HOF AND SCHRAM—MIOCENE STOMATOPODS





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, $\times 1.2$.

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, al-though 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.

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

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*. *Ptery*- gosquilla 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