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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 altamirensis* 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 Maastrichtian of Nigeria (Förster, 1982). To date there are 25 species of fossil unipeltatan stomatopods known, apart from poorly described 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-

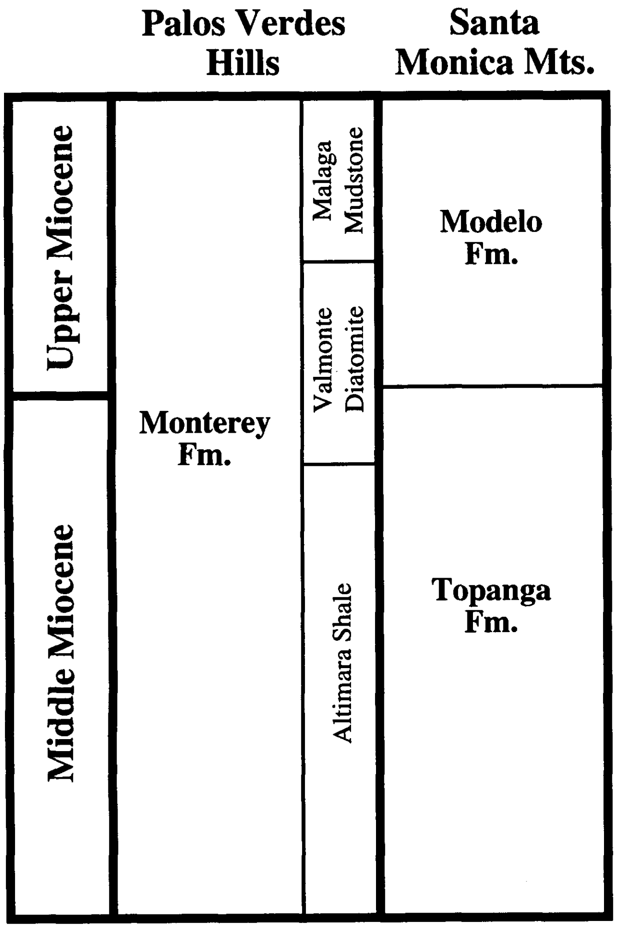

FIGURE 1—Stratigraphy of the middle and upper Miocene in southern California. The chart roughly correlates rock units found in the Palos Verdes Hills and the Santa Monica Mountains. Based on geographic and lithologic evidence, the fossil stomatopods from localities 1 and 2 appear to be from the lower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

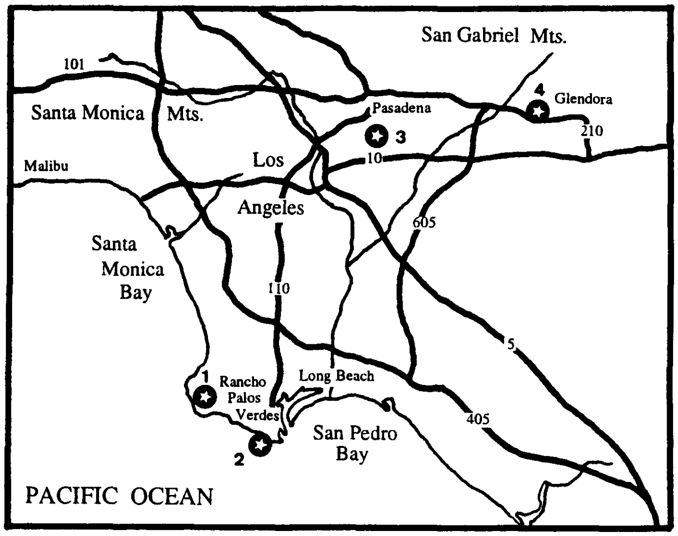

FIGURE 2—Localities for fossil stomatopods in Los Angeles County, California. Numbers correspond to the following localities: 1 = LACMIP locality 12020, Palos Verdes Hills, Los Angeles; 2 = LACMIP locality 15618, beach west of Point Fermin, Los Angeles; 3 = LACMIP locality 2542, 838 Lyndon St., South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

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 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

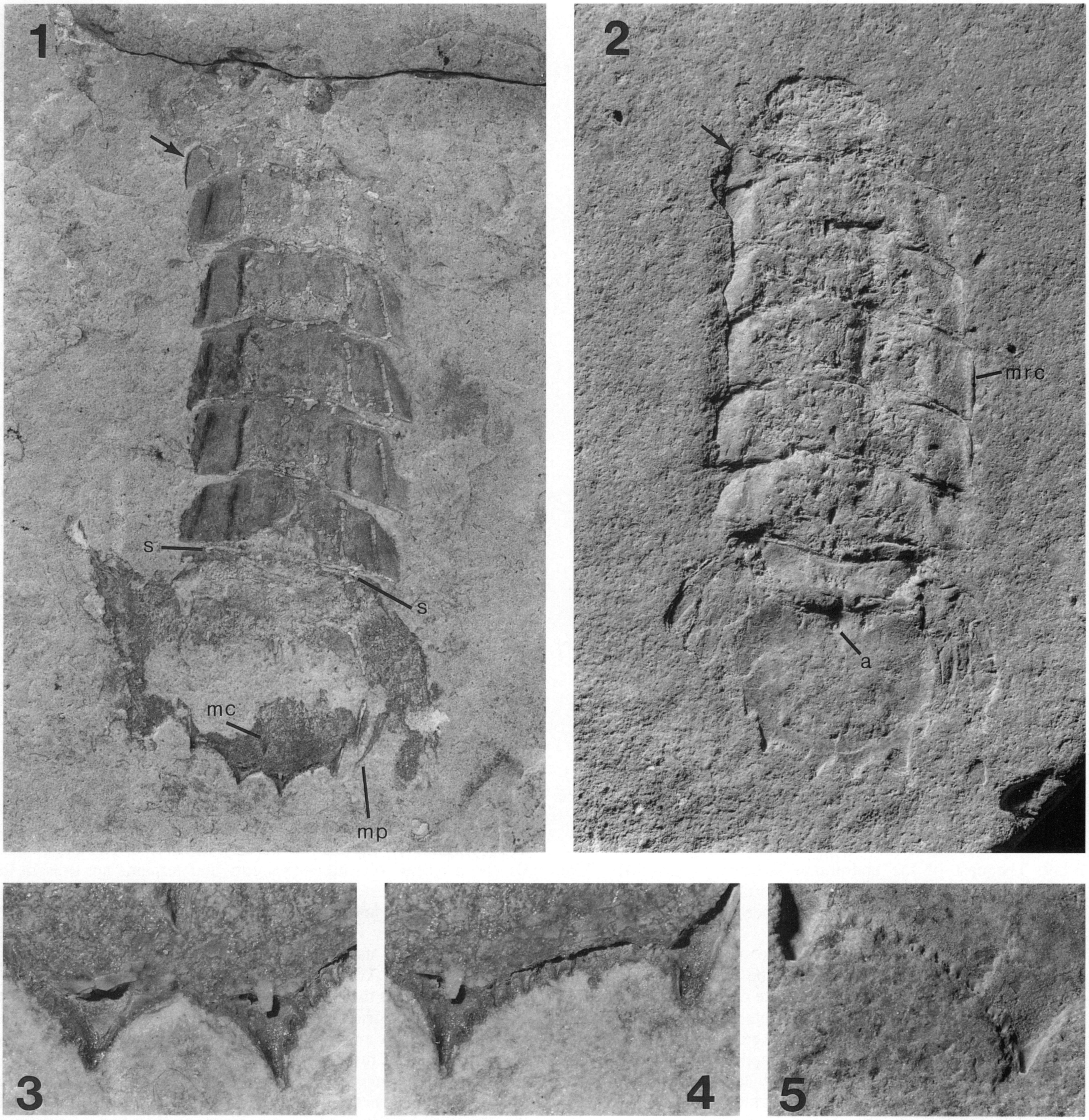

FIGURE 3—*Squilla laingae* new species. *1, 3, 4,* holotype, LACMIP 7959. *1,* dorsal impression in negative relief showing part of the eight thoracic, first five abdominal somites, telson, and partially preserved left uropod, arrow = anterolateral plate of first abdominal segment, s = socket for articulation of fifth and sixth abdominal segments, mc = median carina, mp = medial process of the basal prolongation of the uropod, ×2; *3,* close-up of submedian area of telson, ×10; *4,* close-up of intermediate area with intermediate denticles, ×10. *2, 5,* paratype, LACMIP 7960. *2,* a dorsal abraded cast of the abdominal somites, the remains of the basal parts of the uropods, and an impression of the venter of telson, arrow = anterolateral plate of first abdominal segment, mrc = marginal carina of an abdominal tergite, a = anus, ×1.75; *5,* close-up of intermediate area with intermediate denticles, ×10.

edges of the tergites. The intermediate carinae are visible as sharply defined grooves extending the entire length of the tergites. On the first tergite, the anterior impressions are slightly deeper than those posterior. Small holes at the posterior end of the intermediate carinae of somites four and five indicate the presence of posterior spines. The lateral carinae are discernible as sharp grooves of constant depth along the tergites. Similar to the intermediate carinae, the lateral carinae of somites four and five show traces of posterior spines. Only an impression of the left marginal carina of the first tergite remained in LACMIP

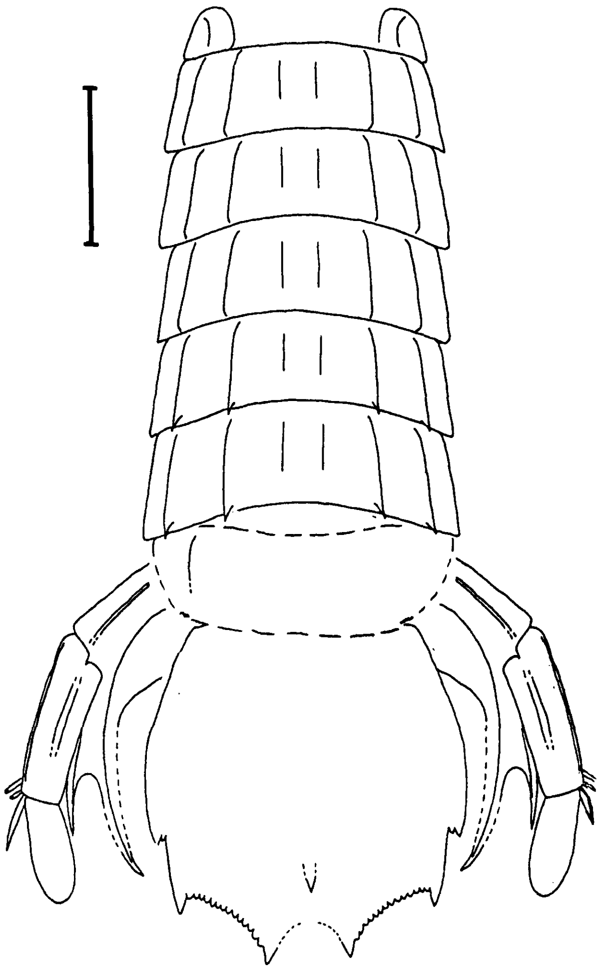

FIGURE 4—Reconstruction of *Squilla laingae* new species, showing dorsal side of abdominal somites, telson and uropods. Scale = 1 cm.

7959. The cast of the abdominal somites of LACMIP 7960 shows the slightly inflated marginal carinae on at least the first four somites (Figure 3.2, mrc). All other cuticular ornaments in LACMIP 7960 are distorted.

In LACMIP 7959, abdominal somite six is preserved only as an impression of the anterior part of the lateral carinae and the oblique anterior part of the intermediate carinae. Clearly visible, however, are the remains of the sockets (Figure 3.1, s), which are part of the pivoting structure between somites five and six and located on the onset of the intermediate carinae. The sediment filling of somite six shows faint, tanned casts of the anterior margin of the sternite of this segment. In LACMIP 7960, abdominal somite six shows the mineralized remains of a smooth sternite (Figure 3.2).

On both specimens, the telson is clearly preserved. The telson is almost as broad as long. In LACMIP 7959, the telson is filled with sediment. Only the posterior and left lateral margin are observable. Within the sediment filling, a sharp impression of the posterior part of a dorsal median carina is visible, deepening towards the posterior margin of the telson and ending abruptly about 1.5 mm in front of the telson's edge (Figure 3.1, mc). The visible margin of the telson preserves a sagittal section along with the dorsal inner side of the cuticular remains of the marginal denticles and teeth. In LACMIP 7960, an impression of the anus and a very short post-anal carina is visible (Figure 3.2, a).

Both specimens show paired submedian and intermediate teeth (Figure 3.1–3.5). In LACMIP 7959, only the left lateral tooth is preserved (Figure 3.1), in LACMIP 7960, both lateral teeth are visible (Figure 3.2). The area of the prelateral lobes is not preserved in LACMIP 7959. This area is visible in LACMIP 7960, although the margin of the impression is disturbed (Figure 3.2). The actual presence of prelateral lobes seems unlikely. All marginal teeth are armed with fixed apices. The relative depth of the impressions of the teeth (LACMIP 7959, Figure 3.3, 3.4) suggests the presence of inflated bases.

The margin of the telson between the submedian teeth has a gentle V-shaped form (Figure 3.3). In LACMIP 7959, the presence of a median slit cannot be checked because this area is obscured by sediment. However, the manner in which the matrix in this area is deformed in LACMIP 7960 suggests the presence of a median slit in the telson. In both specimens, submedian denticles are not visible (Figure 3.3, 3.5). It is not clear whether these are really missing or just not exposed.

Between the submedian and intermediate teeth 14 intermediate denticles are clearly visible (LACMIP 7959, Figure 3.4; LACMIP 7960, Figure 3.5). The intermediate denticles form a concave line from halfway up the submedian tooth to the base of the intermediate tooth. The denticles are rounded and about equal in size. Single lateral denticles are present, visible between the left lateral and intermediate teeth of both LACMIP 7959 and LACMIP 7960.

Of all the uropods, the left one of LACMIP 7959 is the best preserved (Figure 3.1). The limb consists of a protopod with a bifurcate basal prolongation on the ventral side, a two-segmented exopod, and an endopod. A deep imprint on the protopod, just above the base of the exopod, indicates the presence of a sharp dorsal spine at this position. Cuticular traces on the protopod indistinctly show the remains of two, most probably dorsal, longitudinal ridges. The medial process of the basal prolongation is visible in outline (Figure 3.1, mp), the lateral is missing on LACMIP 7959, but visible on LACMIP 7960. The nebulous outline of the medial process fails to reveal any possible armature on its inner margin, or the presence of a lobe on its outer margin. However, the presence of large spines, or a large lobe, is very unlikely. The exopod clearly consists of two segments. On the proximal one numerous cuticular remains are present in both the specimens. These fragments seem to indicate the presence of a median and lateral ridge. In LACMIP 7959, there are at least three partly visible spines on the outer distal margin. The distal segment of the exopod can be seen as a tanned, paddle-shaped outline (LACMIP 7959, Figure 3.1). Only a small portion of the base of the uropodal endopod is preserved along with some more distal fragments.

Discussion.—A reconstruction of what is known about this species is offered in Figure 4.

Although the anterior half of the animal is missing on both specimens, the general habitus of the abdomen and telson, and the structure of the uropod, provide enough information for a generic assignment of these specimens.

The presence of a complete set of carinae on the abdomen, a sharp median carina on the telson, the marginal teeth of the telson lacking movable apices, and more than four intermediate denticles serve to place this species within the superfamily Squilloidea (see Manning, 1980, 1995). This superfamily currently consists of two families, the Harpiosquillidae and the Squillidae. Diagnostic characters of the Harpiosquillidae include erect spines on the upper margin of the propodus of the raptorial claws, and the deeply excavated posterolateral margin of the carapace. Both raptorial claws and carapace are missing in these specimens. However, it seems unlikely that this species belongs to the large to very large-sized Harpiosquillidae. Focusing on

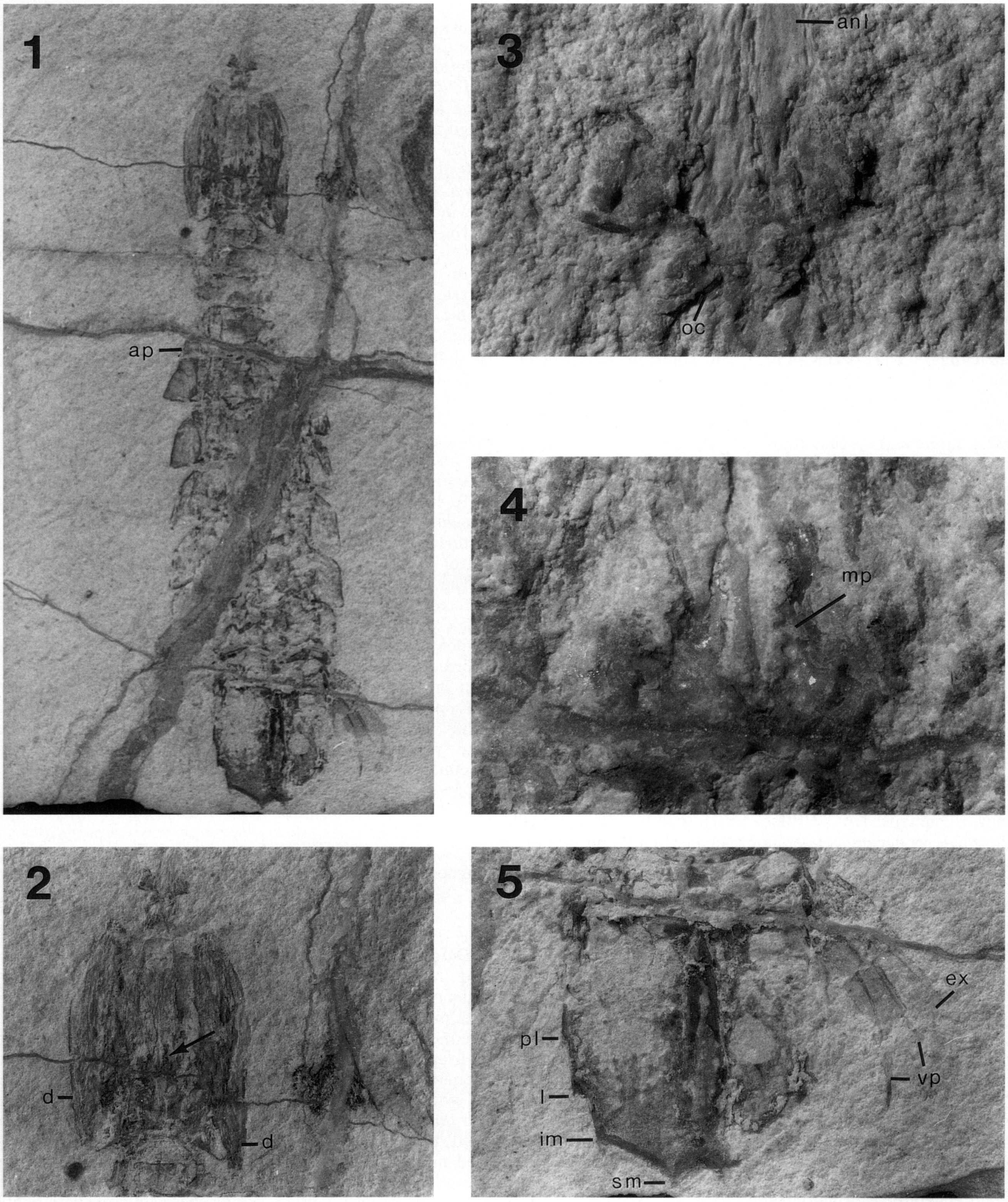

FIGURE 5—*Angelosquilla altamirensis* new genus and species. *1–5,* holotype, LACMIP 7961, part. *1,* general view, ap = anterolateral plate, ×1.2; *2,* close-up of cephalon and anterior thorax, d = dactyls of second thoracopods, arrow = area of mandible remains, ×2; *3,* close-up of cephalon with eyes and antennular peduncles, oc = ocular scale, anl = first segments of antennular peduncles, ×11.5; *4,* close-up of mandibles, mp = molar process, ×15; *5,* close-up of tail fan, ex = exopod of uropod, vp = ventral processes of basal prolongation, pl = prelateral lobe, l = lateral tooth, im = intermediate tooth, sm = submedian tooth, ×2.5.

overall size and the morphology of the abdomen and the telson, a comparison of our species with the 11 known harpiosquillid species did not render any similarity. The family Squillidae contains 40 genera. The absence on our material of movable apices on the submedian teeth of the telson, presence of a complete set of carinae on the anterior five abdominal tergites, and the lack of clear spines on the inner margin of the basal prolongation of the uropods, reduces the number of possible genera significantly.

The relative high number of 14 intermediate denticles is only observed in species of the genera *Alima* and *Squilla*. The questionable presence of submedian denticles on these fossils precludes a species to species comparison. We assign this species to *Squilla* based mainly on the shape of the telson. According to Manning's generic diagnosis (Manning, 1969, p. 127) the telson of *Alima* is more elongated.

Etymology.—The species is named in honor of the collector of the paratype, Ms. Melody Laing.

Type material.—Holotype, LACMIP 7959 (Figure 3.1), a tanned negative dorsal intaglio of the right half of the eighth thoracic tergite and the abdominal tergites one to six, an outline of the left uropod with some cuticular remains, and a telson filled with sediment showing only the lateral and posterior margin. Paratype, LACMIP 7960 (Figure 3.2), a dorsally abraded cast of the first five abdominal somites, an impression of the ventral side of abdominal somite six and the telson, and the remains of the basal parts of the uropods. Both types are deposited in the invertebrate collection of the Los Angeles County Museum of Natural History.

Measurements.—LACMIP 7959: width of the abdomen 2.2 cm, abdominal length 4.3 cm (without telson). Telson width 1.8 cm, telson length 1.7 cm. LACMIP 7960: width of the abdomen 2.5 cm, abdominal length 4.2 cm. Telson width 1.9 cm, telson length 1.7 cm. The estimated total length of this species is about 10 cm (based on the body proportions of *Squilla mantis*).

Localities.—Holotype: LACMIP loc. 12020, middle Miocene, Altamira Shale exposed in the Palos Verdes Hills section, Los Angeles County, California. The exact location is unfortunately unknown. Paratype: LACMIP loc. 15618, middle Miocene, Altamira Shale, collected as float along the beach at Point Fermin, Los Angeles County, California.

The Altamira Shale is the lowest of three members of the Monterey Formation (see Figure 1), a Miocene deposit in the Los Angeles Basin (Woodring et al., 1946; Rowell, 1981). Based on analysis of the benthic foraminiferans and molluscs found in this member, Woodring et al.(1936) suggested these layers represent a shallow neritic to deeper-water facies.

Taphonomy.—The fact that both specimens consist of only the posterior half of the body indicates that a period of decay and transport occurred before the actual burial event. Experimental research, as well as a taphonomic review of the stomatopod fossil record, reveals that stomatopod carcasses tend to separate in the region of the last thoracic somites (see Hof and Briggs, 1997). Although the abdominal tergites of both specimens are still connected, the first signs of further fragmentation can be observed. LACMIP 7959 shows that some tergites are separated laterally, especially somite four and five (Figure 3.1).

In both the specimens the sixth abdominal somite is preserved in a different way than the anterior five. This is most probably due to the morphological and structural differences between the sternites of these somites. The uropods of the sixth abdominal somite originate from the lateral sides of the sternite, compared to the ventrally attached pleopods of the first five abdominal somites. The sternite of the sixth abdominal somite, therefore, forms a relatively large plate. Observation of extant stomatopods shows that this sternite is usually also more sclerotized than the anterior five.

In all the impressions of the thoracic and abdominal carinae of LACMIP 7959, tiny, white cuticular fragments are visible, as there are on the anterior and posterior margins of the tergites (Figure 3.1). Apparently only the more sclerotized parts of the cuticle were mineralized while the thinner portions decayed. However, the counterpart of this specimen is lacking so we will never exactly know which parts of the cuticle were preserved and in what way.

The impressions of the sixth abdominal tergite and the telson of LACMIP 7959 are filled with sediment. Both parts show traces or remains of ventral structures. A faint tanned cast of the anterior margin of the sternite can be seen in somite six. A part of the filled telson is tanned and covered with tiny pieces of cuticle. These are probably the remains of the ventral side of the telson. Also the impression of the median carina is lined with cuticular remains. A remarkable feature of the preservation of the telson is that the depth of the impression of the marginal teeth exceeds the depth of the impression of the median carina. Apparently the midfield of the telson has been compressed during fossilization. The filling of these parts also indicates a period of transport and decay prior to actual burial.

To the right of the telson, an amorphous mass of cuticular remains can be seen. The only structures that can be discerned in this mass are several curved spines or setae, most probably not of stomatopod origin.

The paratype, LACMIP 7960, is preserved in a completely different way. The abraded cast of the abdomen shows an irregular cross section at the height of the lateral carinae. The abdomen is filled with sediment, but in many places internal mineralized remains are visible. Only studies with a scanning electron microscope can determine the soft-tissues mineralized in this specimen. Also, cuticular mineralized remains are abundantly present, especially in the uropods. The telson of the paratype specimen is an impression of the ventral side with traces of cuticular remains at the margins.

Genus Angelosquilla new genus

Type species.—*Angelosquilla altamirensis* new species.

Diagnosis.—Since only one species is known at present, the diagnosis of the genus is the same as that of the species.

Angelosquilla altamirensis new species
Figures 5.1–5.5, 6, 7

Diagnosis.—A moderate-sized stomatopod around 10 cm long. Moderate-sized eyes, separated subtruncate ocular scales. Antennular peduncle slightly shorter than carapace. Rostral plate with median carina, carapace with at least anteriorly median and intermediate carinae. Dactylus of raptorial claw slender, armed with approximately 16 teeth. Last three thoracic somites with submedian and intermediate carinae. First five abdominal tergites with longitudinal, paired submedian, intermediate, lateral, and marginal carinae. Telson as broad as long with well-developed, broad, basally notched median carina; margin with submedian, intermediate, and lateral teeth all with fixed apices, prelateral lobes present; submedian denticles of telson very small or absent; about 14 to 15 small, sharp, intermediate denticles present and one lateral denticle. Telson ornamented with radiating rows of circular decorations. Inner margin of basal prolongation of uropod smooth or with minute armature.

Description.—The specimen, LACMIP 7961, exhibits an ophthalmic somite bearing the stalked eyes. Both ocular peduncles are poorly preserved (Figure 5.1–5.3). Parts of the cornea are preserved, indicating cylindrical-shaped eyes of moderate size (see Manning et al., 1984, for eye shape terminology). On the

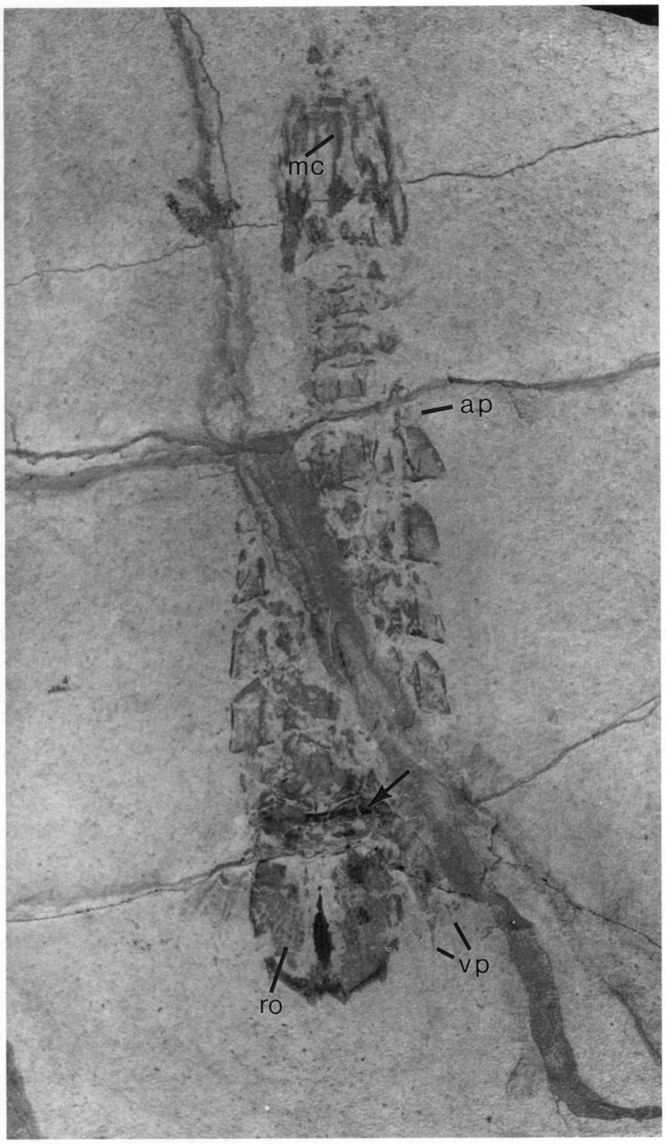

FIGURE 6—*Angelosquilla altamirensis* new genus and species. Holotype, LACMIP 7961, counterpart, mc = median carina carapace, ap = anterolateral plate, arrow = sternite sixth abdominal somite, vp = ventral processes of basal prolongation of uropod, ro = radiating ornamentation on telson, ×1.2.

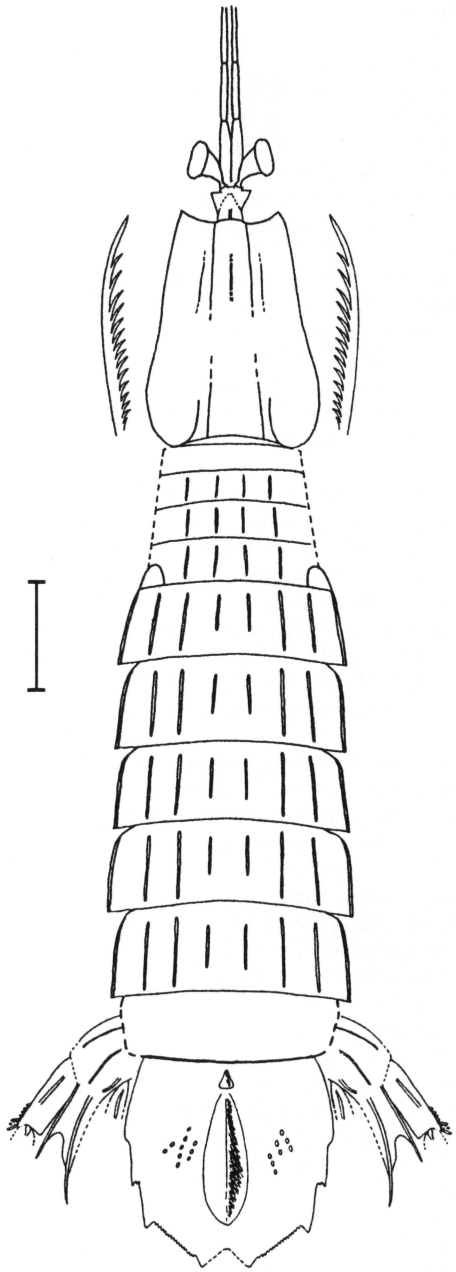

FIGURE 7—Reconstruction of *Angelosquilla altamirensis* new genus and species. Scale = 1 cm.

part, the left of the paired ocular scales is clearly visible on the dorsal side of the ophthalmic somite (Figure 5.3, oc). The ocular scales are separated and subtruncate. Posterior to the ophthalmic somite the anterior portion of the antennular somite can be seen. The dorsolaterally situated antennular processes are visible, although only as vague outlines. The antennules are stretched out anteriorly, laying side by side. They emerge from beneath the ophthalmic somite just between the eyes (Figure 5.3, anl). Three peduncular antennal segments are visible, subequal in length. The total length of the antennular peduncle is slightly shorter than the carapace. The fossil is unfortunately cut off just at the end of the third antennular segment depriving us of information on the flagella. Faint remains of the antennal peduncles and scales are hardly visible.

Only the base of an apparently subtriangular rostral plate is preserved. The rostral plate seems broader than long, and with traces of a median carina. The carapace is narrowed anteriorly. The median field shows traces of a dorsal median carina (Figure 6, mc) and intermediate carinae on the counterpart. The lateral plates of the carapace are poorly preserved, their margins disturbed by the underlying remains of the second pair of thoracopods. The molar processes of the mandibles can be seen (Figure 5.2, arrow) in the posterior area of the carapace. The right one is best preserved and shows one of the two dentate folds of the molar process with at least 8 teeth (Figure 5.4, mp). The posterior median margin of the carapace is only slightly curved (Figure 5.1, 5.2). The posterolateral angles extend posteriorly, the reflected portions of the marginal carinae are clearly visible.

The second thoracopods are large, slender, raptorial claws. The specimen shows the preserved dactyls, propodi, and meri jack-knifed on each other (Figure 5.1, 5.2). The dactyls are slender and almost as long as the carapace (Figure 5.2, d). The remains of 14 teeth are discernible and the total number of teeth is estimated at 16. It is not possible to clearly distinguish the separate segments of the raptorial claws apart from the dactyls. The only detail that can be recognized is one of the movable teeth of the inner proximal edge of the propodal groove of the right propodus. The remains of the tooth are displaced sideways beneath the lateral field of the carapace.

Fragments of both sternites and tergites of the last four thoracic somites are visible. The only recognizable traces of dorsal carination are the sharp, paired, submedian and intermediate carinae of tergites six, seven, and eight (Figure 6).

The first five abdominal somites preserve only the remains of the tergites. The lateral parts of these tergites are clearly visible, but the median area is disturbed by a filled crack that divides the abdomen diagonally. A complete set of paired submedian, intermediate, lateral, and marginal carinae on the dorsal abdominal tergites can be seen on somite one (Figure 6). This somite also shows the remains of both anterolateral plates (Figures 5.1, 6, ap). Apart from the marginal carinae, which can be seen on all somites (Figures 5.1, 6), the more medial carination of the remaining abdominal segments is only partly preserved. Intermediate carinae can be seen on somites two, four, and five of the counterpart (Figure 6), lateral carinae on somites four and five of the part (Figure 5.1), and three, four, and five on the counterpart again (Figure 6). Of the sixth abdominal somite only the sternite is preserved (Figure 5.5, but much better in Figure 6, arrow).

The telson is as broad as long and bears a distinctive broad median carina that is basally notched (Figures 5.1, 5.5, 6). The telson is ornamented with rows of radiating circular decorations posterolateral from the base of the median carina (Figure 6, ro). Paired submedian, intermediate, and lateral teeth are present as are prelateral lobes (clearly visible on Figure 5.5, pl). The tips of the teeth are not preserved in fine detail, but the presence of any movable apices seems unlikely. The area of the submedian denticles is disturbed and only a superficial median slit can be seen (Figure 5.5). The margin of the intermediate area is almost linear and occupied with very small, sharp denticles. Although the denticles are not well preserved, information from both the sides results in an estimation of 14 to 15 denticles. Between the intermediate and lateral teeth, one lateral denticle is present.

Both of the uropods are partially preserved (Figures 5.1, 5.5, 6). The right one (on both part and counterpart), and the left one (counterpart only) show the basal segment with the bifurcate ventral projection (Figure 5.5, 6, vp). The outline of the right, two-segmented exopod can be seen vaguely (Figure 5.5, ex), including the remains of at least seven movable spines on the posterolateral margin of the proximal segment. On the counterpart (Figure 6), the spines of the basal prolongation show very faint serial cuticular remains on the inner margin. It is not clear whether this margin is smooth or provided with minute tubercles or spines.

Discussion.—A reconstruction of this species is offered in Figure 7.

Without question this species belongs to the superfamily Squilloidea (see Manning, 1980, 1995), a stomatopod superfamily accommodating only two families. The absence of a deeply excavated posterolateral margin of the carapace, a diagnostic character of the family Harpiosquillidae, ascribes this stomatopod to the family Squillidae.

When comparing the features of this stomatopod with the diagnoses of the genera within the Squillidae, the large number of teeth on the dactylus of the raptorial claw is conspicuous. Ten or more teeth are only known from the genera *Pterygosquilla* and *Natosquilla,* and the species *Squilla decimdentata. Pterygosquilla* can be excluded because species of that genus exhibit spiniform ocular scales, have movable apices on the submedian teeth of the telson, and bear erect spines on the inner margin of the basal prolongation of the uropods (see Manning, 1969). The monotypic genus *Natosquilla* is characterised by 10 to 18 teeth on the dactyls of the raptorial claw. However, characteristic features of this genus, such as the large eyes and the small ocular scales (Manning, 1978), do not match with those of the described fossil. The species *Squilla decimdentata* bears raptorial claws armed with 10 or 11 teeth only (Manning, 1970). Consequently, the unique combination of characters justifies the erection of a new genus.

Etymology.—The generic name is formed from "Angeles," because the type material was found in the vicinity of Los Angeles, in combination with the generic name *Squilla.* The species name refers to the stratum from which the type material originates.

Type material.—Holotype, LACMIP 7961 (Figures 5.1, 6), a well-preserved stomatopod in part and counterpart. Both halves show the ophthalmic region, including the eyes, the first three segments of the antennules, the base of the rostral plate, the carapace, some internal structures of the thorax, the folded raptorial claws, thoracic somites five to eight, the tergites of the first five abdominal somites, the sternite of abdominal somite six, the uropods, and the telson. Part and counterpart mainly show a sagittal view of the dorsal side. The type is deposited in the fossil invertebrate collection of the Los Angeles County Museum of Natural History.

Measurements.—Total length of LACMIP 7961 about 9 cm (corrected for natural filled cracks). Carapace length 1.7 cm. Rostral plate basal width 0.2 cm. Dactylus raptorial claw 1.7 cm. Abdominal width 2 cm (coarse estimation). Telson width 1.7 cm; length 1.7 cm.

Localitiy.—LACMIP loc. 12020, middle Miocene, probably Altamira Shale as exposed in the Palos Verdes Hills section, Los Angeles County, California. Unfortunately the exact location is unknown.

Taphonomy.—*Angelosquilla altamirensis* is the best preserved stomatopod specimen of all those available for this study from the Monterey Formation. The complete preservation with the raptorial claws folded underneath the carapace, indicates a rapid burial. [This specimen is figured in Hof and Briggs (1997) as an example of a rapidly buried stomatopod.] During the course of diagenesis, the more sclerotized parts of the cuticle were mineralized. The thinner parts are preserved as tanned areas. These thin cuticular portions sometimes show a "floppy" appearance, a feature also observed in experimental studies on the taphonomy of stomatopods (Hof and Briggs, 1997). The partly preserved mandibles are remarkable. Also the densely packed remains of the posterior thoracic sternites are well preserved. Fragments of the delicate thoracic epipods are present but it is not possible to determine the exact number. The coarse granular structure of the matrix unfortunately obscures the observation of very fine details such as the marginal armature of the basal prolongation of the uropods.

Superfamily LYSIOSQUILLOIDEA
Giesbrecht, 1910
Family LYSIOSQUILLIDAE Giesbrecht, 1910
Genus TOPANGASQUILLA new genus

Type species.—*Topangasquilla gravesi* new species.

Diagnosis.—Since only one species is known at present, the diagnosis of the genus is the same as that of the species.

TOPANGASQUILLA GRAVESI new species
Figures 8.1–8.4, 9

Diagnosis.—A moderate-sized stomatopod around 10 cm long. Triangular, moderate sized eyes. Antennal scale slender, about five times longer than wide. Rostral plate broader than long with rounded apex. Carapace subrectangular in shape, broader posteriorly than anteriorly. Dactyls of raptorial claws robust, not basally inflated, armed with six teeth. Longitudinal carinae on the exposed thoracic and at least the first abdominal tergites. Telson ovate, about twice as broad as long, lacking movable submedian teeth; marginal armature of telson masked by fusion of submedian denticles; submedian teeth covered by dorsal surface of the telson, no other marginal teeth traceable. Dorsal surface of telson with median low triangular boss and apparent radiate decoration. Uropods robust; uropodal endopod lacking strong proximal fold on outer margin.

Description.—The remains of moderate-sized triangular eyes are visible on the anterior part of the cephalon (Figure 8.1, e). The ophthalmic somite itself is not preserved well enough to reveal the presence of any ornamentation. The antennular somite is poorly preserved and partly covered by the remains of the rostral plate. Of the rostral plate only the rounded apex can be recognized; assuming that the basis of the rostral plate is as wide as the midfield of the carapace, the rostral plate must be broader than long. Only the basal parts of the proximal segments of the antennules are visible, extending anteriorly in between the eyes. The protopodal parts of the antennae are vaguely discernible. On both sides of the specimen the laterally directed, slender scaphocerites (e.g., Figure 8.1, sc) are clearly visible as are the onsets of the antennal endopods. The margins of the scaphocerites are not preserved in fine detail, however, the preservation is good enough to estimate a dimension of about five times longer than wide.

The carapace is clearly preserved, and a median and two lateral fields can be easily distinguished (Figure 8.1). The carapace is subrectangular in shape, broader posteriorly than anteriorly. An indistinct median line can be distinguished, extending the whole length of the carapace. It is not clear whether this line represents a true median carina on the carapace or resembles a linear structure beneath the carapace.

Of the first five thoracopods only the remains of the second pair are recognizable (Figure 8.2), and only the dactyls are preserved in complete detail (Figure 8.1, d, 8.2, d, 8.4). The dactyls are provided with 6 slender teeth, increasing in size distally. The two most proximal teeth are positioned close together. Apart from the terminal tooth, the teeth tend to bend their tips distally (Figures 8.4, arrow, 9).

Traces of the sternites, tergites, and internal endophragmal connectives of the thoracic somites five to eight can be discerned. The remains of the sternites are too poorly preserved to show any detail. Remarkably, however, the well-preserved tips of the paired copulatory organs cross each other near the seventh thoracic sternite (Figure 8.2, arrow), indicating that we are dealing with a male stomatopod. Although poorly preserved, some traces of carination could be observed on the last three thoracic tergites. Paired submedian carinae are present on tergites six and seven at least (Figure 8.1). Tergite eight possesses paired submedian and intermediate carinae (Figure 8.2, 8.3). The median line clearly visible on this somite might represent a dorsal median carina on the tergite, or a sharp ventral keel on the sternite. The coxa of the walking legs on the last three thoracic somites are all preserved (Figure 8.2, wl). The width and degree of sclerotization of these segments increases posteriorly. Some remains of the more distal segments are preserved, but these are too vague to reveal any detail.

The abdomen is crudely preserved, the remains that are visible are fragmented and no more than color differences on the matrix. The two anterolateral plates of the first somite are visible and appear to be relatively large (Figure 8.1, ap). Only remains of the first three abdominal tergites are preserved well enough to show cuticular ornamentation (Figure 8.2, 8.3). The first tergite at least bears paired submedian, intermediate, and lateral carinae. The sub- and intermediate carinae are visible as sharp lines (Figure 8.3, small arrows), but they are not preserved well enough to determine whether they extend from margin to margin. The second tergite seems to bear sub- and intermediate carinae too, although less easily recognizable. A lateral carina is relatively well preserved on this tergite. The third tergite is poorly preserved but clearly shows a lateral carina and the lateral margin of the tergite. More heavily tanned patches on this margin indicate the presence of a marginal carina (Figure 8.3, mc).

The lateral carinae appear to be the most remarkable (Figure 8.3, large arrows). These carinae are broader than the more median carinae. It is clear on the second abdominal tergite that the broad lateral carinae extend the whole length of the tergite, tapering towards the anterior and posterior margins.

The remains of the fourth, fifth, and sixth abdominal tergites are largely covered with a veneer of sediment (Figure 8.1). Removal of this layer reveals a fragmented and cracked mass of cuticular remains, from which no further information can be gained.

The ovate telson is relatively well preserved (Figure 8.1). The maximum width is almost twice the length. The only clear structure on the surface is a small U-shaped, median arch close to the posterior margin, the convex side directed posteriorly. The position of this arch is best visible on the part with the poor telson remains (Figure 8.2, ma). This little arch is most likely the posterior remnant of a low triangular boss. Unfortunately the median area of the telson is not well preserved, so the presence of such an elevated structure remains unclear. The marginal armature seems to consist of paired intermediate teeth only (Figure 8.1, im). The margin of the telson is incompletely preserved so the presence of small additional teeth can not be excluded. Only the left intermediate tooth is relatively well preserved. The faint preservation of this tooth relative to the margin of the telson indicates a location just beneath the margin. The dorsal surface of the telson shows traces of small irregular decorations. On both parts the position of the ventral anus is clearly visible (Figure 8.1, 8.2, a).

Remains of both uropods are present (Figure 8.1). The specimen seems to provide a view on both ventral and dorsal side of these appendages. Their general appearance is that of relatively short, robust limbs. The protopods are about twice as long as broad. The ventral view shows a circular structure at the base of the protopod (Figure 8.1, uo). This structure resembles the margin of the opening on the sixth abdominal sternite, where the anterior part of the uropod is attached. The uropods are robust and provided with a basal bifurcate prolongation on the ventral side. Only the medial spine of this projection is completely visible (Figure 8.1, arrow). The proximal segments of the exopods and endopods are partly visible. The endopods lack a strong proximal fold on the outer margin, the basal segment of the exopod is ornamented with a lateral fold. The distal parts of the endo- and exopods are not visible.

Discussion.—A reconstruction of this species is provided in Figure 9.

The broad, ovate form of the telson, the absence of a distinct median carina on the telson, and the absence of movable apices on the visible marginal teeth of the telson, allies this specimen to the superfamily Lysiosquilloidea (Manning, 1980, 1995; Manning and Camp, 1993). Five families are currently recognized

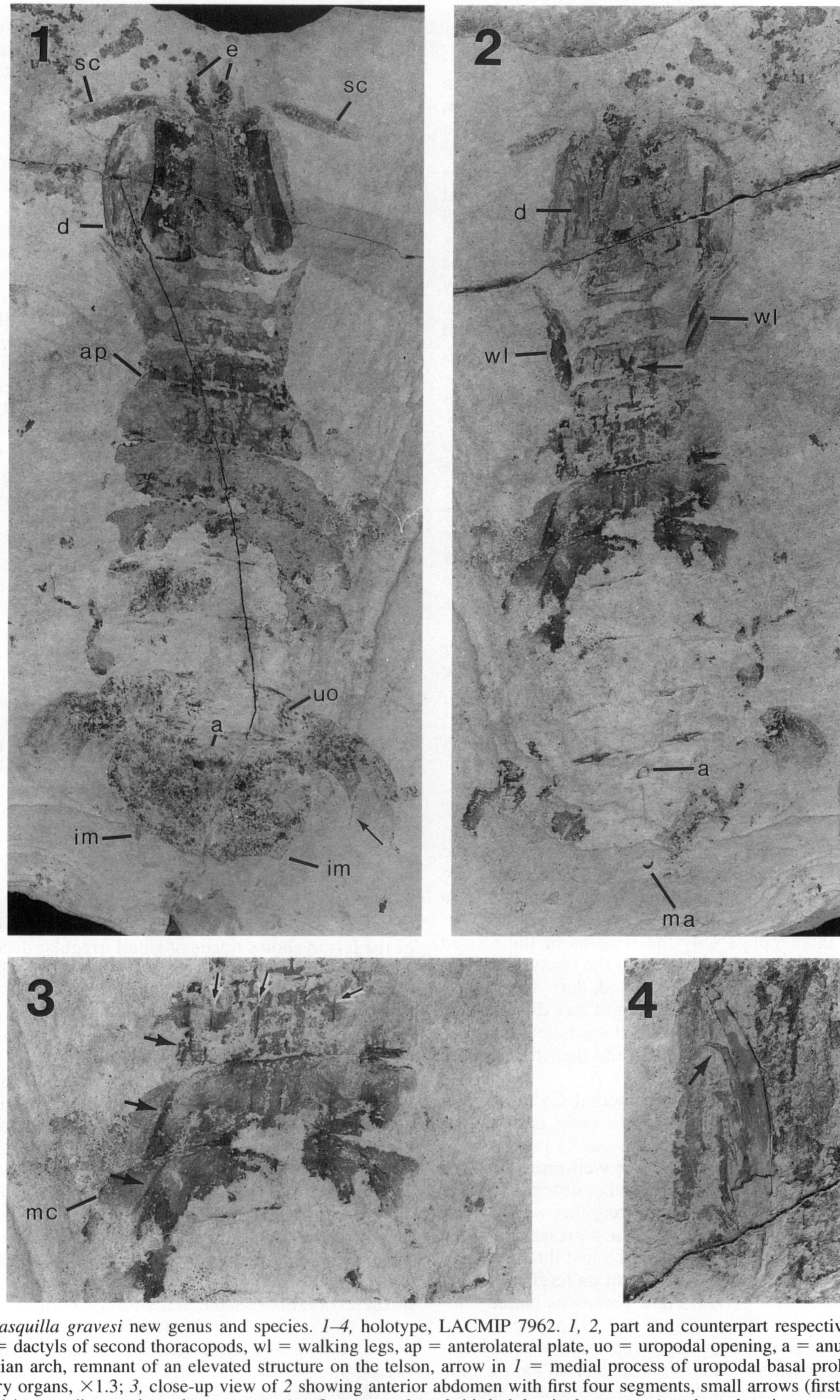

FIGURE 8—*Topangasquilla gravesi* new genus and species. *1–4,* holotype, LACMIP 7962. *1, 2,* part and counterpart respectively, e = eyes, sc = scaphocerites, d = dactyls of second thoracopods, wl = walking legs, ap = anterolateral plate, uo = uropodal opening, a = anus, im = intermediate tooth, ma = median arch, remnant of an elevated structure on the telson, arrow in *1* = medial process of uropodal basal prolongation, arrow in *2* = male copulatory organs, ×1.3; *3,* close-up view of *2* showing anterior abdomen with first four segments, small arrows (first abdominal segment) = submedian and intermediate carinae, large arrows (on first, second, and third abdominal segments) = lateral carinae, mc (on third abdominal segment) = marginal carina ×1.8; *4,* close-up view of *2* showing dactyl of second thoracopod, arrow = bent tip of one of the tooth, ×3.

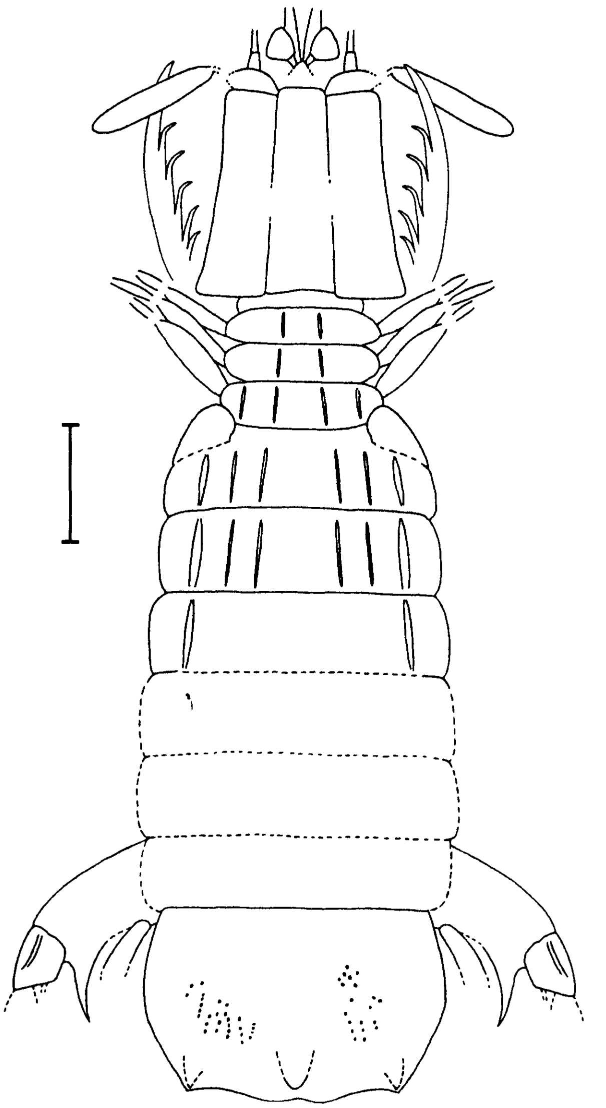

FIGURE 9—Reconstruction of *Topangasquilla gravesi* new genus and species. Scale = 1 cm.

within the Lysiosquilloidea. The family Coronididae can be excluded here because *T. gravesi* lacks the basally inflated dactyls that are diagnostic for the Coronididae. The characters used to distinguish the four remaining families focus on the morphology of the uropodal endopods and the anterior two walking legs. Unfortunately these appendages are only partly preserved in the specimen examined here. Most of the diagnostic characters used to distinguish genera within these four families also are not visible or incompletely preserved in the specimen at hand. However, the size of this specimen makes it rather unlikely that it belongs to the family Nannosquillidae, of which all members are rather small and elongated (see stomatopod lengths provided in Müller, 1994). The family Tetrasquillidae can be excluded because members of this family all bear four teeth on the dactyls of their raptorial claws. The telson of members of the recently erected new family Heterosquillidae (Manning, 1995), is armed with movable submedian marginal teeth, thus excluding this family also from our consideration. Consequently by the process of elimination, we conclude that this fossil stomatopod most probably lies within the family Lysiosquillidae.

The family Lysiosquillidae was recently revised and accommodates three genera to date (Manning, 1995). The lack of movable submedian teeth on the telson and the slender antennal scales seem to ally our specimen to the genus *Lysiosquilla.* However, although similar in size and shape to species of the genus *Lysiosquilla,* this specimen posses longitudinal carinae on the carapace, and on the thoracic and abdominal tergites. The origin of the median line on the midfield of the carapace is unclear. In our opinion it does not resemble a true median carina, but rather a more sclerotized median area. However, the carinae on the thoracic and first abdominal tergites are unmistakable. Although not very well preserved, their straightness and demarcation by the tergal margins excludes the misinterpretation of underlying mineralized soft-tissue. Longitudinal abdominal carinae are typically absent in the genus *Lysiosquilla* and very rare within the Lysiosquilloidea altogether. The presence of longitudinal carinae on at least the first abdominal tergites, justifies the erection of a new genus within the family Lysiosquillidae.

Several fossil stomatopod species are ascribed to the family Lysiosquillidae. *Lysiosquilla antiqua* (Münster, 1842) from the upper Eocene deposits of Monte Bolca in Italy, was placed in this family by Secretan (1975). Although we believe certain characters were misinterpreted by her (personal observations C.H.), *Lysiosquilla antiqua* most likely belongs to the genus *Lysiosquilla. Lysiosquilla nkporoensis* Förster, 1982, from the lower Maastrichtian of Nigeria, lacks to many features for a proper generic diagnosis. None of these two fossil lysiosquillid species show a carination pattern as *Topangasquilla gravesi.*

Etymology.—The generic name is a combination of "Topanga," after the Topanga Canyon Formation from where the type material originated, with the generic name *Squilla.* The species name refers to the name of the collector, Dr. William Graves.

Type material.—Holotype LACMIP 7962, part and counterpart of an almost completely preserved stomatopod (Figure 8.1, 8.2). The remains are preserved on both portions as tanned prints or thin sheets of mineralized cuticle. The type is deposited in the fossil invertebrate collection of the Los Angeles County Museum of Natural History.

Measurements.—Total length 9.5 cm. Carapace length 1.6 cm. Rostral plate length 0.21 cm; width 0.34 cm. Antennal scale length 1.2 cm; width 0.22 cm. Dactylus raptorial claw about 1.8 cm. Abdominal width 3.0 cm (estimation based on one half of the fifth somite). Telson width 2.54 cm; length 1.5 cm.

Locality.—LACMIP loc. 2542, Miocene, Topanga Canyon Formation. Exposure at 838 Lyndon Street, South Pasadena, Los Angeles County, California. This locality shows as Topanga Formation on the geologic map of the Elysian Park-Repetto Hills area, Los Angeles County, California (Californian Division of Mines Special Report 101, pl. 1). The specimen was collected in 1971.

Taphonomy.—The completeness of the body and the folded second thoracopods indicate a rapid burial, as experimentally demonstrated by Hof and Briggs (1997). The second thoracopods are not folded as subtly as in *Angelosquilla altamirensis* and the dactyls were slightly displaced during diagenesis. Although the animal is completely preserved, the quality of the cuticular preservation is poor. Thin cuticular parts are visible as colored outlines only, while the more sclerotized cuticle seems to be mineralized in places. The well-preserved lateral fields of the carapace are remarkable. Their clear preservation is most probably due to the mass of the underlying second thoracopods. The telson and uropods are apparently so much compressed that dorsal and ventral parts are visible in the same horizontal field. The most interesting taphonomic feature of this specimen is one of the dactyls of the raptorial claws. This dactylus shows traces of mineralized soft-tissue enclosed by cuticular remains (Figure 8.4).

Order STOMATOPODA incerta sedis

Remarks.—Three poorly preserved specimens that originate from the Miocene Topanga Canyon Formation. Precise taxonomic identification is impossible, but these specimens do provide information on several features of taphonomy.

Locality.—Locality, LACMIP loc. 1292, Miocene, Topanga Canyon Formation, consisting of thick beds of sandstone with thin interbedded shales. The locality record notes, "Fish scales and plant impressions were common in the shale. First roadcut on northside of Freeway 210 entering west end of south hills in Glendora. Glendora Avenue passes under freeway to west, Los Angeles County, California. The specimens were collected somewhere in this road cut. Four thousand feet east and 0 to 500 feet south of the intersection T1S, R9W (USGS topographic map, 7.5 min, San Dimas, California quadrangle, 1954, scale 1:24,000)." This site was mapped as Topanga Formation by Californian Division of Mines Bulletin 170, Chapter II, pl. 1. The specimens were collected August 1970, by Mrs. William E. Meyer and her children, Glendora, California.

Taphonomy.—From a taphonomic point of view these specimens are certainly interesting. Each specimen represents one of the typical tagmata compositions in which most fossil stomatopods are found (Hof and Briggs, 1997): a complete animal with the second thoracopods more or less folded underneath the carapace (LACMIP 7963; Figure 10.1), abdomen with the telson (LACMIP 7964; Figure 10.4), and a telson with at least the sixth or more of the posterior abdominal somites (LACMIP 7965; Figure 10.5).

The relatively completely preserved specimen, LACMIP 7963, was possibly buried alive or immediately after death. The segments of the raptorial claws show some displacement due to diagenesis. The inferior margin of the left dactylus is preserved as a sharp impression filled with cuticular remains (Figure 10.2). Near this margin fragments of the cuticular lining of inner side of the dactylus are preserved (Figure 10.2, arrows). A minute fragment of these remains was examined with a scanning electron microscope by Hof and Briggs (1997). This fragment clearly showed the presence of so called "muscle scars," the mineralized remains of muscle attachments.

Superfamily LYSIOSQUILLOIDEA Latreille, 1803
Family, genus and species indeterminate
Figures 10.1–10.3, 11.1–11.2

Description.—The specimen, LACMIP 7963, only preserves clearly the dactyls of the second pair of thoracopods (Figure 10.1–10.3). The dactyls of these raptorial limbs have nine slender teeth that increase in size distally (Figure 11.1). Although there are many tanned areas and tiny pieces of cuticle in the region of the cephalothorax, no other parts can be identified with certainty.

The fossil preserves both the dorsal and ventral surface remnants of the animal. The remains of the last three thoracic somites are visible as colored residues of the central parts of these segments. Traces of a median and paired submedian carinae are visible as faint, dark lines (Figure 10.1, c). The archlike, tanned impressions in this area resemble the endophragmal connectives between the tergites and sternites (Figure 10.1, ph).

The remains of the abdominal sternites, obscuring most of the remains of the tergites, are easily recognizable by the circular outline of the pleopodal openings (abdominal somites two, three, and four; Figure 10.1, po). On some sternites an oval outline of the median keel can be seen (somite two, three, and four; Figure 10.1, mk). Fragmented remains of the protopodal parts of the pleopods are visible in and around all the sternal pleopodal openings. The remains of the more sclerotized anterior margin of sternite six are distinct (Figure 10.1, large arrow).

The telson shows the proximal anus (Figure 10.1, a). That portion of the lateral margin of the telson that is preserved shows no signs of marginal armature.

Measurements.—LACMIP 7963, total length about 7.5 cm, telson width about 1.6 cm (approximate estimation).

Remarks.—The only relatively well-preserved parts of this specimen are the dactyls of the second thoracopods. These slender dactyls certainly belong to a "spearer," a morphological type of stomatopod that can be found in all of the Recent superfamilies (Caldwell and Dingle, 1975; Dingle and Caldwell, 1978). The number of teeth on the dactylus might help in resolving the closer taxonomic affinities of this specimen. Nine teeth are a relatively high number among stomatopod spearing claws. Such a number excludes spearing members of the Gonodactyloidea and the monotypic Erythrosquilloidea. All of the remaining superfamilies contain genera with identically or almost identically shaped and armored dactyls to this specimen. The only other character preserved in this specimen that might contribute to the resolution of its taxonomic identity, is the shape of the telson. Although very faintly and only partly preserved, it shows a rounded margin without distinctive teeth or denticles. Such a shape of the telson is most likely to be found among members of the superfamily Lysiosquilloidea.

Only the faint preservation of carinae on the thoracic tergites, is evocative of *Topangasquilla gravesi.* However, the vague nature of these carinae and the variable nature of dactyl claws in stomatopods as a group, make further taxonomic identification of this specimen at this point difficult.

Superfamily SQUILLOIDEA Latreille, 1803
Family SQUILLIDAE Latreille, 1803
Genus and species indeterminate
Figures 10.4, 11.2

Description.—Only fragmented portions and an outline of both sternites and tergites of the abdominal somites on LACMIP 7964 (Figure 10.4) are observable. Traces of marginal, lateral, and intermediate longitudinal carinae can be seen on the few tergal remains visible (Figures 10.4, 11.2). A sharp impression is present all along the center of the abdominal segments. It is not clear which stomatopod structure this impression represents. The circular remains of a socket (Figure 10.4, small arrow), part of the pivot articulation between abdominal somites five and six, is conspicuously present.

The remains of the sternites, covering most of the tergites, are easily recognizable by the circular outline of the pleopodal openings (somites two, three, and four; Figure 10.4, po). On some sternites, an oval outline of the median keel can be seen (somites one and three). Fragmented remains of the protopodal parts of the pleopods are visible in and around all the sternal pleopodal openings. The remains of the more sclerotized anterior margin of sternite six are distinct (Figure 10.4, large arrow). Although the telson is only partly preserved, the remains indicate its dimensions must have been about as long as broad. A small circular structure, close to the anterior margin, probably represents an impression of the anus, although it is positioned off-center. A sharp linear median impression represents either a ventral post-anal spine or a dorsal median carina. Unfortunately the posterior margin of the telson is missing. The visible parts of the lateral telson margin show no clear traces of armature.

Measurements.—LACMIP 7964, total length estimated 8 to 9 cm, telson width approximately 1.5 cm.

Remarks.—Lacking all the diagnostic characters used in stomatopod identification, the taxonomic place of this specimen is

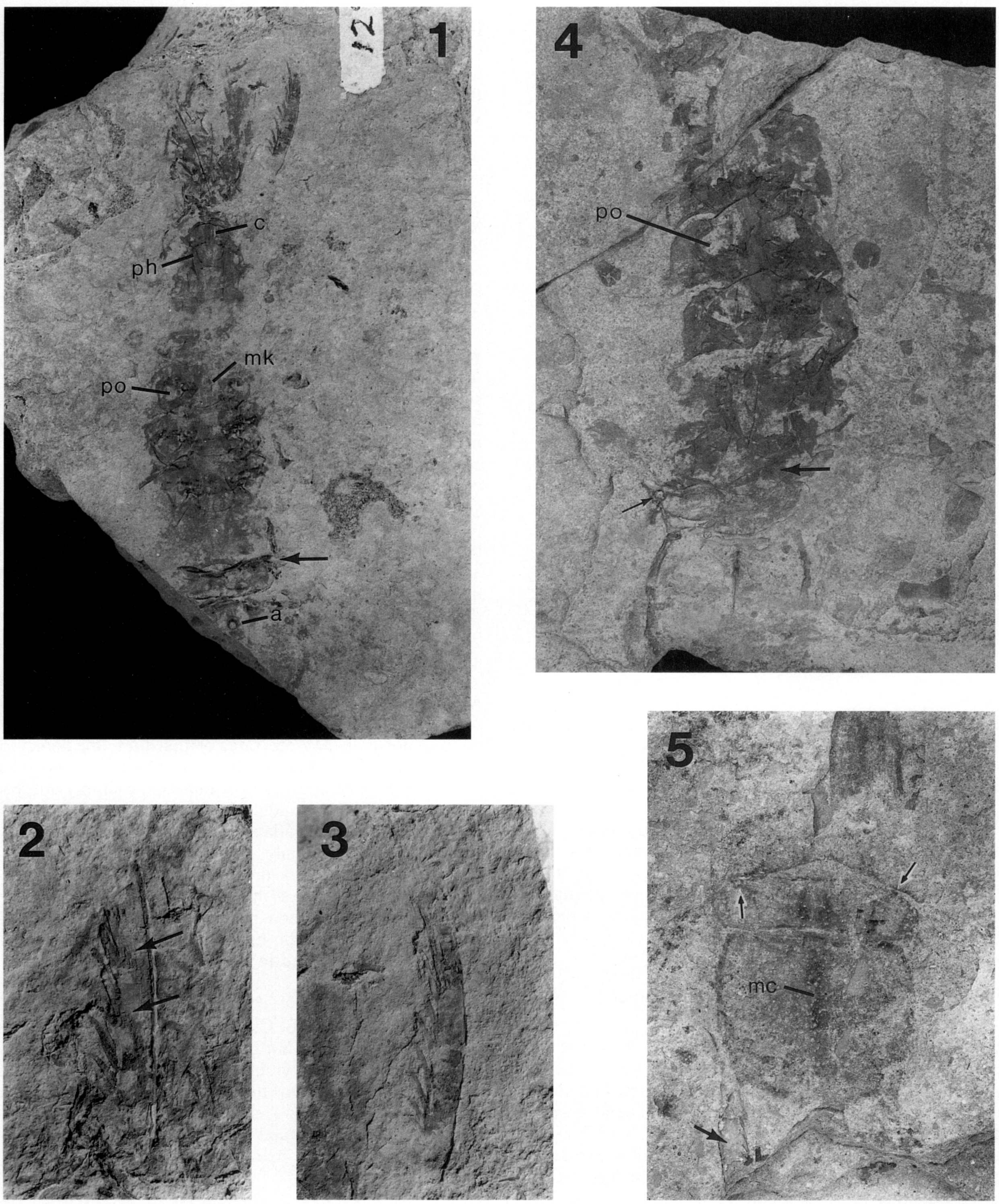

FIGURE *10*—Indeterminate stomatopod remains from the Topanga Formation. *1–3,* LACMIP 7963, lysiosquilloid; *1,* venter of whole body, c = carinae on thoracic somite, ph = endophragmal arches, po = pleopodal opening of an abdominal sternite, mk = outline of base of median keel, a = anus, large arrow = anterior margin sixth abdominal sternite, ×1.2; *2, 3,* close-up views of second thoracopod dactyls, arrows = fragments of the cuticular lining on inner side, ×3.5; *4,* LACMIP 7964, squilloid abdomen and part of telson, po = pleopodal openings, small arrow = articulating sockets, large arrow = anterior margin sixth abdominal sternite, ×1.8. *5,* LACMIP 7965, squilloid posterior abdomen and telson, mc = median carina, small arrows = articulating sockets, large arrow = stray second thoracopod dactyl, ×2.

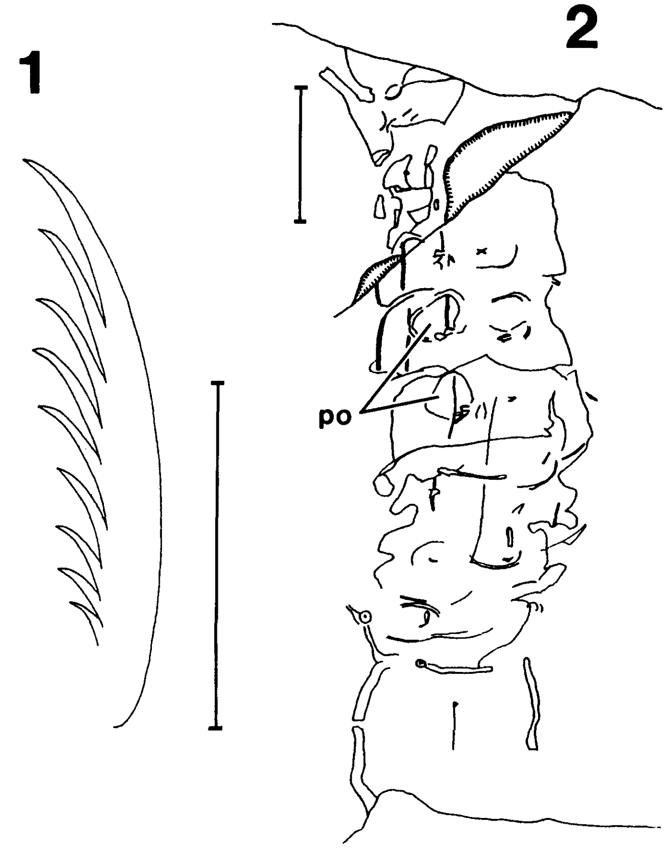

FIGURE *11*—*1,* Reconstruction of dactyls in Figure 10.2 and 10.3. *2,* Line drawing of Figure 10.4., po = pleopodal opening of abdominal sternites. Scales = 1 cm.

difficult to determine. The presence of the longitudinal abdominal carinae and the shape of the telson, make accommodation within the superfamily Squilloidea the most likely position. The moderate size of the animal indicates that we are dealing with a member of the family Squillidae rather than with a member of the large Harpiosquillidae.

Superfamily SQUILLOIDEA Latreille, 1803
Family, genus, and species indeterminate
Figure 10.5

Description.—LACMIP 7965 (Figure 10.5) preserves only the posterior abdomen and the telson. The carination of the sixth abdominal tergite consists of inflated, paired submedian carinae, intermediate carinae (of which the anterior parts bend laterally), and lateral carinae. Like in *Squilla laingae* (LACMIP 7959), the sockets of the pivoting connection between tergites five and six are recognizable (Figure 10.5, small arrows). The telson is provided with a distinctive median carina, preserved as a darkened band (Figure 10.5, mc). The margin of the telson is partly missing and vaguely preserved. No marginal teeth or denticles can be clearly discerned. The outline of the posterior margin of the telson only suggests the presence of intermediate teeth.

Just posterior to the remains of the telson lies a fragment of a second thoracopod dactyl (Figure 10.5, big arrow). Not much can be discerned concerning this and it is not clear whether it even belongs to the individual it is next to.

Measurements.—LACMIP 7965, telson width 1.7 cm; length 1.5 cm.

Remarks.—Lacking almost all the diagnostic characters used in stomatopod identification, taxonomic accommodation of this specimen is a problem. However, based on the presence of a clear median carina on the telson, the shape of the telson and the carination on the sixth abdominal tergite, this specimen resembles a squilloid.

DISCUSSION

Fossilized stomatopods can be characterized as rare, based on their record to date, yet these animals live in habitats that should lend themselves to easy fossilization. Many of them prefer muddy or sandy bottoms into which they burrow or lie covered with sediment as they patiently wait for their prey. In these circumstances, the apparent scarcity of stomatopod fossils becomes difficult to explain.

On the other hand, in one relatively small area in the southwestern corner of the United States, in a series of closely linked formations in the Miocene, we encounter a series of good to superbly preserved mantis shrimp specimens. The quality of most of this material even allows detailed comparison with living forms. Not only that, the occurrence of stomatopods in these Miocene formations reveals a modicum of diversity, since the best four specimens at hand are clearly arrayed in three separate genera in two distinctive superfamilies of Stomatopoda. If we include the fossil stomatopod *Pseudosquilla adelaidensis* Rathbun 1926, also originating from the Californian Monterey shales and belonging to the superfamily Gonodactyloidea, our California record embraces the three large stomatopod superfamilies. A similar fossil stomatopod richness is known from the Miocene of Korea (Yun, 1985), although the five species from this locality all belong to the family Squillidae.

It seems clear, based on the experience documented here, as well as other discoveries made in collections around Europe (descriptions in preparation), that the problem with fossil stomatopods is not that they are rare, or that they are poorly or infrequently preserved. Rather, the proper facies are not adequately examined by paleontologists or material is simply not recognized as such by collectors and collection managers. Material of striking preservation is available and that material, linked with rigorous phylogenetic analysis of the group, will provide a time-stratigraphic framework upon which we can strive to better understand the history of the Stomatopoda. This will hopefully include not only the pace of morphologic evolution among mantis shrimps, but also the historic aspects of their biogeography, especially if considered in a plate tectonic context.

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