

STOMATOPODS (CRUSTACEA: MALACOSTRACA) FROM THE MIOCENE OF CALIFORNIA

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ABSTRACT—The scarce fossil record of stomatopod crustaceans is extended with three new species and two new genera described from the Miocene of California. *Squilla laingae* new species and *Angelosquilla atamirensis* new genus and species show clear affinities to the Recent family Squillidae. *Topangasquilla gravesi* new genus and species can be accommodated within the Recent family Lysiosquillidae. These new species occur in the Monterey and Topanga Formations in Los Angeles County. In addition, three other specimens are described from the Miocene Topanga Formation. The preservation of these stomatopods is among the best noted for any fossils of this group. These specimens show characteristic stages of decay that clearly correspond with those noticed in taphonomic experiments with Recent stomatopods.

INTRODUCTION

STOMATOPODS, COMMONLY known as mantis shrimp, have been recognized as a distinct group of crustaceans since Latreille defined the order in 1817. The Recent representatives of this group can be found on most of the world's tropical and subtropical coral reef, sand, mud, and rubble strewn coasts. These crustaceans, 1 to 35 cm in length, are active, alert, highly visual predators exhibiting intense agonistic behavior while defending their burrows and cavities (Caldwell and Dingle, 1975). The chief morphological characteristic of the group is enlargement of the second thoracopods used in prey capture and agonistic interactions (Dingle and Caldwell, 1978). Although seldom seen because of their secretive habits, these animals, due to their numbers, often constitute a major predatory force in sub- and intertidal marine communities (Caldwell and Dingle, 1975, 1976).

Fossil evidence indicates that the ancestors of the stomatopods probably diverged from other malacostracans in the Devonian (Schram, 1969a, 1969b, 1981, 1982; Reaka, 1975; Kunze, 1983). Schram (1986) recognized essentially two types of fossil stomatopods: those Mesozoic and Cenozoic forms assignable to the living suborder Unipeltata, and the Paleozoic suborder Archaeostomatopodea. The Archaeostomatopodea currently contain only one family, the Tyrannophontidae (Schram, 1984). This family appears to form an anatomical intermediate between the Unipeltata and the extinct order Palaeostomatopoda (Schram, 1986).

Of the Unipeltata, only the Jurassic Sculdidae cannot be assigned to any of the living families. Some species of the deep-water superfamily Bathysquilloidea seem to resemble an intermediate form between the Sculdidae and the extant stomatopods (Manning et al., 1990). Schram (1986) therefore placed the Sculdidae within the superfamily Bathysquilloidea. However, there seems little precise morphological justification for doing so, based on restudy of the species of *Sculda* (personal observations C.H.). All other fossil forms are essentially assignable to extant families, although many descriptions are based on imperfectly preserved material. Berry (1939) comprehensively summarized the taxonomic history of the Sculdidae and other fossil stomatopods known until then. Holthuis and Manning (1969) provided a short overview of the fossil stomatopods, indicating the uncertain affinities of most of them. Relatively recent records are known from Tertiary deposits in Korea (Yun, 1985), Japan (Karasawa and Nakagawa, 1992; Karasawa, 1996) and Germany (Förster, 1982; Lienau, 1985), and the early Maastriichtian of Nigeria (Förster, 1982). To date there are 25 species of fossil unipeltatan stomatopods known, apart from poorly de-

scribed and dubious records. Geary et al. (1991) presented a way to extend the geologic record of stomatopods by identifying their distinct predatory traces in fossil shell deposits; Pether (1995) employed a similar approach.

In this paper, we describe two new species of fossil squilloid stomatopods, one in a new genus, from the middle Miocene, Monterey Formation of Los Angeles County, California. We also recognize a third species, a lysiosquilloid placed in a new genus, from the Miocene Topanga Formation, South Pasadena, California. In addition, three specimens also representing stomatopods have been collected from Glendora in the Topanga Formation. These deposits form major elements in the Miocene of the Los Angeles Basin (Figure 1).

This material was discovered in the fossil invertebrate collection of the Los Angeles County Museum of Natural History (LACMIP). Although the specimens had been recognized as stomatopods and had been in the collection for years, they were never described. The material comes from a series of localities (Figure 2) scattered in and around the city of Los Angeles in southern California. With the description of these new species, reports of the scarce stomatopod fossil record receive a significant boost.

Morphological terms employed in this paper adhere to the usage of Manning (1969, p. 8–15), and measurements follow Manning's standard metrics and indices for stomatopods. The measurements for incomplete specimens are estimations based on the bilateral symmetry of the animals or ratios known for species typical of the family to which they belong.

The species descriptions in this paper include information on morphological details that are not used in standard stomatopod taxonomy. This extra information might prove its usefulness in a possible future phylogenetic analysis of the stomatopod taxa.

Special attention has been given to the taphonomic features of the material, utilizing information gained from experimental studies on stomatopod decay and mineralization (Hof and Briggs, 1997).

SYSTEMATIC PALEONTOLOGY

- Class MALACOSTRACA Latreille, 1806
- Subclass HOPLOCARIDA Calman, 1904
- Order STOMATOPODA Latreille, 1817
- Suborder UNIPELTATA Latreille, 1825
- Superfamily SQUILLOIDEA Latreille, 1803
- Family SQUILLIDAE Latreille, 1803
- Genus SQUILLA Fabricius, 1787

Diagnosis.—Body compact with smooth or minutely punctate cuticle; size moderate to large, total length up to 20 cm, generally 15 cm or less. Eyes moderate to large. Ocular scales sep-

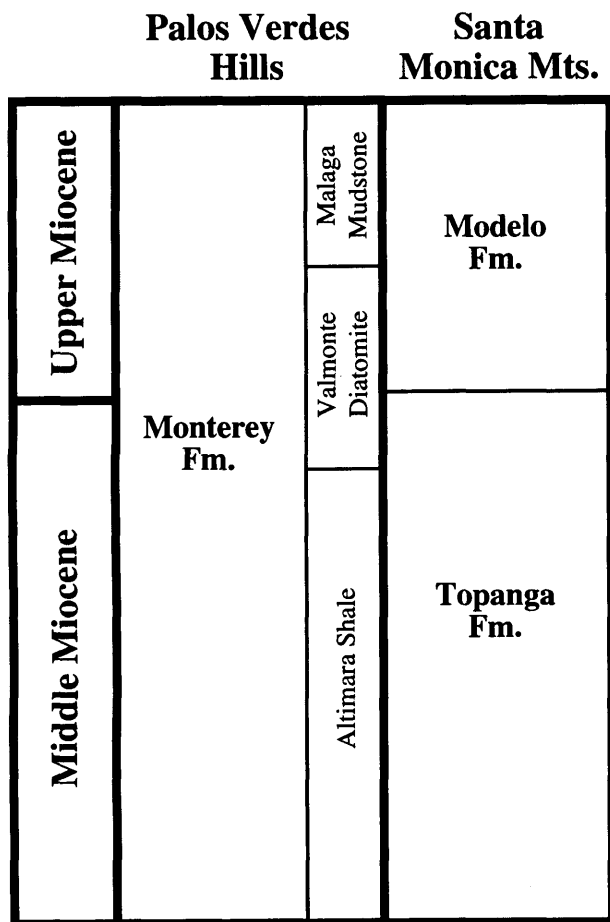


FIGURE 1—Stratigraphy of the middle and upper Miocene in southern California. The chart roughly correlates rock units found in the Palos Verdes Hills and the Santa Monica Mountains. Based on geographic and lithologic evidence, the fossil stomatopods from localities 1 and 2 appear to be from the lower Altamira Shale, while those from localities 3 and 4 probably originated from the upper part of the Topanga Formation.

arate, subtruncate, rounded, or acute. Rostral plate variable in shape, median carina present or absent. Carapace narrowed anteriorly, carinae well formed, normal complement present (one median, two intermediates, laterals, and marginals), median carina often with anterior bifurcation; cervical groove distinct; posterior median margin of carapace usually evenly concave, occasionally with obscure obtuse median projection; anterolateral angles of carapace armed. Last three thoracic somites with submedian and intermediate carinae, intermediate occasionally armed, lateral process of fifth thoracic somite a single, variously shaped spine or lobe, usually an anteriorly curved spine; lateral processes of next two somites usually bilobed, posterior lobe usually much the larger. Dactylus of raptorial claw with five to seven teeth, usually six; upper margin of propodus evenly pectinate and with three movable teeth at base, middle smallest; ischiomeral articulation terminal; endopods of walking legs linear. Abdomen compact, carinae well formed, first five somites with eight carinae (paired submedians, intermediates, laterals, and marginals), sixth somite with six. Telson with median carina, supplementary dorsal carinae present or absent; three pairs of marginal teeth present, submedians with fixed apices; prelateral lobes usually present; ventral surface of telson usually with post-anal keel; inner margin of basal prolongation of uropod typically

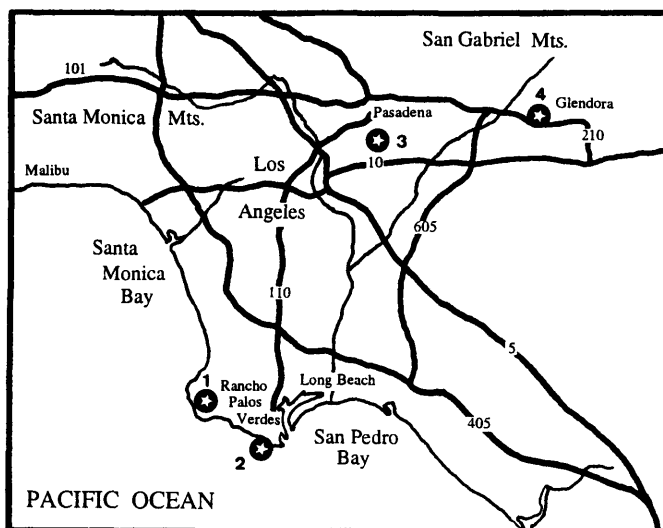


FIGURE 2—Localities for fossil stomatopods in Los Angeles County, California. Numbers correspond to the following localities: 1 = LACMIP locality 12020, Palos Verdes Hills, Los Angeles; 2 = LACMIP locality 15618, beach west of Point Fermin, Los Angeles; 3 = LACMIP locality 2542, 838 Lyndon St., South Pasadena; 4 = LACMIP locality 1292, roadcut on Freeway 210 at Glendora Ave., Glendora.

tuberculate, occasionally provided with slender spines; medial spine of basal prolongation with lobe on outer margin.

Remarks.—The above diagnosis of the genus is derived from Manning (1969). It includes those characters most likely to be preserved on fossils. The genus *Squilla* contains 26 extant species. Several fossil stomatopod species have been assigned to this genus, although some of them certainly do not represent true *Squilla*. In other cases, possible species of *Squilla* were ascribed to distinct genera (Holthuis and Manning, 1969).

SQUILLA LAINGAE new species
Figures 3.1–3.5, 4

Diagnosis.—A moderate-sized stomatopod about 10 cm long. First five abdominal tergites with longitudinal, paired submedian, intermediate, lateral, and marginal carinae; at least intermediate and lateral carinae of somites four and five posteriorly armed with small spines. Telson almost as broad as long with well-developed median carina; margin with submedian, intermediate, and lateral teeth all with fixed apices, prelateral lobes absent. Submedian denticles of telson very small or absent, 14 rounded intermediate denticles present and one lateral denticle. Ventral side of telson bears a short post-anal carina.

Description.—The visible part of the left half of the eighth thoracic somite shows the impression of an intermediate carina (LACMIP 7959, Figure 3.1). The lateral margin of the pleuron of this somite is unfortunately partially covered by the anterolateral plate of the first abdominal tergite.

The first abdominal tergite is provided with distinctive anterolateral plates. In LACMIP 7959, the right anterolateral plate is especially clear showing the extension of the first abdominal lateral carina and a slightly inflated lateral margin (Figure 3.1, arrow). In LACMIP 7960, the left anterolateral plate is clearly visible (Figure 3.2, arrow).

The first five abdominal tergites are armed with longitudinal, paired submedian, intermediate, lateral, and marginal carinae. All the impressions of abdominal tergites one to five (LACMIP 7959, Figure 3.1) display the submedian carinae as slight imprints, less clearly developed towards the anterior and posterior