

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, paddleshaped 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

## HOF AND SCHRAM—MIOCENE STOMATOPODS

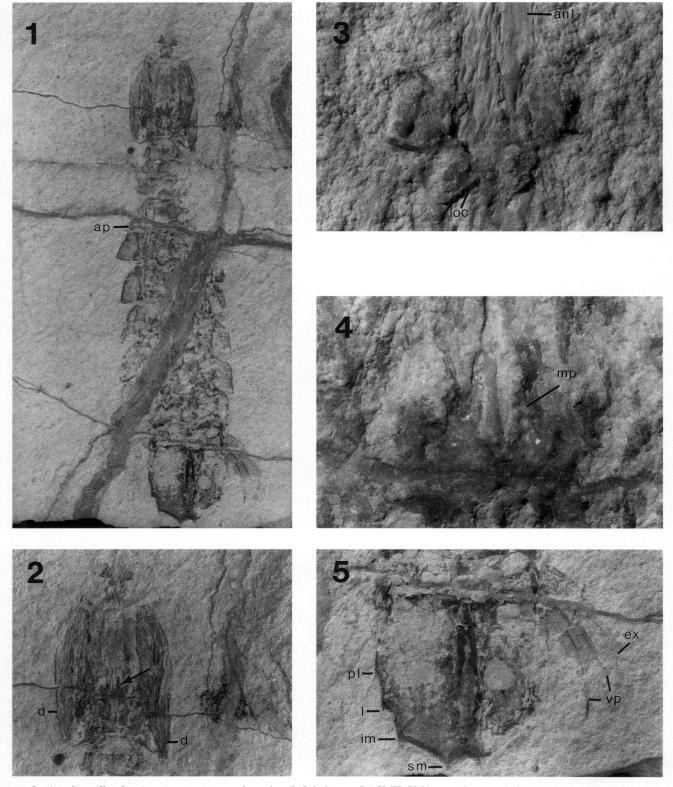


FIGURE 5—Angelosquilla altamirensis new genus and species. 1–5, holotype, LACMIP 7961, part. 1, general view, ap = anterolateral plate,  $\times 1.2$ ; 2, close-up of cephalon and anterior thorax, d = dactyls of second thoracopods, arrow = area of mandible remains,  $\times 2$ ; 3, close-up of cephalon with eyes and antennular peduncles, oc = ocular scale, anl = first segments of antennular peduncles,  $\times 11.5$ ; 4, close-up of mandibles, mp = molar process,  $\times 15$ ; 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,  $\times 2.5$ .

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