the posterior margin is lined with long, moveable spines, a distinctive feature of Sculdidae. Schram & Müller (2004), however, reassigned the Colombian specimen to *Pseudosculda* on the basis of the raptorial claw. The dactyli of the raptorial claws of the Colombian specimen resemble those of pseudosculdids, but it is noteworthy that the raptorial claws of *Sculda* are presently unknown. The Colombian specimen is certainly not *Pseudosculda*, and it is doubtful that it belongs to Pseudosculdidae either.

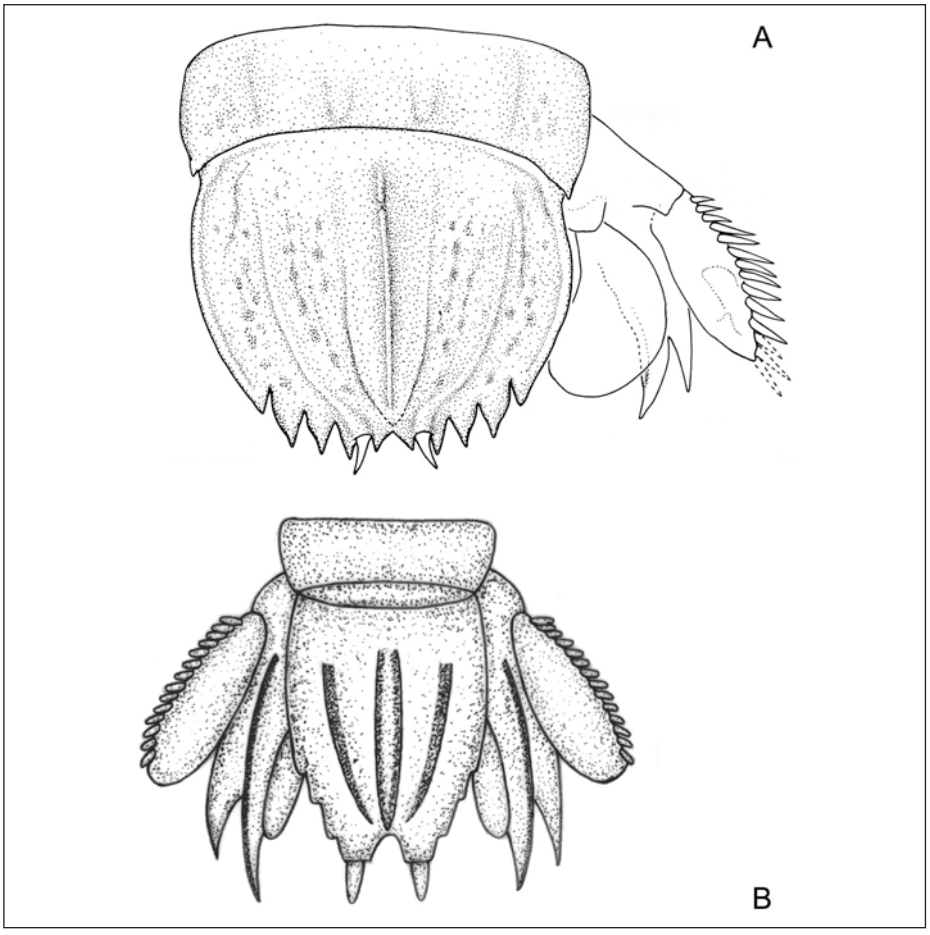

Fig. 4 - Comparison of the tail fans (confronto dei ventagli caudali): A) *Archaeosculda phoenicia* n. gen., n. sp.; B) *Pseudosculda laevis* (Schlüter, 1872).

Discussion

Cladistic analyses of the Stomatopoda have recognised Sculdidae and Pseudosculdidae as stem-lineage unipeltatans, with the pseudosculdids as sister to crown-group Unipeltata (Hof, 1998b; Ahyong & Harling, 2000) (Fig. 5). The chief character excluding sculdids and pseudosculdids from the crown-group is the plesiomorphic uropodal exopod segmentation, being unisegmental rather than bi-segmental. Sculdidae, as presently composed, can be diagnosed by several apomorphies such as the broad, dorsoventrally depressed body, the absence of a median carina on the telson, and most importantly, the posterior telson margin lined with

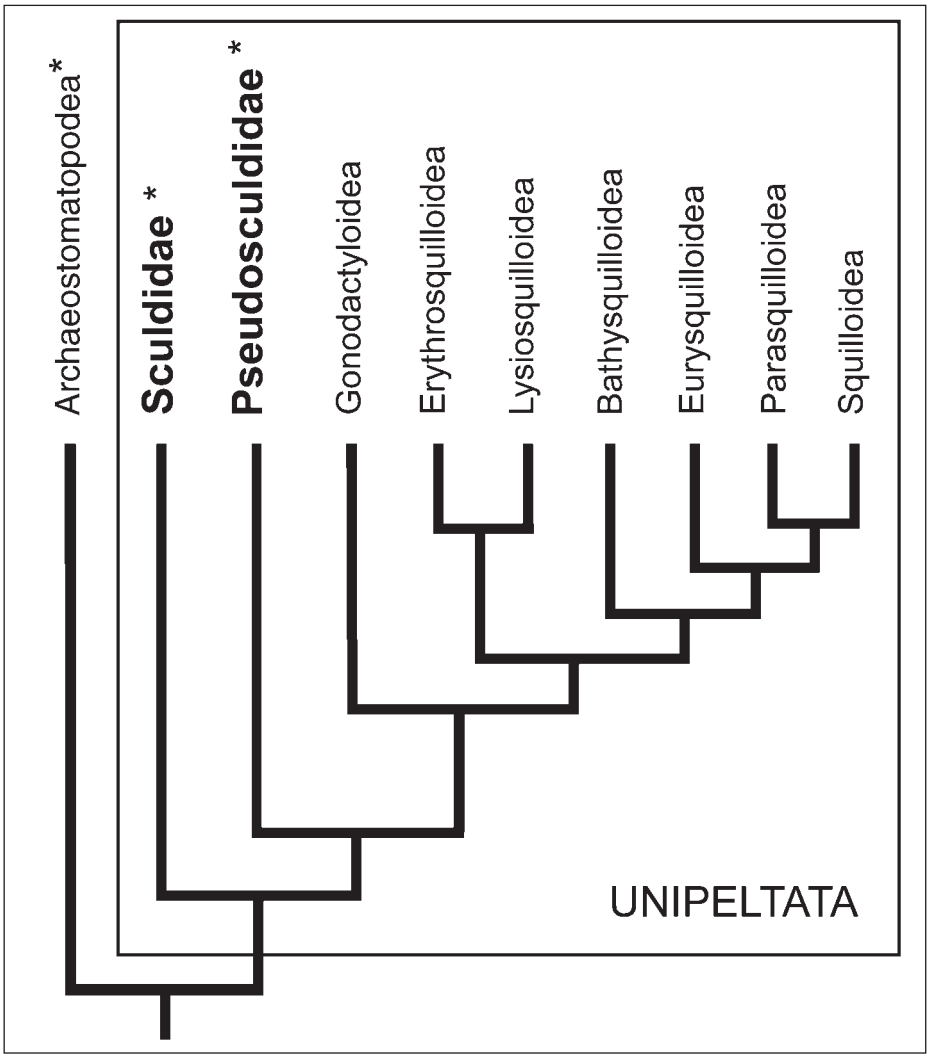

Fig. 5 - Phylogenetic relationships within Unipeltata. Extinct taxa indicated*. Based on Ahyong & Harling (2000).

Fig. 5 - Relazioni filogenetiche degli Unipeltata. Taxa estinti indicati con*. Da Ahyong & Harling (2000).

Fig. 6 - *Hemisquilla australiensis* Stephenson, 1967 (Hemisquillidae). Male TL 121 mm, New Zealand, NIWA. Dactylus and propodus of right raptorial claw (dactylus e propodus dell'appendice raptatoria destra).

moveable spines. Unfortunately, the raptorial claws of sculdids, being unknown, cannot be compared to those of pseudosculdids. Pseudosculdidae is distinguished from Sculdidae by the narrower, more subcylindrical body form, the median carina on the telson, and in having only the submedian primary telson teeth articulated. Hof (1998b) and Schram & Müller (2004) regarded the well-sclerotized scythe-like dactylus of the raptorial claw as a defining feature of Pseudosculdidae. The raptorial claws of members of the crown-group Hemisquillidae Manning, 1980 (superfamily Gonodactyloidea), however, are structurally similar to pseudosculdids, albeit with proportionally shorter dactyli and propodi. The raptorial claw of *Hemisquilla australiensis* Stephenson, 1967 is shown in Fig. 6. The differences between the raptorial claws of hemisquillids and pseudosquillids are essentially morphometric, so care should be taken to avoid placing undue emphasis on the raptorial claws in defining and assigning taxa to Pseudosculdidae. Note also that *Hemisquilla* Hansen, 1895 is basal in the Gonodactyloidea (Ahyong & Harling, 2000), so its raptorial claw morphology perhaps reflects the stem-lineage condition. Other recognized characters of Pseudosculdidae are not unique — the subcylindrical body is a plesiomorphy inherited from archaeostomatopodeans and retained by the modern gonodactyloids and parasquilloids; and the telson with a

distinct median carina and moveable submedian telson teeth is retained by almost all modern unipeltatans. Consequently, no robust synapomorphies are presently known that unite *Pseudosculda* and *Archaeosculda* raising the possibility that Pseudosculdidae is paraphyletic. The anterior cephalic appendages of *Pseudosculda* and *Archaeosculda* are incompletely known and more complete fossils may reveal synapomorphies. Nevertheless, the discovery of *Archaeosculda phoenicia* is significant, not only for expanding the rare Mesozoic stomatopod fossil record, but also in increasing knowledge of the morphospace occupied by stem-lineage unipeltatans.

At present, sculdids are known reliably from the Upper Jurassic to Middle Cretaceous and the pseudosculdids from the Upper Cretaceous. Pinna (1985) listed two ill-preserved stomatopod fossils from the Lower Jurassic (Sinemurian) of Osteno in northern Italy, representing the oldest known unipeltatans. Hof (1998b) indicated that the Osteno specimens represent an undescribed *Pseudosculda*-like species. If the Osteno specimens are pseudosculdids, and if current phylogenetic hypotheses are correct, then both the Pseudosculdidae and Sculdidae are considerably older than presently recognized.

Fossil record of unipeltatan Stomatopoda

Schram & Müller (2004) listed 31 named and unnamed species of fossil Unipeltata, to which we add *Archaeosculda phoenicia* n. gen., n. sp.. *Chloridella angolia* Berry, 1939, was placed in *Clorida* by Schram & Müller (2004), presumably because the generic name *Chloridella* Miers, 1880, was an unnecessary replacement for the valid generic name *Clorida* Eydoux & Souleyet, 1842. Nomenclatural confusion in the six decades following 1880 led several authors to incorrectly replace *Squilla* Fabricius, 1787, with *Chloridella*. Therefore, *Chloridella angolia* is herein referred to *Squilla* following Holthuis & Manning (1969), Reaka & Manning (1987) and Berry's (1939) account and figure. Two other changes to the Schram & Müller (2004) list follow Ahyong (2005). Thus, *Topangosquilla gravesi* Hof & Schram, 1998, originally referred to Lysiosquillidae, is a squillid. Similarly, *Ursquilla yehoachi* (Remy & Avnimelech, 1955), placed in Ursquillidae by Hof (1998a), is nested among other squillid genera, and is thus referable to Squillidae (Ahyong, 2005).

Mesozoic forms:
Family Pseudosculdidae Dames, 1886
Archaeosculda phoenicia n. gen., n. sp. (Upper Cretaceous – Lebanon)
Pseudosculda laevis (Schlüter, 1872) (Upper Cretaceous – Lebanon)
Family Sculdidae Dames, 1886
Sculda pennata Münster, 1840 (Upper Jurassic – Germany)
Sculda pusilla Kunth, 1870 (Upper Jurassic – Germany)
Sculda spinosa Kunth, 1870 (Upper Jurassic – Germany)
Sculda syriaca Dames, 1886 (Upper Cretaceous – Lebanon)
Family Lysiosquillidae Giesbrecht, 1910
Lysiosquilla nkporoensis Förster, 1982 (Upper Cretaceous – Nigeria)

Family Squillidae Latreille, 1802
Squilla cretacea Schlüter, 1868 (Upper Cretaceous – Germany)
Ursquilla yehoachi (Remy & Avnimelech, 1955) (Upper Cretaceous – Israel, Jordan)
Family uncertain
Paleosquilla brevicoxa Schram, 1968 (Upper Cretaceous – Colombia)

Cenozoic forms:
Family Bathysquillidae Manning, 1967
Bathysquilla wetherelli (Woodward, 1879) (Eocene – Great Britain)
Family Gonodactylidae Giesbrecht, 1910
Neogonodactylus oerstedii (Hansen) (middle Miocene-Recent – North America)
Family Hemisquillidae Manning, 1980
Hemisquilla adelaidensis Rathbun, 1926 (middle Miocene – North America)
Family Lysiosquillidae Giesbrecht, 1910
Lysiosquilla antiqua (Münster, 1842) (lower-middle Eocene – Italy)
Lysiosquilla messinai De Angeli, 1997 (Oligocene – Italy)
Family Pseudosquillidae Manning, 1977
Pseudosquilla wulfii Förster, 1982 (upper Eocene – Germany)
Pseudosquilla berica De Angeli & Messina, 1996 (middle Oligocene – Italy)
Family Squillidae Latreille, 1802
Angelosquilla altamirensis Hof & Schram, 1998 (middle Miocene – North America)
Harpiosquilla harpax de Haan, 1844 (Holocene-Recent – Australia).
Leesquilla bajee Yun, 1985 (lower-middle Miocene – Korea)
Leesquilla sunii Yun, 1985 (lower-middle Miocene – Korea)
Oratosquilla sp. Karasawa & Nakagawa, 1992 (Miocene – Japan)
Pohsquilla neonica Yun, 1985 (lower-middle Miocene – Korea)
Pohsquilla scissodentica Yun, 1985 (lower-middle Miocene – Korea)
Shako tomidai Karasawa, 1996 (lower Miocene – Japan)
Squilla angolia (Berry, 1939) (Eocene – Angola)
Squilla empusa Say, 1818 (Pleistocene-Recent – North America)
Squilla hollandi Förster, 1982 (upper Eocene – Germany)
Squilla laingae Hof & Schram, 1998 (middle Miocene – North America)
Squilla miocenica Lovisato, 1894 (Miocene – Italy, Spain)
Squilla sp. Yun, 1985 (lower-middle Miocene – Korea)
Topangosquilla gravesi Hof & Schram, 1998 (middle Miocene – North America)

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