**Squilla taulinanus** n. sp. (Crustacea, Stomatopoda, Squillidae) from the Burdigalian (Miocene) of Taulignan, south-eastern France

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**Abstract**

Mantis shrimps (Crustacea: Stomatopoda) are rather rare in the fossil record. Nineteen species have been assigned to Squillidae, of which 12 species have been recorded from the Miocene. We describe herein a squillid, *Squilla taulinanus* n. sp., from the Miocene of Taulignan, south-eastern France. The exceptionally well-preserved specimen is remarkable in apparently having abdominal somites 5–6 conjoined; such somatic abnormality is rare in stomatopods. A taxonomic reassessment of the fossil species assigned to *Squilla* is provided.

Keywords: Crustacea, Stomatopoda, Squillidae, Burdigalian, Miocene, France.

**Resumen**

Las mantis marinas (Crustacea: Stomatopoda) son raros en el registro fósil. Diecinueve especies han sido asignadas a Squillidae, de las cuales 12 especies se registran en el Mioceno. Se describe aquí el esquilido, *Squilla taulinanus* n. sp., del Mioceno de Taulignan, suroeste de Francia. El ejemplar excepcionalmente bien preservado es notable por aparentemente presentar las somitas abdominales 5–6 conjuntas; esta anomalía somática es rara en los estomatópodos. Se presenta una reevaluación taxonómica de las especies fósiles asignadas a *Squilla*.

Palabras Clave: Crustacea, Stomatopoda, Squillidae, Burdigaliano, Miocene, Francia.

**1. Introduction**

The mantis shrimps, Order Stomatopoda Latreille, 1817, are well known as highly efficient predators with remarkably developed vision and for their second maxillipeds modified into powerful raptorial claws. The crown-group stomatopods belong to Verunipeltata Haug et al., 2010, with almost 500 extant species arrayed in seven superfamilies, the largest of which is Squilloidea Latreille, 1802. The verunipeltatan fossil record, however, is sparse, with fewer than 40 fossil species known in total and 12 named species recorded from the Miocene. At present, 19 fossil species are assigned to the Squillidae (Ahyong et al., 2007; De Angeli and Beschin, 2006; Schram, 2010), of which eight fossil species
are assigned to *Squilla Fabricius*, 1787: *Squilla angolia* (Berry, 1939) (Eocene, Angola); *Squilla breoniensis* De Angelis and Beschin, 2006 (middle Eocene, Italy); *Squilla cretacea* (Schlüter in von der Mark and Schlüter, 1868) (Late Cretaceous, Germany); *Squilla empusa* Say, 1818 (Pleistocene to recent, North America); *Squilla hollandi* Förster, 1982 (late Eocene, Germany); *Squilla laingae* Hof and Schram, 1998 (Miocene of California); *Squilla miocenica* Lovisato, 1894 (Miocene, Italy and Spain); and *Squilla sonomana* (Rathbun, 1926) (Pliocene, California). In the present paper, we describe a new species of Miocene squillid from the Burgidalian of France, and reassess the taxonomic placement of fossil species assigned to *Squilla*.

2. Materials and Methods

The specimen derives from Miocene (Burgidalian) marine strata at Taulignan (La Croix de Bouchet), Drôme department, France. It is preserved in dorso-ventral aspect and comprises a part and counterpart in which details of the dorsal and ventral surfaces are preserved. Morphological terminology follows Ahyong (2001, 2012). Total length (TL), measured from the rostral tip to the submedian teeth of the telson, is estimated for the specimen owing to its incompletely preserved posterior telson. Carapace length (CL) is measured along the dorsal midline and excludes the base of rostral plate; intermediate, lateral and reflected marginal carinae distinct, well developed; posterolateral margin obtusely angled. Thoracic somite 5 (pereonite 5) lateral process a simple straight, evenly tapering spine, directed anterolaterally; thoracic somite 6–7 lateral processes triangular, anterior margin sinusous with low lobe anteriorly; thoracic somite 6–8 and abdominal somites (pleonites) with distinct submedian carinae. Telson without accessory median carinae; prelateral lobe as long as carina of lateral primary tooth, with blunt, angular apices.

**Description.** Eye large, not extending beyond antennular peduncle segment 1 (Figure 1A, B). Short, subquadrate ocular scales, inclined anteriorly. Short triangular antennular somite dorsal processes, directed anterolaterally. Antennular peduncle segments subequal in length, total length shorter than carapace. Antennal peduncle reaching beyond midlength but not apex of antennular peduncle segment 1; article 2 and 3 subequal in length. Antennal scale about 0.4CL. Antennal protopod (= coxa + basipod) unarmed.

Rostral plate longer than wide, apex rounded. Carapace with short but distinct anterolateral spines; anterolateral margins sloping posteriorly; gastric and cervical grooves distinct; median carina with uninterrupted anterior bifurcation, base of bifurcation near midpoint between base of rostral plate and dorsal pit; intermediate, lateral and reflected marginal carinae distinct, well developed; posterolateral margin obtusely angled. Posterior margin unarmed, faintly biconcave.

Thoracic somite 5 (pereonite 5) lateral process a simple straight, evenly tapering spine, directed anterolaterally (Figure 1C). Thoracic somite 6–7 lateral processes triangular, anterior margin sinusous with low lobe anteriorly. Thoracic somite 6–8 with distinct submedian, intermediate and lateral carinae.

Right pereopods 1–3 preserved, folded laterally across respective thoracic somites, length about equal to corresponding somite width. Abdominal somites (pleonites) with distinct submedian, intermediate lateral and marginal carinae; submedian carinae on somites 1–3 subparallel, slightly divergent on posterior 2 somite, unarmored on somites 1–4, possibly posteriorly armed on last somite; intermediate and lateral carinae of posterior four somites apparently with broken posterior apices. Abdominal somite 1 pleural plate anteriorly rounded. Specimen aberrant, with somites 5 and 6 apparently conjoined, somite demarcation not evident dorsally, but evident ventrally by juxtaposition of abdominal somite 5 pleopod insertions and abdominal somite 6 sternite; somite 6 sternite posteriorly unarmored (Figure 1D).

Telson incomplete. Dorsal surface with strong median carina, interrupted proximally; accessory median carinae absent; dorsolateral surface with curved rows of shallow
Squilla taulinanus n. sp. from the Burdigalian of Taulignan, south-eastern France

Figure 1. Squilla taulinanus n. sp. from the Miocene (Burdigalian) of Taulignan, Drôme department, France. A–B, holotype MNHN.F.A42046, complete specimen in dorsal and ventral views. C, detail of the lateral process of thoracic somite 5, ventral view and pereopods 1–3. D, detail of the conjoined abdominal somites 5 and 6, ventral view. Abbreviations: s6 = abdominal somite 6; pl1–3 = pereopods 1–3; pl4–5 = pleopod 4–5 insertion; t5 = lateral process of thoracic somite 5. Photos: P. Loubry and C. Lemzaouda
The conjoined abdominal somites in *S. taulignanus* are thus all the more unusual in being symmetrical. Despite its symmetry, however, we regard the conjoined somites in *S. taulignanus* as an abnormality because the species is clearly recognisable as a species of *Squilla* and such fusion is not known in any other stomatopod. Moreover, the ‘crowding’ of the sternites of the last two abdominal somites, in addition to the complete pleuron with marginal carinae on the last abdominal somite, could have probably restricted full movement of the uropod, suggesting an abnormal condition.

**Discussion.** *Squilla taulinanus* n. sp. can be distinguished from the eight other fossil species previously assigned to *Squilla* as follows:

- *Squilla angolia* differs from *S. taulinanus* n. sp. in the much longer prelateral lobe and the presence of accessory median carinae on the telson;
- *Squilla breoniensis* is readily separated from *S. taulinanus* n. sp. by lacking abdominal submedian carinae. Furthermore, *S. breoniensis* appears to lack a median carina on the carapace and has four or five teeth on the dactylus of the raptorial claw; it does not belong to *Squilla* but may instead be closely related to members of the “Meiosquilla group” in Squillidae (Ahyong, 2005);
- *Squilla cretacea* is a poorly known species. The minimal original description and crude figure of the holotype (Schlüter *in von der Mark and Schlüter, 1868*; pl. 54, fig. 7), however, show a lysiosquilloid-like non-carinate carapace and about nine teeth on the dactylus of the raptorial claw. This indicates that Schlüter’s species represents neither *Squilla* nor Squilloidea and is more likely to belong to the Lysiosquilloidea or Eurysquilloidea;
- *Squilla empusa* is readily separable from *S. taulinanus* n. sp. by the longer anterolateral spines on the carapace, reaching anteriorly slightly beyond the base of the rostral plate (rather than falling well short) and the wider than long rostral plate (rather than longer than wide), as well as the position of the base of the anterior bifurcation of the median carina of the carapace (much closer to the dorsal pit than anterior margin of the carapace);
- *Squilla hollandi* has median carinae on the thoracic and abdominal somites, absent in *S. taulinanus* n. sp.;
- *Squilla sonomana* differs from *S. taulinanus* n. sp. by the fully rounded, rather than obtusely angular, posterolateral margin of the carapace;
- *Squilla laingae* has weakly developed instead of prominent submedian carinae on the abdomen, and lacks submedian denticles on the telson. Unfortunately, the cephalothorax of *Squilla laingae* is not presently known, but based on telson shape and apparent absence of submedian denticles on the telson, *Squilla laingae* might be closer to *Pterygosquilla* Hilgendorf, 1890, than *Squilla* Fabricius, 1787;
- *Squilla miocenica* is known only from the dactylus of the raptorial claw, but given that it is eight-toothed, it is unlikely to represent *Squilla*, whose known species have six dactylar teeth.
Of the extant species of *Squilla*, *S. taulinanus* n. sp. most closely approaches *Squilla brasiliensis* Calman, 1917, and *S. caribaea* Manning, 1969, both from the western Atlantic, in sharing a distally rounded rostral plate, distinct anterior bifurcation of the median carina of the carapace that is not interrupted at the base, an obtusely angular posterolateral margin of the carapace and lateral processes of thoracic somites 6–7 that have a low lobe or swelling on the anterior proximal margin. The new species can be separated from *S. caribaea* by the distinctly sloping anterolateral margins of the carapace (almost transverse in *S. caribaea*) and position of the base of the anterior bifurcation of the median carina of the carapace (almost equidistant from dorsal pit anterior margin of carapace versus about two-thirds of distance from anterior margin of carapace to dorsal pit). From *S. brasiliensis*, *S. taulinanus* n. sp. can be separated by its straight, rather than falcate lateral process of thoracic somite 5.

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