# External Morphology of the Genus *Aegla* (Crustacea: Anomura: Aeglidae)

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# ABSTRACT

Martin, Joel W., and Lawrence G. Abele. External Morphology of the Genus *Aegla* (Crustacea: Anomura: Aeglidae). *Smithsonian Contributions to Zoology*, number 453, 46 pages, 19 figures, 1988.—External morphology of aeglid "crabs," unusual freshwater anomuran decapods endemic to South America, is described in detail for common members of the genus *Aegla* from the Arroyo San Antonio in southern Uruguay. Comparisons are made with available species descriptions in the literature. General aeglid morphology resembles that of members of the marine family Galatheidae, with which aeglids are traditionally grouped in the superfamily Galatheoidea. Several morphological features distinguish aeglids from marine members of the Galatheoidea. Of special interest are branchial morphology and sutures of the carapace. The occurrence of characters similar to those seen in *Aegla* in non-galatheoid anomuran families casts doubt upon the presently accepted phylogenetic placement of the Aeglidae. The hypothesis that aeglids may be related to members of the Paguroidea is presented. A list of all species of the family is included.

# Contents

# External Morphology of the Genus *Aegla* (Crustacea: Anomura: Aeglidae)

## Joel W. Martin
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## Introduction

The Recent Aeglidae are freshwater crab-like decapod crustaceans endemic to South America. They occur in lakes, streams, salt marshes, and caves from Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay (Bahamonde and López, 1961; Hobbs, 1979; Manning and Hobbs, 1979; Schmitt, 1942b). These decapods are presently considered to belong to a single genus, *Aegla,* consisting of some 40 currently recognized species and subspecies, several of which have been described recently (Buckup and Rossi, 1977; Hebling and Rodrigues, 1977; Hobbs, 1979; Jara, 1977, 1980b, 1982, 1986; Jara and López, 1981). Although widely distributed across temperate South America, they are perhaps the least known of the freshwater decapod crustaceans.

The group is interesting for several reasons. First, with the possible exception of one fossil species (*Haumuriaegla glaessneri* Feldmann) from New Zealand (see Feldmann, 1984), they are restricted to temperate and subtropical South America, the only anomuran family thus restricted. Schmitt (1942b:431) noted: "There are no freshwater Crustacea at all like *Aegla* anywhere else in the world." Thus, their distribution poses some interesting biogeographical as well as ecological questions. Second, their evolutionary relationships are unknown. Morphologically the aeglids appear similar to members of the family Galatheidae (infraorder Anomura, superfamily Galatheoidea) and are included with the galatheids, porcellanids, and chirostylids in the superfamily Galatheoidea Samouelle, 1819. However, all members of the Galatheidae and even of the Galatheoidea, except the aeglids, are restricted to marine habitats (an exception is the porcellanid *Petrolisthes*

*robsonae* Glassell; see Gore and Abele, 1976). In addition, there are some important morphological differences between aeglids and galatheids. In *Aegla,* males have vestigial abdominal appendages, whereas these appendages (pleopods) are usually well developed in male galatheids (e.g., Pike, 1947; Tirmizi, 1966). Apart from being of systematic importance, this absence of functional pleopods in aeglid males poses the interesting problem of how sperm transfer occurs. Sutures of the aeglid carapace are unlike those found in any galatheids. The gill structure, traditionally considered an important systematic character in decapod Crustacea (e.g., Huxley, 1878; Bate, 1888; Glaessner, 1960, 1969) is "penicillate" [trichobranchiate] in the aeglids, yet "foliose" [phyllobranchiate] in the galatheids (terminology after Dana, 1852). Other morphological peculiarities of aeglids include a border of scales along the cutting edges of the chelae and a spoon-shaped lobe on the palm of the cheliped in some species (e.g., *A. schmitti* Hobbs; see Hobbs, 1979). Finally, aeglids constitute an ecologically unique group of decapod crustaceans in that, during the mating season, females of some species leave the water and congregate beneath stones or logs at the water's edge; they are sometimes found associated with spiders, ants, isopods, and scorpions during this spawning period (Bahamonde and López, 1961; Burns, 1972).

The gaps in our knowledge of aeglid crabs are large. The present study, in anticipation of a re-examination of the phylogenetic placement of aeglids in relation to other decapods, begins to address the question of aeglid origins by examining the external morphology of the genus *Aegla.*

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## Annotated History of Aeglid Systematics

Latreille (1818, pl. 308: fig. 2) first illustrated, without description, an aeglid under the name *Galathea laevis*. Schmitt (1942b) suggests that Latreille may have been unaware that the specimen came from freshwater, as the genus in which Latreille placed it is entirely marine. According to Schmitt (1942b), "a crustacean of this type was recognized (but not described) as early as 1782 (pp. 206, 347; 1789, p. 182) by Molina in his 'Saggio sulla Storia Naturale del Chile' as *Cancer apancora*." However, Molina's description is vague and may not have been of an aeglid:

The *apancora* (Cancer apancora) is larger than the talicuna. The shell is oval and wholly denticulated, the claws are hairy, and the tail of a triangular form and very long. [From the 1808 English translation.]

The specific name selected by Molina may stem from the fact that the common name for these crabs in parts of Chile is *pancora* (Burns, 1972). Leach (1821) recognized that Latreille's species represented a distinct genus, and it was he who chose the genus name *Aegla*, probably after Aegle, one of the Hesperides who guarded the garden of golden apples of the Isles of the Blest at the western end of the earth in Greek Mythology.

A number of early carcinologists reproduced the figure of Latreille, some introducing inaccuracies and some reproducing the figure only crudely. These workers included Desmarest (1825), who introduced the misspelling *Aeglea*, Griffith and Pidgeon (1833), H. Milne Edwards (1837), who first mentioned

the habitat (the coasts of Chile), and the "Disciples Edition" of Cuvier's (1837) *Le Régne Animal*. The contributions of these workers are discussed in more detail by Schmitt (1942b).

Prior to 1849, the genus was still considered monotypic, the sole species being *A. laevis* (Latreille). Although distinct species were described by Nicolet (1849), Girard (1855), and Muller (1876), Ortmann (1892, 1902) continued to refer to the genus as monotypic, and only after Schmitt's (1942a,b) work was the diversity of the group appreciated. Schmitt's (1942b) monograph on *Aegla* remains the primary taxonomic reference. In that paper, he examined specimens of *Aegla* from Argentina, Brazil, Chile, and Uruguay, described 13 new species and 2 new subspecies, and included a key to the identification of the 20 forms recognized by him.

In the years since Schmitt's monograph several new species have been described (Bahamonde and López, 1963; Buckup and Rossi, 1977; Hebling and Rodrigues, 1977; Hobbs, 1979; Jara, 1977, 1980a,b, 1982, 1986; Jara and López, 1981; Ringuelet, 1948a,b, 1960b; Türkay, 1972) so that there are now approximately 40 currently recognized species and subspecies of the genus *Aegla* (Appendix II). While this is not a small number of species, it is in no way comparable to some other families of freshwater Decapoda. North American crayfishes, for example, comprise well over 300 species in approximately 9 genera and 19 subgenera (Hobbs, 1972, 1974). It is possible that the smaller number of species known in *Aegla* reflects a lack of adequate sampling in temperate and subtropical South America.

## Morphological Studies of *Aegla*

Most authors agree that the aeglids are a branch of the galatheid crabs that invaded fresh water. Schmitt (1942b:431) stated that "Its nearest relatives are marine and probably to be found somewhere among the galatheids (tribe Galatheidea)." However, no authors have ventured to guess which group of the galatheids is most closely related to the aeglids. This stems probably from the absence of any detailed morphological examination of the aeglids. Traditional characters illustrated in descriptions of aeglids are those proposed by Schmitt (1942b) for distinguishing species; these are limited to the shape of the rostrum, outline of the carapace, anterolateral angle of the second abdominal somite, ventral margin of the second pereiopod, armature of the fourth thoracic sternum, and several characters of the cheliped (palmar lobes, basal teeth, and spination of the ischium). It is known that many of these characters are extremely variable among individuals (e.g., see Hobbs, 1979; Jara, 1980a; Ringuelet, 1948b, 1949a,b; Vaz-Ferreira, Gary, and Vaz-Ferreira, 1945). An additional problem is that in the literature often only one or two of the above characters are illustrated, with other characters either incompletely described in the text or omitted from the description. Few papers exist in which aeglid characters other than those proposed by Schmitt are described. H. Milne Edwards (1837)
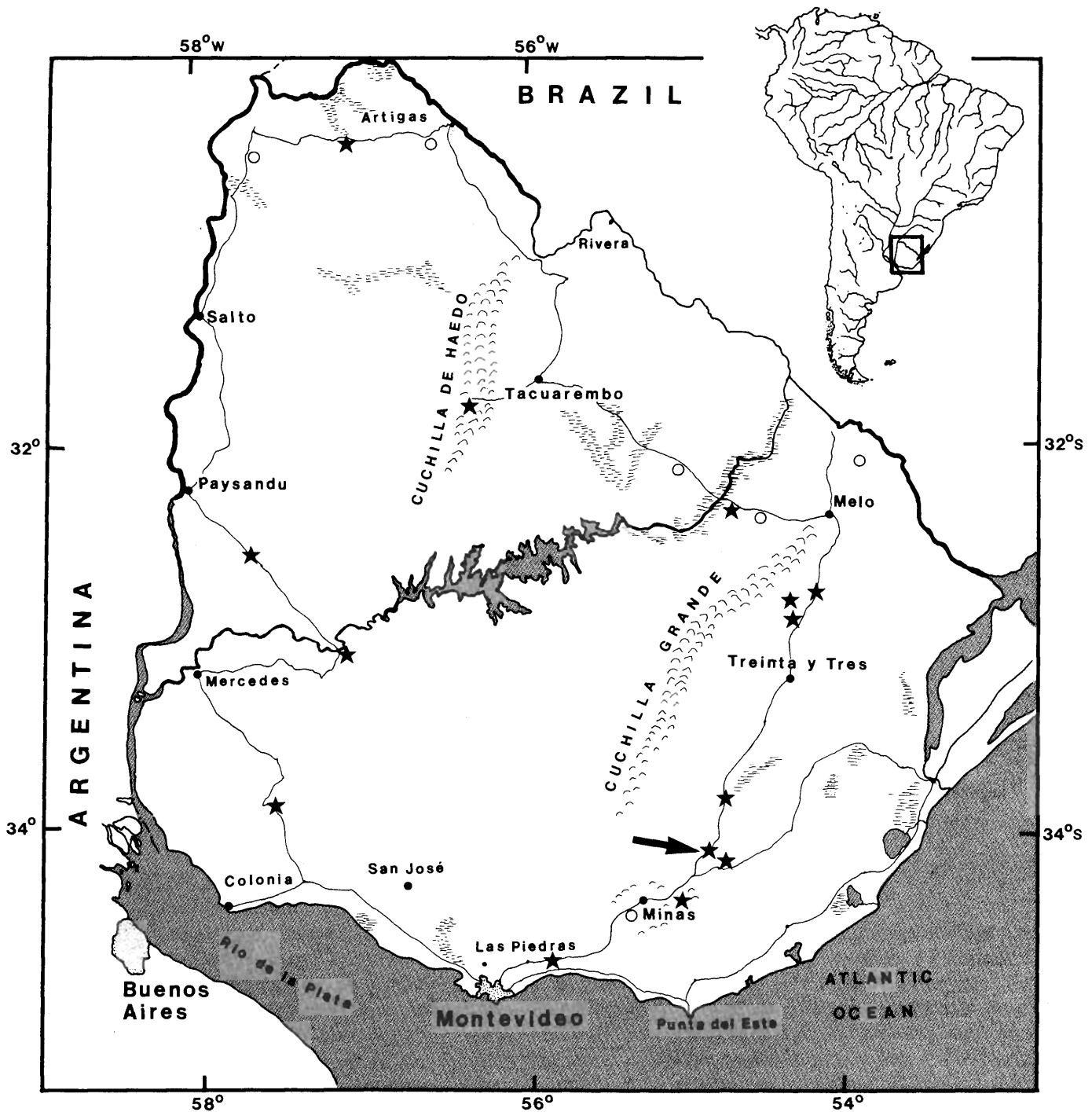
FIGURE 1.—Collecting localities visited by one author (JWM) in Uruguay. Stars indicate collecting sites where aeglids were found; large arrow indicates approximate site of the Arroyo San Antonio from which live aeglids were collected.

presented a brief diagnosis of the genus, Dana (1852) briefly discussed the nature of the carapace sutures and outlined (somewhat erroneously) the characters of the genus, Mocquard (1883, pl. 6: figs. 133–135) published surprisingly detailed figures of the foregut of *A. "laevis,"* and Ortmann (1892) crudely illustrated the mouthparts of *A. "laevis."* Mouchet (1931a,b, 1932a,b) figured parts of the gills in a study of the

parasites of aeglids. Snodgrass (1950) included a schematic diagram of the protocephalon and gnathal region of *A. prado*. With the exception of Mocquard's and Dana's work these papers do not provide any basis for comparisons of aeglids with other anomurans at the family or superfamily level; characters are either insufficiently illustrated (Mouchet) or else do not differ from the same structures in many other anomuran
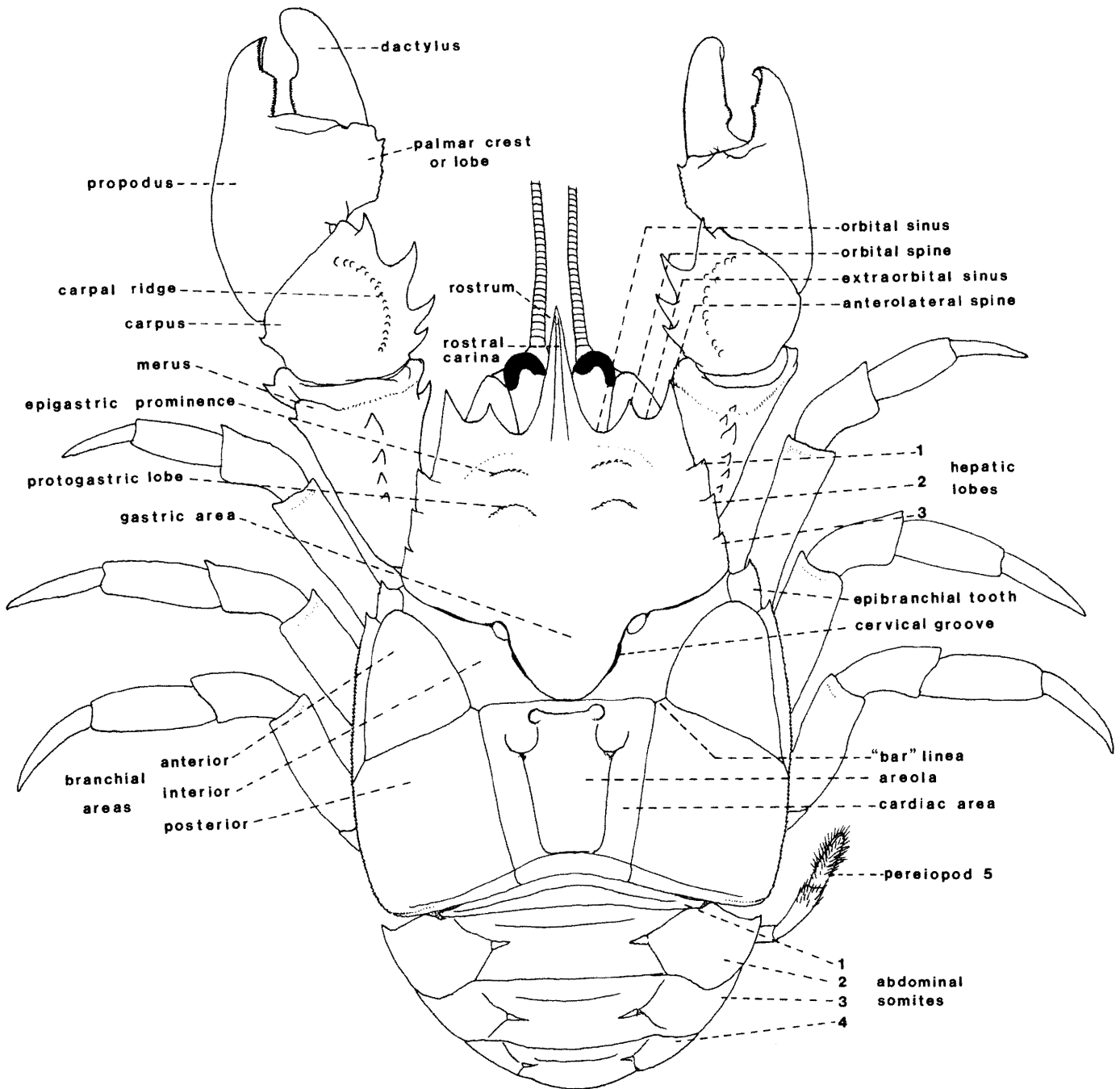
FIGURE 2.—Schematic view of a typical aeglid crab (based on an adult male *A. platensis*).

groups (Ortmann). Recent work by Lopretto (1978a,b, 1979, 1980a,b, 1981) describes in detail the morphology of the male fifth pereiopod coxa, a structure that holds promise for clarification of within-family systematics. Below we describe the complete external morphology of aeglids for the first time.

**Materials and Methods**

Live aeglid crabs were collected by dipnet from the Arroyo San Antonio, southern Uruguay (Figure 1). The San Antonio, a tributary of the Rio Cebollati, is a shallow (<1.0 m) second order freshwater stream with a bed of loose gravel and stones. Water temperature at the time of collection (19 April 1984) was 22°C; air temperature was 20°C. The current of the stream varied from 0.8 m/sec in the center to <0.01 m/sec in deeper pools and along the shallow sides of the stream. Density of the crabs, estimated by throwing a 0.5 m$^2$ metal quadrat and
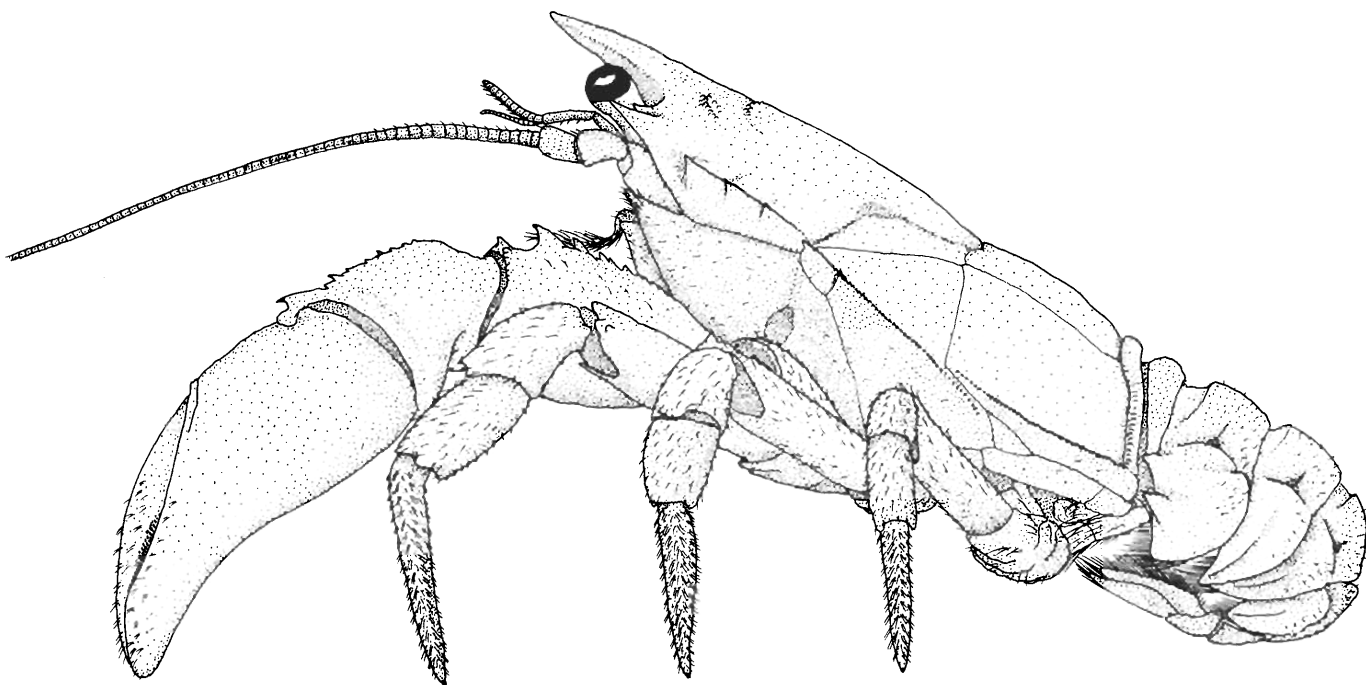
FIGURE 3.—*Aegla platensis*, lateral view of adult male.

removing all stones and crabs from within its confines, varied from 6 to 48 individuals/m². Crabs were collected three hours before departure from Uruguay and placed in styrofoam chests with crushed ice; towels were added to reduce the risk of damage during shipping and to give the aeglids something to which they could cling. This collection yielded numerous specimens of *A. platensis* Schmitt and *A. uruguayana* Schmitt. Additional specimens of both species were preserved in 10%–20% formalin in the field and later transferred to 70% ethanol. Through the kindness of Dr. R.B. Manning at the National Museum of Natural History, Smithsonian Institution, specimens of the Argentine *A. jujuyana* were borrowed for comparative purposes, and Dr. Enrique Boschi graciously sent a collection of preserved *A. platensis* from Argentina. Fortunately all three of the above named species have been considered to represent "primitive" species of *Aegla* (see Schmitt, 1942b; Ringuelet, 1949c) so that this examination may serve as a baseline study for further investigations into aeglid morphology.

Illustrations were made from crabs preserved in the field and later transferred to ethanol. In addition, many of the structures were dissected from live crabs in the laboratory; this allowed observation of function as well as form. Other live aeglids were allowed to air dry before they were examined and/or dissected, and a few illustrations were aided by photography of the live crabs (e.g., Figure 3). Illustrations are of *A. platensis* and *A. uruguayana*. Comparisons of them with aeglids other than *A. jujuyana* are made through accounts in the literature.

Terminology follows that of Glaessner (1969), Schmitt (1942b), and Pike (1947) for characters of the carapace and appendages, Kunze and Anderson (1979) for setal morphology, and Snodgrass (1951, 1952a,b) for characters of the protocephalon. Abbreviations used in the figures are explained in Appendix I.

## Results

### CARAPACE AND ROSTRUM

CARAPACE (Figures 2–4, 16).—Perhaps the single most remarkable feature of the genus *Aegla* is the carapace; it distinguishes the group not only from other members of the Galatheoidea but from all other decapod crustaceans. As with nearly all features employed in aeglid taxonomy, the carapace displays considerable variation among and within species. However, some features are consistent and unique to the family. The following description is based upon *A. platensis*, but applies to all species of the genus except where noted.

The carapace is extremely depressed and gives the animal an overall flattened appearance (Figure 4b,d). The dorsal surface is divided by a distinct cervical groove (Figure 2; cg, Figure 4) into a narrow anterior region and a much wider posterior region. The carapace may be nearly smooth or obviously granulate; small, often setiferous punctations are common on the dorsal surface. Small simple setae are frequent especially along the ventral borders.

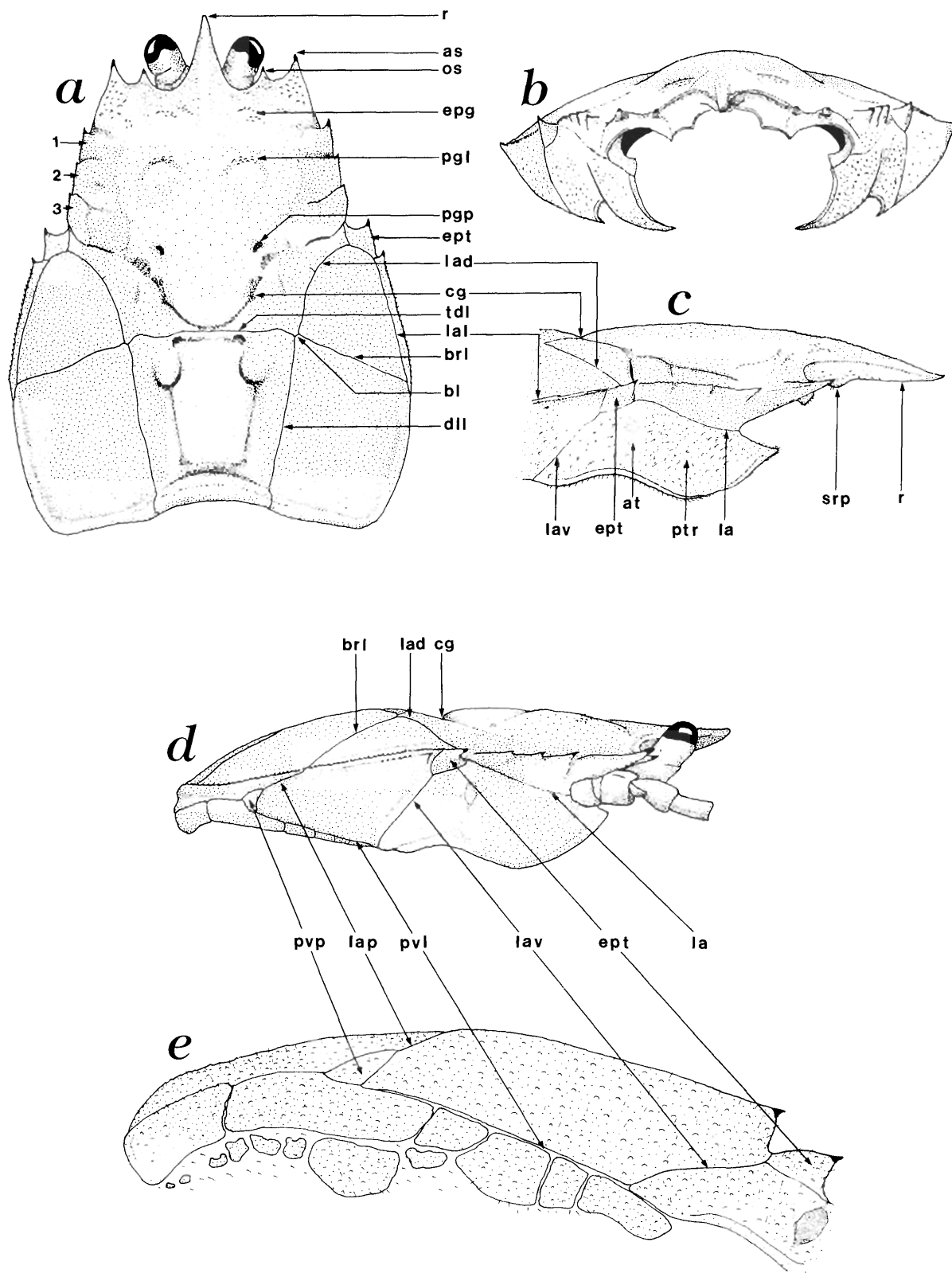*Anterior Region:* The anterior region is marked by a well-developed rostrum usually with a strong dorsal carina

FIGURE 4.—The aeglid carapace: *a*, dorsal view; *b*, frontal view; *c*, lateral view of anterior half of carapace; *d*, lateral view of carapace with eyes and second antennae; *e*, ventrolateral view of posterior half of carapace, higher magnification. *c* is *A. uruguayana;* all others are *A. platensis.*

(see below). The rostral carina typically extends posteriorly onto the carapace only as far as the level of the epigastric prominence or, occasionally, to the protogastric lobe, although in the aberrant *A. denticulata* Nicolet this carina extends the full length of the carapace. On each side of the rostrum a broad shallow excavation on the margin of the carapace forms the orbital sinus (Figure 2), which is flanked ventrolaterally by the orbital spine (os, Figure 4*a*). This spine may be acute with a cornified tip and nearly equal in length to the anterolateral spine (e.g., *A. platensis,* Figure 4*a*) or it may be reduced and coalesced with the anterolateral spine or absent (e.g., *A. concepcionensis* Schmitt, *A. papudo* Schmitt, *A. affinis* Schmitt, *A. maulensis* Bahamonde and López, *A. serrana* Buckup and Rossi, and *A. franciscana* Buckup and Rossi). Therefore the extraorbital sinus separating this spine from the anterolateral spine may be of variable depth, or absent. The anterolateral spine (as, Figure 4*a*) is typically acute with a corneous tip and may exceed the length of the eyestalk (e.g., *A. sanlorenzo* Schmitt) although in most species it extends only as far as the posterior margin of the cornea (e.g., Figures 4*a*, 5*a*).

The anterolateral carapace margin extends posteriorly from the anterolateral spine to the hepatic region. This region is subdivided into three lobes of approximately equal size (Figure 2, and numerals 1–3 in Figure 4*a*). The anterolateral margins of the hepatic lobes are typically acute and tipped with a corneous spine, although in some species these lobes are fused and nearly indistinguishable (e.g., *A. bahamondei* Jara, *A. plana* Buckup and Rossi, and *A. franciscana*). Even when the hepatic lobes are indistinct, the demarcation between the first lobe and the posterior limit of the dorsal anterolateral carapace area is almost always readily apparent.

The dorsal surface of the anterior region is slightly elevated centrally and slopes gently down to the lateral carapace margins. At about the level of the first hepatic lobe is a small raised area termed by most authors the epigastric prominence (epg, Figure 4*a*). This prominence may be highly granulate and obvious or it may be inconspicuous or even absent (e.g., *A. plana*). Directly posterior or slightly posterolateral or postero-medial to this prominence is another raised granulate area that Schmitt (1942b) called the anterior margin of the protogastric lobe (pgl, Figure 4*a*). As in the epigastric prominence, the protogastric lobe may be obvious and granulate or indistin-guishable from the surrounding carapace (e.g., *A. plana*). Occasionally the anterior margin of this lobe is marked by a series of small sclerotized tubercles (Figure 5*a*). Posterior to the protogastric lobes is a large, slightly inflated, gastric area usually devoid of granulations but often punctate. On either side of the gastric area is a small sharply defined pit termed by Glaessner (1969) the posterior gastric pit (pgp, Figure 4*a*); these pits are external indications of internal calcareous apodemes supporting a pair of gastric muscle-fiber bundles. In some individuals the pits are faint and not easily seen. From the slightly elevated gastric area the carapace slopes laterally

to the hepatic region and posteriorly to the cervical groove. The grooves separating the lobes of the hepatic region may in some individuals extend onto the dorsal carapace surface; the posterior groove of the third hepatic lobe is very prominent and becomes deep, producing a strong internal apodeme, just lateral to the posterior gastric pits. This groove then becomes shallow and merges with a wide reticulated area marking another internal gastric muscle attachment. Mesial to this wide shallow depression the groove merges with the cervical groove (cg), which curves posteriorly in a wide U-shape. The cervical groove is usually well developed and distinct, separating the anterior and posterior regions. The portion of the cervical groove directly posterior to the shallow depression is deep, producing interiorly a flat transverse apodeme. The posterior portion of the "U" of the cervical groove becomes more shallow but is still distinct in all specimens examined.

The ventral surface of the anterior region can be divided into two parts, an anterior subrostral area and a lateral subhepatic area. The ventral subrostral margin slopes sharply backward from the anterior margin and articulates with the anterolateral borders of the epistome (Figures 4*b*, 5*b,c*); the rostrum and orbital spine bear a weak ventral ridge that in the rostrum is produced basally as a subrostral process (srp, Figure 4*c*). The lateral subhepatic area slopes inward and is divided by a distinct uncalcified line or suture. This linea, although referred to in pagurids as a linea anomurica, is neither a linea anomurica nor a linea thalassinica, since it does not extend posteriorly from the antennal region to the posterior border of the carapace. Instead, this linea slopes obliquely upward toward the epigastric tooth (ept, Figure 4*c–e*) where it bifurcates to continue dorsally and ventrally. This linea extending from the antennal region to the epigastric tooth has no previous name; we have termed it the *linea aeglica* (la, Figure 4*c,d*). Ventral to the linea aeglica the pterygostomial region of the carapace (ptr, Figures 4*c*, 5*b*) curves medially and is bordered by a distinct doublure (db, Figure 5*b*). The pterygostomial region is large and extends posteriorly to the ventral branch of the linea aeglica, the *linea aeglica ventralis* (lav, Figure 4*c–e*). Beneath the bifurcation of the linea aeglica just anterior to the epigastric tooth the pterygostomial region bears an oval depression, an external indicator of the attachment of the adductor testis muscle (at, Figure 4*c*). This depressed area is usually obvious.

*Posterior Region:* The posterior region of the carapace is that portion posterior to the cervical groove. The most anterior part of this region is the epibranchial tooth (ept, Figure 4*a,c–e*). The epibranchial tooth is an acute, spine-tipped lobe, usually with a lateral border of smaller spinules. As noted above, the epibranchial tooth is separated from the pterygostomial and anterior regions of the carapace by the bifurcated linea aeglica. This linea continues dorsally and ventrally to surround and separate the epibranchial tooth from the posterior region of the carapace as well. Dorsally the linea aeglica passes between the base of the epibranchial tooth and the posterolateral border of

the third hepatic lobe to extend posteriorly over the dorsum of the carapace; it is then referred to as the *linea aeglica dorsalis* (lad, Figure 4*a,c,d*). The dorsalis is a prominent linea that curves medially and posteriorly on the surface of the carapace. Its anterior part is curved laterally to join the extended linea aeglica and the linea aeglica ventralis (lav, Figure 4*c–e*), the latter passing dorsally posterior to the epibranchial tooth. The dorsalis typically has a very small linea extending at right angles to the dorsalis in the direction of the cervical groove; this small linea leads nowhere and is a "dead end" (Figure 4*a*). Posteriorly the dorsalis appears to intersect a long transverse linea. Closer inspection reveals not an intersection but a confluence of several lineae; a short linea termed by Ringuelet (1948b) the "bar" linea connects four different lineae on the aeglid carapace (Figure 2; bl, Figure 4*a*). The *bar linea* is more or less transverse, so that if extended the two bar lineae would intersect in the posterior region of the carapace. In two species, *A. neuquensis affinis* Schmitt and *A. papudo,* the bar linea is instead sublongitudinally oriented so that if extended the lineae would intersect in the anterior region of the carapace.

It may be that the dorsalis is the continuation of the posterior longer linea, the *dorsal longitudinal linea* (dll, Figure 4*a*); this was believed by Dana (1852). However, it may also be that the dorsalis represents an anterior branching of the *transverse dorsa linea* (tdl, Figure 4*a*). Because the homologies of these various lineae are not understood, it seems appropriate to give them separate names rather than assume correspondence. Extending posterolaterally from the bar linea is a fourth major linea, the *branchial linea* (brl, Figure 4*a,d*), which extends to the margin of the carapace. The branchial linea there merges with the *linea aeglica lateralis* (lal, Figure 4*a,c*), a posterolateral continuation of the dorsalis that extends posteriorly from the epibranchial tooth. These two lineae (branchial and lateralis) merge into the *linea aeglica posterioris* (lap, Figure 4*d,e*), which continues ventrally along the ventrolateral carapace border.

Thus, the dorsal posterior surface of the aeglid carapace is subdivided into several distinct areas. The central area is usually termed the cardiac (Figure 2), although it most likely represents a combination of the cardiac and intestinal areas of other anomurans. Within this cardiac area is a distinct convex region termed by Schmitt (1942b) the areola (Figure 2). The anterior demarkation of the areola is a deep groove producing internally a large apodeme. The lateral termini of the groove are deep circular pits. From these pits, the grooves separating the areola from the cardiac region curve posteriorly and then laterally, creating two semicircular depressions (Figures 2, 4*a*). The posterolateral borders of the areola are nearly parallel to the dorsal longitudinal lineae, and the posterior margin descends sharply toward the posterior carapace groove (Figure 4*a*). The remaining regions of the carapace were collectively termed branchial areas by Schmitt (1942b). The "inner" branchial area is delimited by the cervical groove, the dorsalis, the linea aeglica, and the transverse dorsal linea. The anterior

branchial area is delimited by the dorsalis, the lateralis, and posteriorly by the branchial linea. The posterior branchial area is delimited by the branchial linea, the dorsal longitudinal linea, and the posterolateral margin of the carapace (Figure 2).

The lateral margin of the posterior region of the carapace is sharply defined (Figure 4*b*) and clearly separates dorsal from ventral aspects of the carapace. This margin is typically spinose, although in some species it is nearly smooth, and in a few species (e.g., *A. denticulata* Jara, *A. araucaniensis* Jara, *A. rostrata* Jara, and *A. spectabilis* Jara) the spination has given rise to a row of spiniform teeth so that the lateral margin appears serrate.

The ventral surface of the posterior region of the carapace is subdivided into a series of plates, much as is the dorsal surface. From the epibranchial tooth the linea aeglica ventralis (lav, Figure 4*d,e*) extends posteroventrally, separating the anterior pterygostomial region from the triangular branchiostegal region. The branchiostegite bears, just posterior to the epibranchial tooth (ept, Figure 4*c–e*), a large anterior tooth that is followed posteriorly by a series of small spinules. The posterior border of the branchiostegite is delimited by the merged branchial linea and linea aeglica lateralis, now called the linea aeglica posterioris, on the ventral surface (lap, Figure 4*d,e*). This linea bifurcates to surround a triangular plate, the posteroventral plate (pvp, Figure 4*d,e*). The ventral margin of this plate is marked by yet another linea, the *posteroventral linea* (pvl, Figure 4*d,e*), which extends obliquely backward from the lower border of the pterygostomial region. Below the level of the posteroventral linea the carapace is divided into a number of different-sized ossicles set in a flexible membranous matrix. These small plates differ in size and number among individuals, but there is usually a pair of larger rectangular plates toward the posterior margin and several smaller more widely separated plates anterior and ventral to these larger plates (see Figure 4*e*).

*Variations:* Feldmann (1984) described the only known fossil aeglid (but see Secretan, 1972) from Cretaceous fragments from New Zealand. The differences between that species (*Haumuriaegla glaessneri* Feldmann) and extant aeglids are such that Feldmann noted that, with additional material, the new form could perhaps be placed in a separate family. One of the major differences is that in the fossil aeglid, the dorsal carapace lineae are poorly developed at best. Feldmann noted the presence of poorly developed "branchial lineae" but no other lineae; his branchial lineae, which may represent grooves and not true lineae (see "Discussion"), correspond to our linea aeglica dorsalis. All extant forms are as described above, although the lineae may at first appear faint in some individuals.

ROSTRUM (Figures 2–4, 5*a*).—The rostrum is treated separately from the carapace because of the significance that many authors have attributed to this character. The aeglid rostrum is well developed and extends anteriorly beyond the orbital or anterolateral teeth. Schmitt (1942b) noted that aeglids
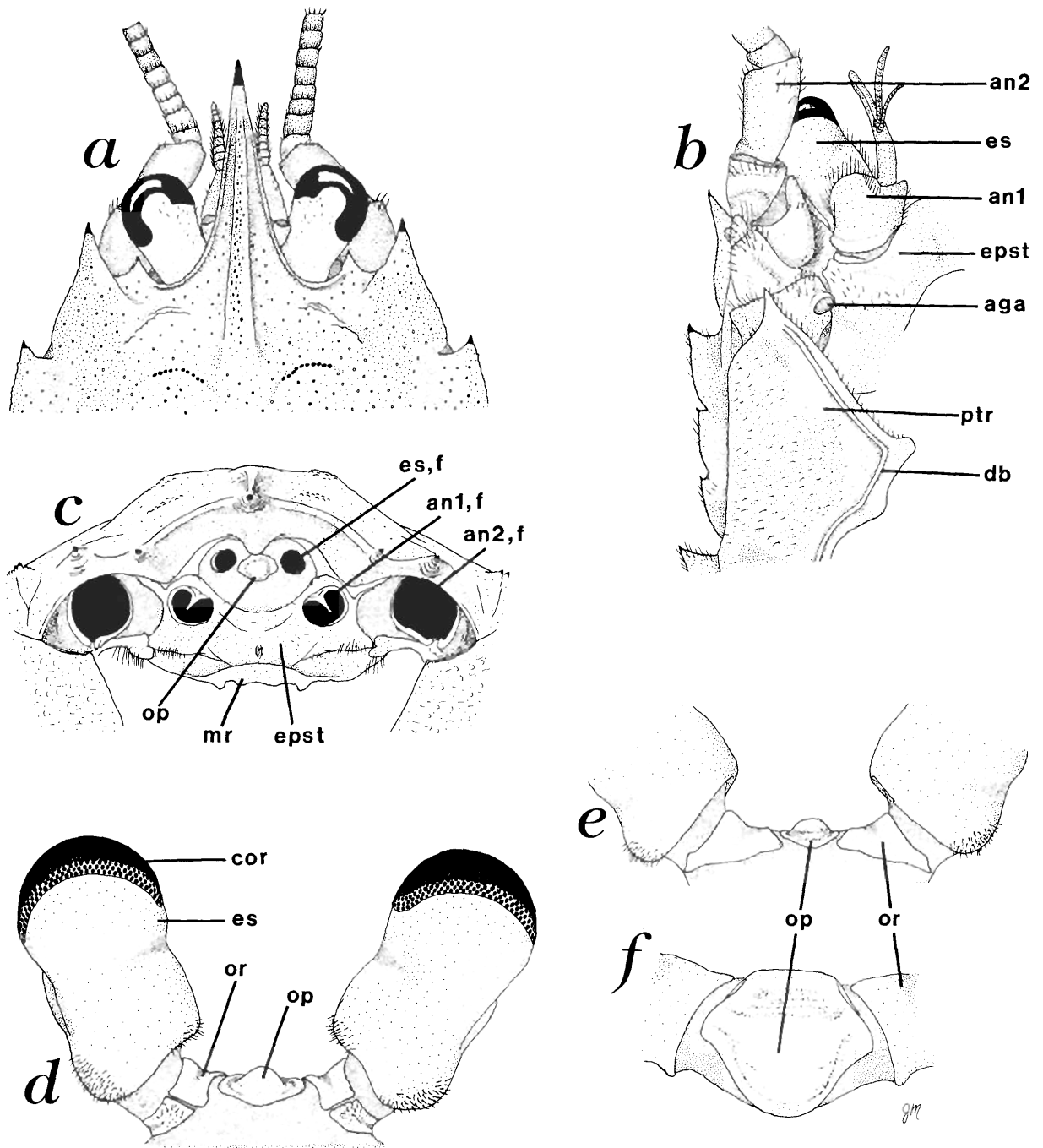
FIGURE 5.—Protocephalon of *A. uruguayana: a,* dorsal view of anterior carapace; *b,* ventral view of right side of protocephalon with mouthparts removed; *c,* frontal view of protocephalon with all appendages removed but with epistome intact; *d,* ventral view of eyestalks and associated sclerites; *e,* dorsal view of eyestalk sclerites; *f,* frontal view of eyestalk sclerites.

could be divided into two large groups on the basis of rostral morphology. The "Atlantic" group, comprising species from eastern South America, has a rostrum with a distinct longitudinal carina that extends to the tip of the rostrum and that is more or less triangular in cross section. The lateral surface of the carina descends at a 45° or sharper angle to the lateral surface of the rostrum. An example of this rostral type is seen in *A. uruguayana* (Figure 5a). The "Pacific" group, containing species west of the Andes Mountains, has a more flattened rostrum with a carina not extending to the tip and not triangular in cross section; this rostral type also tends to be slightly curved upward at the tip and troughed or excavate on
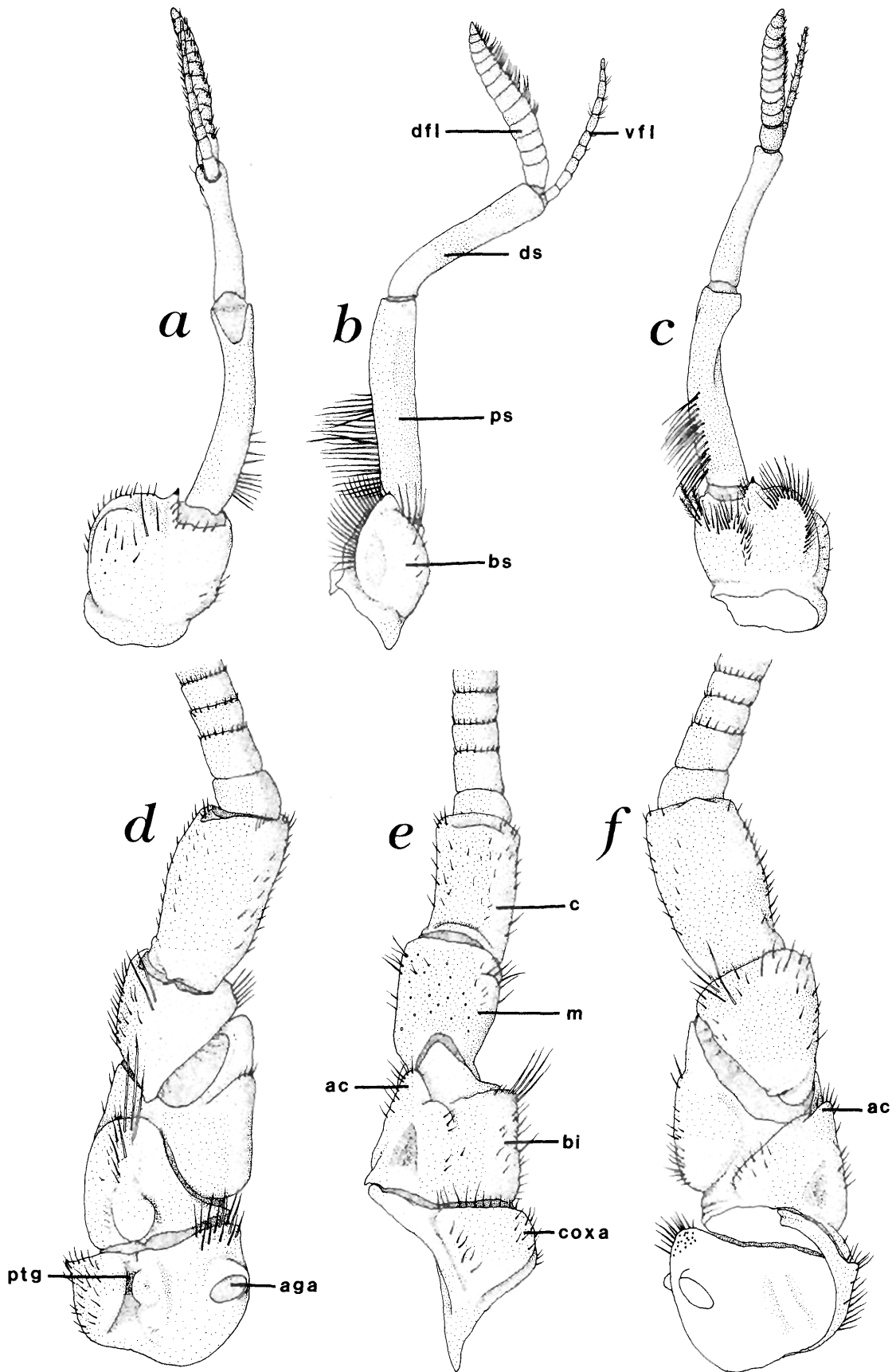
either side of the low carina. Although many authors have continued to assign species to one group or the other, it should be made clear that there is some uncertainty as to the significance of such a character. There are several eastern South American forms with rostral types approaching that of the "Pacific" group. Schmitt (1942b) notes that the rostrum of *A. franca, A. jujuyana,* and some specimens of *A. prado* resembles that of the "Pacific" group. Similarly some Chilean species have rostral types that approach morphologically that of the "Atlantic" group (e.g., *A. manni*). In at least one case, Schmitt (1942b:500) felt that two species, *A. jujuyana* and *A. humahuaca,* were closely related *despite* rostral morphology: "This species [*A. humahuaca*] and *A. jujuyana* so resemble each other in general appearance that one cannot escape the conviction that they may be very closely related in spite of the fact that *A. humahuaca* possesses a palmar crest and has a bluntly ridged rostrum, characters definitely differentiating the two." In light of the recent finding by Feldmann (1984) of a fossil aeglid from the Pacific that seems to have a carinate "Atlantic form" rostrum, assumptions concerning aeglid origins or affinities as related to rostral morphology may be unwarranted.

As an example of a typical aeglid rostrum, the rostrum of *A. uruguayana* is illustrated in Figures 4c and 5a. The rostrum is definitely carinate and of the "Atlantic" group of Schmitt (1942b), with the carina extending fully to the tip of the rostrum. The dorsal surface of the carina bears several scattered, minute, sclerotized granules and few punctations. The upper and lower (ventral) portions of the rostrum are separated by a line of small granules extending from near the lateral distal margin to the inner margin of the orbital tooth; this line of granules is extended on the dorsal surface as a distinct lateral border (Figure 5a).

## PROTOCEPHALON

Snodgrass (1951, 1952a,b) considered the eyes, first and second antennae, epistome, and labrum to constitute a more or less discrete unit corresponding to the primitive head of the Decapoda. The protocephalon is technically not covered by the carapace, as the carapace stems from the dorsum of the mandibular somite and so extends over the gnathal and thoracic regions (Snodgrass, 1952b); in most extant decapods the carapace extends forward so as to shield dorsally the protocephalon as well. Although in aeglids, as well as in many other decapods, the protocephalon does not detach readily from the gnathal region, we follow Snodgrass in treating this region as separate from the carapace proper and its underlying gnathal and thoracic regions.

EYES (Figure 5).—The eyes are typical of many decapod crustaceans. The slightly dilated cornea (cor, Figure 5d) is highly pigmented and is separated from the eyestalk (es, Figure 5b,d) ventrally by a smoothly curving border. Dorsally the eyestalk extends into the region of the cornea in a rounded lobe (Figure 5a). The eyestalk has a slight longitudinal depression on the lateral border, a shallow transverse groove about half way along its length (Figure 5d), and a small ventromedial pit (not illustrated) just proximal to this groove. Scattered, short, simple setae occur on the basal portion of the eyestalk and on the dorsal surface near the cornea. The proximal region of the eyestalk is weakly calcified and flexible. This membranous area is supported by an ocular ring (or, Figure 5d,f) consisting of small basal sclerites that encircle the eyestalk. These sclerites are not fused and allow expansion of the eyestalk as well as freedom of movement. Between the bases of the eyestalks is a single large sclerite, termed by Snodgrass (1951) the ocular plate (op, Figure 5d), that probably functions in supporting the eyestalks. In ventral (Figure 5d) and dorsal (Figure 5e) views this ocular plate is seen to consist of a flat sclerite with a large medial protuberance; in frontal view (Figure 5c,f) the ocular plate is roughly trapezoidal with a distended lower border.

*Variations:* The cornea of the troglobitic *A. cavernicola* Türkay is reduced and tapered toward the distal end. Another cavernicolous species, *A. strinatii* Türkay, appears to have normal eyes (see Türkay, 1972; Hobbs, Hobbs, and Daniel, 1977). Eyestalk development is not described in detail for any other species.

Saint Laurent (1979) noted that in the Reptantia the eyes do not originate independently but instead arise from a single foramen of the protocephalon. In external view this is not apparent; however, when the carapace is carefully removed and the orbital region exposed from the inside, the eyestalks can be seen to originate from a common large foramen.

FIRST ANTENNA (antennule) (Figure 6a–c).—The first antenna is characterized by a globose basal segment (bs) followed distally by a two-jointed stalk, consisting of a proximal (ps) and distal (ds) segment. The distal segment gives rise to a pair of flagella. The basal segment of the stalk, which arises from the anterior of the epistome (Figure 5b,c), is constricted basally and has a shallow lateral depression (Figure 6b). Numerous long simple setae and few plumose and papose setae occur on the dorsal surface, some long simple setae forming a semicircular fringe. Mesially there may or may not occur a short corneous tooth adjacent to the stalk; this is found in *A. uruguayana,* in some specimens of *A. platensis,* but never in *A. jujuyana.* The proximal segment bears long simple setae on the proximal half of the dorsum, and is slightly longer than the distal segment. The distal segment bears few or no simple setae, and gives rise to a dorsal (dfl) and ventral (vfl) flagellum. These structures have been termed exopodites and endopodites by various workers (e.g., Pike, 1947) in other decapods, but this clearly is incorrect as they do not arise from a basipodite. The dorsal flagellum is thick and consists of 10–13 segments,

FIGURE 6.—First and second antennae of *A. uruguayana: a,* first antenna, ventral view (drawn in situ); *b,* same, lateral view; *c,* same, dorsal view; *d,* second antenna, ventral view (drawn in situ); *e,* same, lateral view; *f,* same, dorsal view.
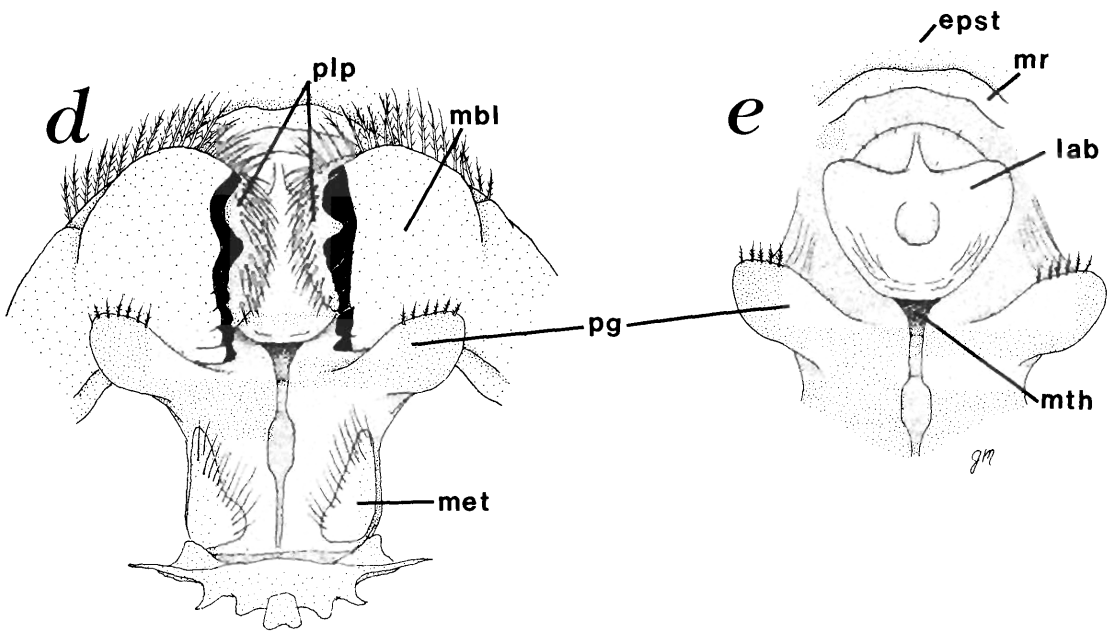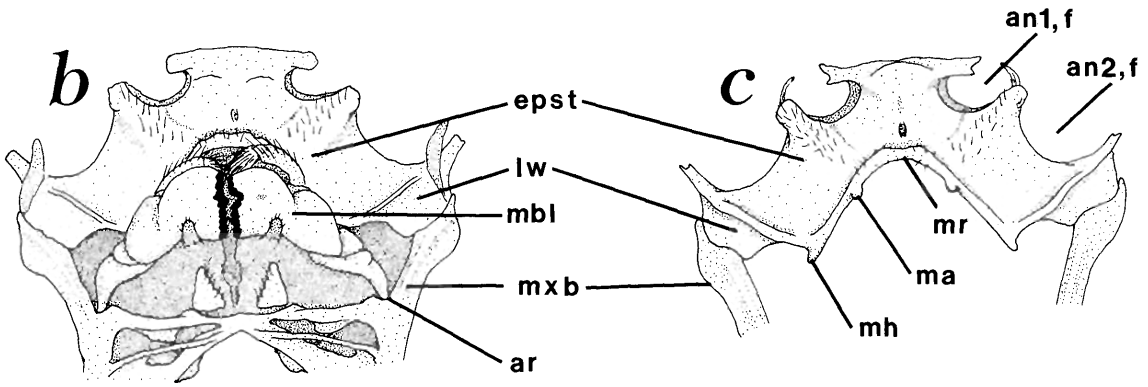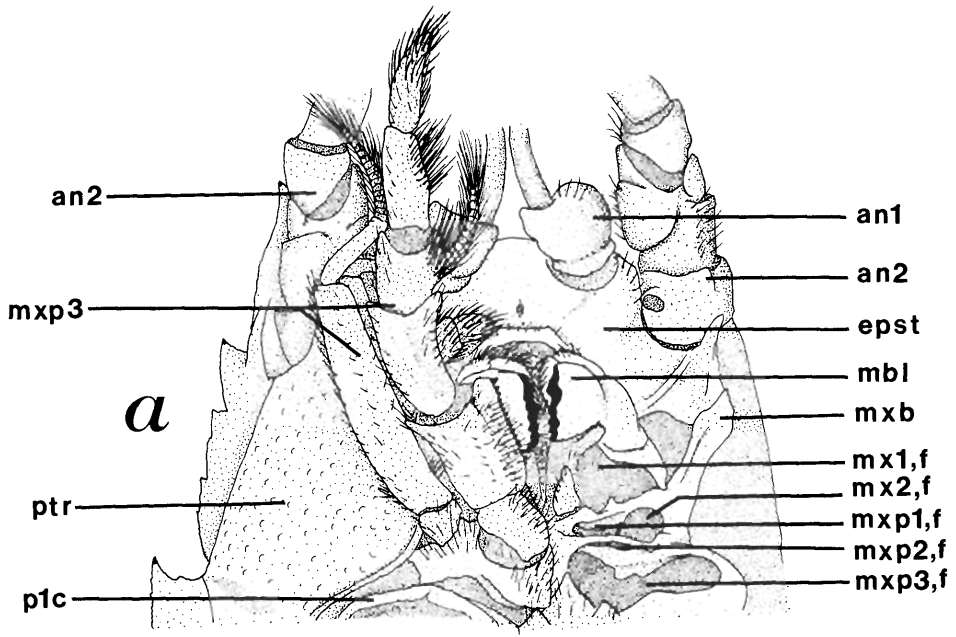
the distalmost of which bear stout simple setae on the ventral border. The ventral flagellum is about equal in length to or slightly shorter than the dorsal flagellum but much more slender and consists of about 10 segments, most with short simple setae.

SECOND ANTENNA (Figure 6d–f).—The second antenna is much longer than the first antenna and may be twice the length of the body. The peduncle is five-segmented, with segments 2 and 3 fused. The basal article (coxa) has a deep ventral groove (ptg, Figure 6d) to accomodate the dorsal border of the pterygostomial region of the carapace, and a large mesial tubercle that bears the aperture of the antennal gland (aga, Figures 5b, 6d). It is very firmly attached to the epistome (Figures 5b, 7a) and almost always remains attached to the epistome when the antenna is removed. The mesial border bears many long simple setae and the lateral border has scattered short setae. The second article is short with a triangular plate extending from its dorsolateral surface; this remnant of an exopod is usually termed a scaphocerite when developed and an antennal scale, squama or acicle (ac) when reduced as in the present case (Glaessner, 1969; McLaughlin, 1980). The distoventral portion of this segment bears long simple setae. The third article is fused with the second, representing the fused basi-ischium (bi). This third segment is longer on the mesial border, which creates an angular articulation; distal segments (four and five) are thereby directed toward the midline so that the antennae appear to originate from under the rostrum (Figures 2, 5a). The fourth article or merus (m) is stout and cylindrical; the fifth article or carpus (c) is slightly longer than the fourth and tapers toward the proximal end. The flagellum is long and multi-articulate, each article except the first having a circle of small simple setae on the distal border. According to Snodgrass (1952a), Schmidt (1915) accounted for seven antennal segments in the crayfish, making the flagellum a modified dactylopodite. Because only five segments plus the flagellum are obvious in *Aegla* and in other anomurans (e.g., Snodgrass, 1952a) our decision to apply the terms coxa, basi-ischium, merus, and carpus may prove inappropriate.

EPISTOME (Figures 5b,c, 7).—The epistome (epst, Figures 5b,c, 7a–c) is a broad medial plate extending from the orbital region posteriorly to the mandibles, and posterolaterally to the carapace at about the level of the mandible. It is not fused to the carapace. Anteriorly it surrounds and supports the first antennae; laterally it supports and is firmly attached to the coxa of the second antennae. Posteriorly the epistome is produced into a thickened bar that supports the labrum and mandibles (Figure 7b,c). This marginal ridge (mr) of the

epistome gives rise posteriorly to paired thickenings, the mesal articulations (ma) of the mandibles. These articulate with the mandible directly below the palp. Continuing posteriorly, the marginal ridge terminates in a pair of calcified protuberances that function as hinges for the mandibles (mh). From these marginal protuberances thickened lateral ridges extend antero-laterally to the carapace. Lateral to this ridge the epistome becomes less calcified and extends by a lateral wing (lw) to the maxillary pleural bridge (mxb). The maxillary pleural bridge, although not part of the epistome, continues the mandibular framework by extending posteriorly and articulating with the proximolateral extremity of the mandible (ar). The ventral surface of the epistome bears two slightly elevated and sparsely setose ridges that separate the foramina of the first and second antennae. A shallow medial depression is almost always found just anterior to the marginal ridge.

*Labrum* (Figure 7d,e): The aeglid labrum (lab) is a membranous globose structure situated just posterior to the marginal ridge of the epistome and just anterior to the mouth (mth). The anterior margin is rounded and gives rise to a narrow ridge that extends ventrally to a flattened, heart-shaped structure that overlaps the mouth. This heart-shaped structure is in direct contact with the mandibular palps (plp, Figure 7d) and during feeding occasionally extends with the palps outward between the cutting edges of the mandible. A medial, ventral, circular depression is almost always present.

SETAL MORPHOLOGY

Before we describe the gnathothorax and associated appendages, we must first mention the types of setae found thereon. Setal morphology in aeglids is mostly unremarkable and similar to that in other anomuran and brachyuran decapods. Most setal types are found on the third maxilliped and this appendage is used (Figure 8) for illustrative purposes. Setal types include comb, serrate, stout serrate, sword, plumose, pappose, pore, simple, and stout simple. Many setae appear intermediate in form and may represent "immature" or undifferentiated stages of more complex types; there is a gradation in length in simple setae and in serrate setae, and a gradation from shorter pappose setae to true comb setae. Some setae are intermediate in form between serrate and stout serrate types.

Terminology of setal types in the above section and in the descriptive sections below follows that of Kunze and Anderson (1979) for pagurid hermit crabs. This is by design; not only the setal types but their location on the mouthparts are essentially identical in hermits and aeglids (see Martin and Felgenhauer, 1986). Possibly unique to aeglids are the composite setae of the fifth pereiopod, and the sword and pore setae of the third maxilliped. Kunze and Anderson (1979) also noted that the eight setal types recognized in pagurid mouthparts are not discrete types; transitional forms exist there as in aeglids.

FIGURE 7.—Protocephalon of *A. platensis: a*, ventral view of protocephalon and mouthparts with appendages of left side removed to show foramina of maxillae and maxillipeds; *b*, epistome with first and second antennae detached but with mandibles intact; *c*, epistome with all appendages and membranous material removed; *d*, high magnification of mandibular region; *e*, oral region with mandibles removed to show labrum, paragnaths and mouth.
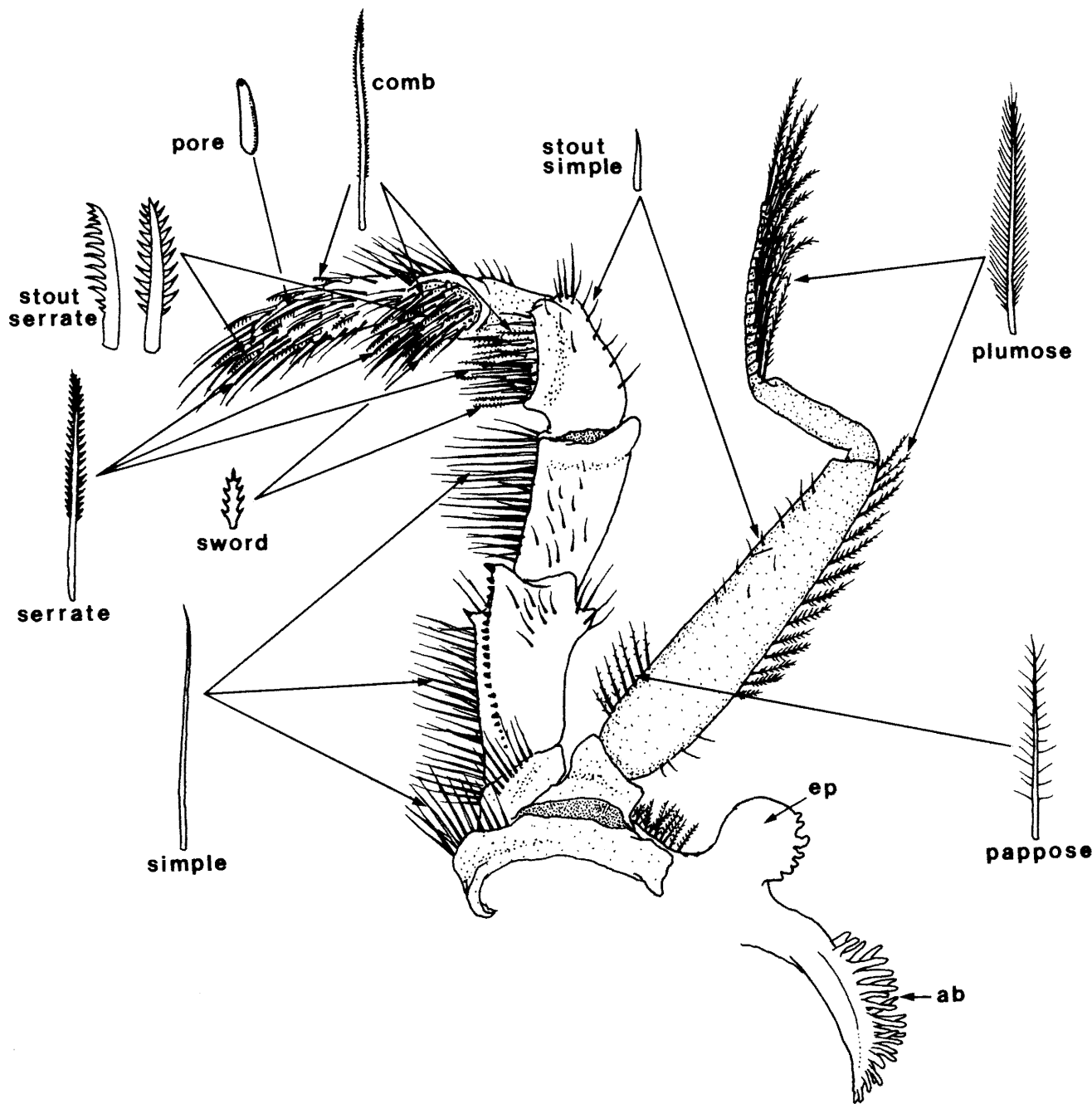
FIGURE 8.—Third maxilliped of *A. platensis,* inner surface, with setal types mentioned in descriptions of aeglid mouthparts. Arrows indicate areas where occurrence of a given setal type is common, and are not meant to be exclusive of presence of a setal type.

## GNATHOTHORAX

Snodgrass (1952b) considered under this heading "the carapace, the branchial chambers and the pleura, the mouth, the ventral skeleton, and the pleurosternal skeleton," or "the part of the animal covered by the carapace." The aeglid carapace was described previously. The pleura (= epimere, epimeron, pleurepimere, pleurite, pleuron, pleural lobe, tergal fold; see McLaughlin, 1980) are described by McLaughlin (1980) as "each lateral part of integument of somite." In other words, these various terms have been advanced to designate the integument of the body where it corresponds to pre-existing somites. Although we recognize a functional gnathothoracic tagma in the fusion of thoracic and gnathal

components under the single dorsal carapace, we treat the gnathal and thoracic regions separately. Although Snodgrass (1952b) chose to treat separately the appendages, we have included description of the appendage with its corresponding somite for the gnathal region.

### Gnathal Region

MANDIBLES (Figures 7a,b,d, 9g,h).—The mandibles stem from the third cephalic somite and are similar to those of many other anomuran and brachyuran decapods. The molar process has been reduced to the point where it is barely visible as a small bump on the interior ventral border (Figure 9g); for practical purposes it is absent. The incisor process is strongly sclerotized and asymmetrical, the right side usually bearing a large blunt tooth that corresponds to an indentation on the left mandible (Figure 7d). The mandible tapers gradually toward the marginal hinge of the epistome (mh) and the articulation point of the mandible (ar) on the maxillary bridge. The mandibular palp (plp, Figures 7d, 9g) is two-segmented. The proximal segment bears several simple and plumose setae on the distal half of the dorsal border; the distal segment is flattened and ovate with many simple, pappose and plumose setae along the entire border. The two segments are approximately equal in length.

The mandibles extend ventrally through a gap between the epistome and the maxillary pleural bridge; their articulation with the gnathothoracic skeleton is described previously under the heading "Epistome".

PARAGNATHS (Figure 7d,e).—The paragnaths (pg) are membranous extensions of the metastomal region. They arise from below (posterior to) the labrum and are situated on either side of the mouth. They are extremely flaccid and weak and their functional role is not readily apparent. Snodgrass (1950) felt that the paragnaths were outgrowths of the metastomal plates (met), structures unique to brachyurans and anomurans. In *Aegla* the distal margin of the paragnath bears few scattered plumose setae; the number may vary somewhat from side to side in a single individual. The metastomal plates (met) are triangular and weakly calcified; they do not extend into the paragnath region but undoubtedly lend support to the paragnaths. These plates arise just posterior to the mouth (mth) and extend anteriorly to just behind the paragnaths. The anteromesial borders bear small simple setae.

FIRST MAXILLA (maxillule) (Figures 7a, 9f).—The first maxilla arises from the fourth cephalic somite and extends ventrally; it is closely adhered to the mandible. The appendage is thin and membranous. The endopod (en) is indistinctly bilobed, with the proximal portion bearing few, long and short, simple setae. The distal portion of the endopod bears few, short, simple setae. The distal endite (de) is fringed with short simple setae and spines; the proximal endite (pe) is spatulate with numerous simple and pappose setae and few short spines. The basal area bears several long, plumose, and simple setae.

SECOND MAXILLA (Figures 7a, 9e).—The second maxilla stems from the fifth cephalic somite and is modified for pumping water over the anterior branchial surfaces. The endopod, distal and proximal endites extend ventrally alongside the maxillule. The endopod (en) is elongate and bears few scattered, simple setae. The distal endite (de) is bilobed, with the distalmost lobe larger and more setose; both lobes of the distal endite bear simple, pappose, and plumose setae. The proximal endite (pe) is bilobed with the proximal lobe much larger; both lobes of the proximal endite bear simple, pappose, and plumose setae. The scaphognathite (scaph) is large and flattened and bordered with numerous plumose setae. The posterior lobe of the scaphognathite extends posteriorly into a respiratory chamber termed by Snodgrass (1952a,b) the pumping chamber (pch; see Figure 14a). This pumping chamber apparently functions in creating high water pressure to facilitate water flow over the posterior branchiae; it is considerably more narrow than the posterior branchial chamber covered by the branchiostegite.

The second maxilla arises far posterior to the first maxilla and appears to be situated posterior to or at the same somite level with the first maxilliped (Figure 7a); its foramen borders on the mesial margin of the maxillary pleural bridge. This is undoubtedly an adaptation for increased respiratory efficiency and is seen in a variety of reptant decapods. The only other illustration of an aeglid gnathal area is that of Snodgrass (1950, fig. 11), in which the foramen of the second maxilla of *A. prado* is also shown posterior to the maxillule and nearly lateral to the first maxilliped.

### Thorax

The first three of the eight thoracic segments bear appendages secondarily modified for feeding: the first, second, and third maxillipeds. These appendages and their corresponding somites are described first because of their affiliation with the true gnathal regions. The functional thorax, i.e., the five pairs of ambulatory appendages and their sterna, are described in the following sections.

FIRST MAXILLIPED (Figures 7a, 9d).—The sixth somite (first thoracic somite) gives rise to the first of three walking appendages that have been secondarily modified for feeding; these are traditionally termed maxillipeds. The first maxilliped, which is thin and only slightly larger than the maxillae, arises posterior to the second maxilla but appears to arise mesial to it (see Figure 7a and second maxilla, above); the foramen is actually located in the narrow confluence of two mesial extensions of the maxillary pleural bridge. The exopod (ex) is 2-segmented with the distal segment a multiarticulated flagellum (fl); both segments bear pappose and plumose setae. The basal portion of the exopod is produced into a large lamellar lobe with plumose setae on its borders. The endopod (en) consists of a reduced, palp-like, terminal lobe and well-developed distal (de) and proximal (pe) endites. The

proximal endite is small and ovoid, with numerous pappose and spinose and few comb setae; the distal endite is larger and subrectangular with numerous pappose, simple, and stout simple setae. The epipod is absent.

SECOND MAXILLIPED (Figures 7a, 9a).—The seventh (second thoracic) somite gives rise to the second maxilliped. The second maxilliped is much larger than the first and assumes more of the grooming and feeding functions, as opposed to being primarily respiratory. This change in function is reflected in the form and setation of this appendage. The maxilliped is pediform, extends anteriorly from the gnathothoracic skeleton, and is not so ventrally oriented as the preceding appendages. The exopod is 2-segmented, with the distal segment developed into a long multiarticulate flagellum bearing numerous, paired, plumose setae. The proximal segment of the exopod is flattened and bears a row of pappose and plumose setae along the lateral margin. The endopod is 5-segmented and more cylindrical in cross section, especially the terminal segments. The dactylus (d) is rounded terminally and bears simple, pappose, serrate, and stout serrate setae; these latter function in grooming as well as feeding. The propodus (p) is short, nearly cylindrical, and bears the same four setal types on the distal border. The carpus (c) is short and articulates with the propodus and merus so as to form nearly a right angle, directing the distal two segments inward toward the mouth; the carpus bears only simple and pappose setae. The merus (m) and fused basi-ischium (bi) are elongate, more flattened than the preceeding segments, and have long simple setae and few pappose setae. The coxal area (coxa) bears long, simple setae and pappose setae. The epipod is absent.
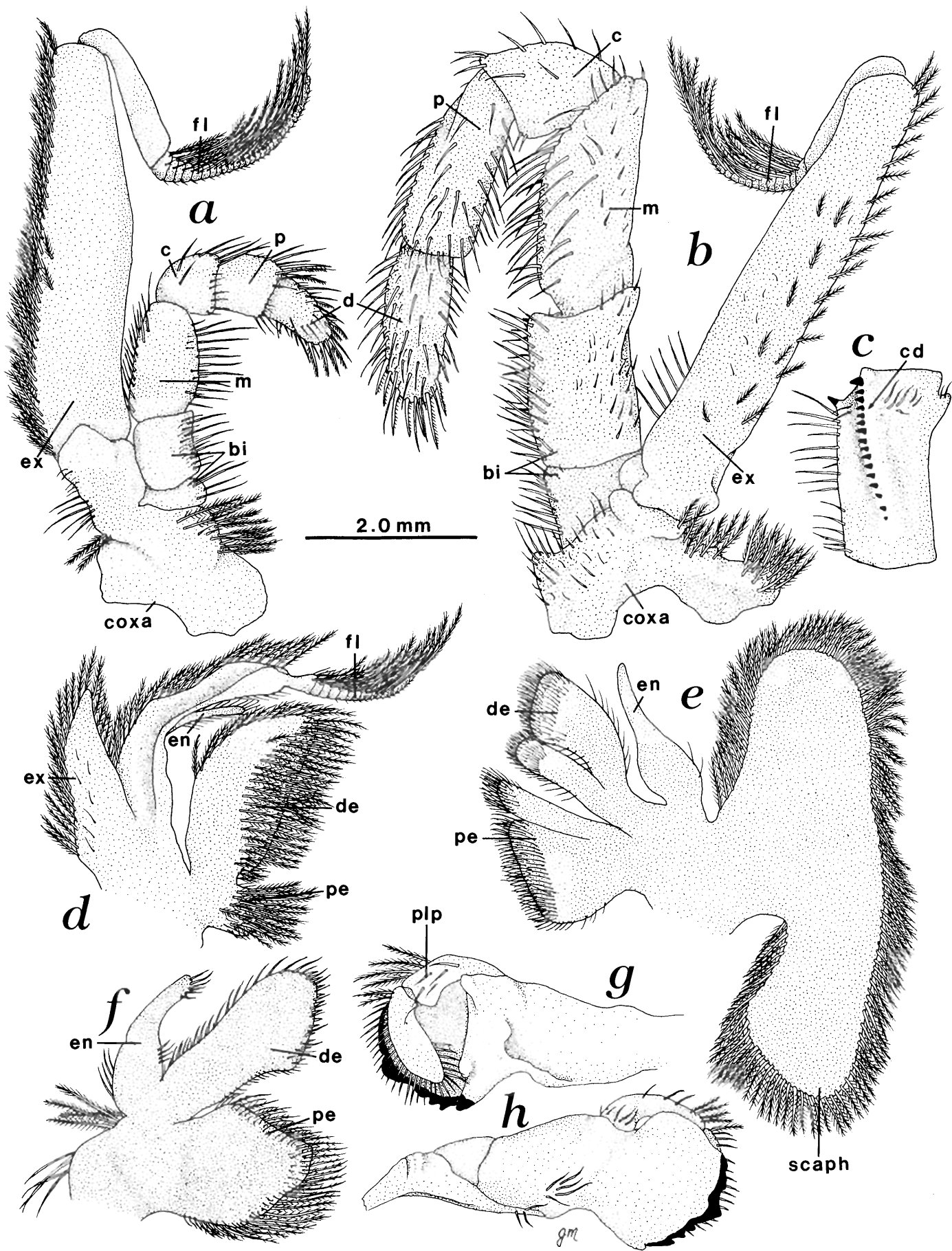
THIRD MAXILLIPED (Figures 7a, 8, 9b,c).—The third maxilliped is pediform and well developed; it functions in grooming and feeding (see Martin and Felgenhauer, 1986). In addition, it is often extended anteriorly when the aeglid appears to be searching for food or shelter and thus may have some sensory capabilities as well. This appendage arises from the eighth (third thoracic) somite and is firmly attached to the ventral thoracic sterna by the coxal segment (see Figure 10a,b). The dactylus is subcylindrical and armed with simple, stout simple, pappose, pore, and serrate setae; most of the serrate setae are located on the distal half. The propodus is slightly longer than the dactylus and bears fewer serrate setae; a circular field of dense setae on the inner surface contains pappose, sword, serrate, and stout serrate setae. The carpus is short and thick with few setae on the outer surface but with a circular field of dense pappose, sword, serrate, and stout serrate setae on the inner surface. This circular field of setae, like that of the propodus, is slightly elevated relative to other areas of the segment. The two circular fields of dense setae on the propodus and carpus combine with the serrate setae of the dactylus to function in grooming and feeding. The merus is subcylindrical and bears numerous long, simple setae along its mesial margin, with scattered simple and pappose setae on the inner and outer surfaces; it is slightly dilated distally. The distal portion of the

merus is concave and allows the carpus to fold tightly against it. The fused basi-ischium is nearly triangular in cross section, and has scattered simple and pappose setae. The mesial margin bears a sharp, corneous, subterminal tooth and many long simple setae. The inner surface is similar to that of many other anomurans in having a row of well-developed corneous tubercles, the crista dentata (cd, Figure 9c). These tubercles become progressively larger toward the distal end of the row and terminate in a large sharp spine. The lateral margin of the basi-ischium bears a blunt subterminal protuberance armed with few simple setae. The coxal area bears simple, pappose, and plumose setae. The epipod is present as a small membranous bud extending posteriorly from the arthrodial membrane proximal to the coxa. There is a small arthrobranch present that is firmly attached to the epimeral plate and is usually lost when the maxilliped is removed. The only other illustrations of aeglid mouthparts are those of Ortmann (1892), which do not allow detailed comparison.

## Thoracic Sterna

The sternal regions of the first and second maxillipeds are reduced and represented by a thin median extension of the maxillary pleural bridge (Figure 7a,b; see also "Gnathal Region" above). The third maxillipeds are closely approximated basally and the corresponding sternum is reduced to a small but well-calcified, conical sclerite, which in some species may be minutely bifurcate or heavily setose. This sclerite forms the apex of a large, sternal, triangular plate (Figure 10a,b) that extends posteriorly to the level of the 7th thoracic somite (pereiopod 4). The sternal plate becomes progressively wider posteriorly. The fourth thoracic sternum, between the coxae of the chelipeds, is of some systematic value in that some species have an anteromedial tubercle or spine on this sternum. This tubercle may be low and rounded (Figure 10b) or it may be sharp and distally cornified (e.g., A. bahamondei Jara and A. perobae Hebling and Rodrigues). In many species no such tubercle is seen, and the anterior margin of the fourth thoracic sternum is nearly smooth. All thoracic sterna bear rather blunt anterolateral projections; those of the third somite articulate with the coxa of the third maxillipeds (Figure 10b). The posterolateral borders of the sterna articulate with a shallow groove or depression in the coxa of the corresponding pereiopod (Figure 10b,c). In A. platensis, A. uruguayana, and A. jujuyana, and probably in all other species, the sternal surfaces are marked by minute pits and scattered simple setae; setation is most dense at lateral and anterolateral sternal borders. All thoracic sterna are fused except for that of the eighth thoracic somite (th8), which is connected to the sternal

FIGURE 9.—Mouthparts of A. platensis: a, second maxilliped; b, third maxilliped; c, ischial portion of fused basi-ischium with crista dentata; d, first maxilliped; e, maxilla; f, maxillule (first maxilla); g, inner view of right mandible; h, external view of right mandible.

*a*

*b*

*c*

*d*

*e*

*f*

*g*

*h*

2.0 mm

fl

c

p

m

d

ex

bi

coxa

p

c

m

ex

bi

coxa

fl

cd

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pe

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en

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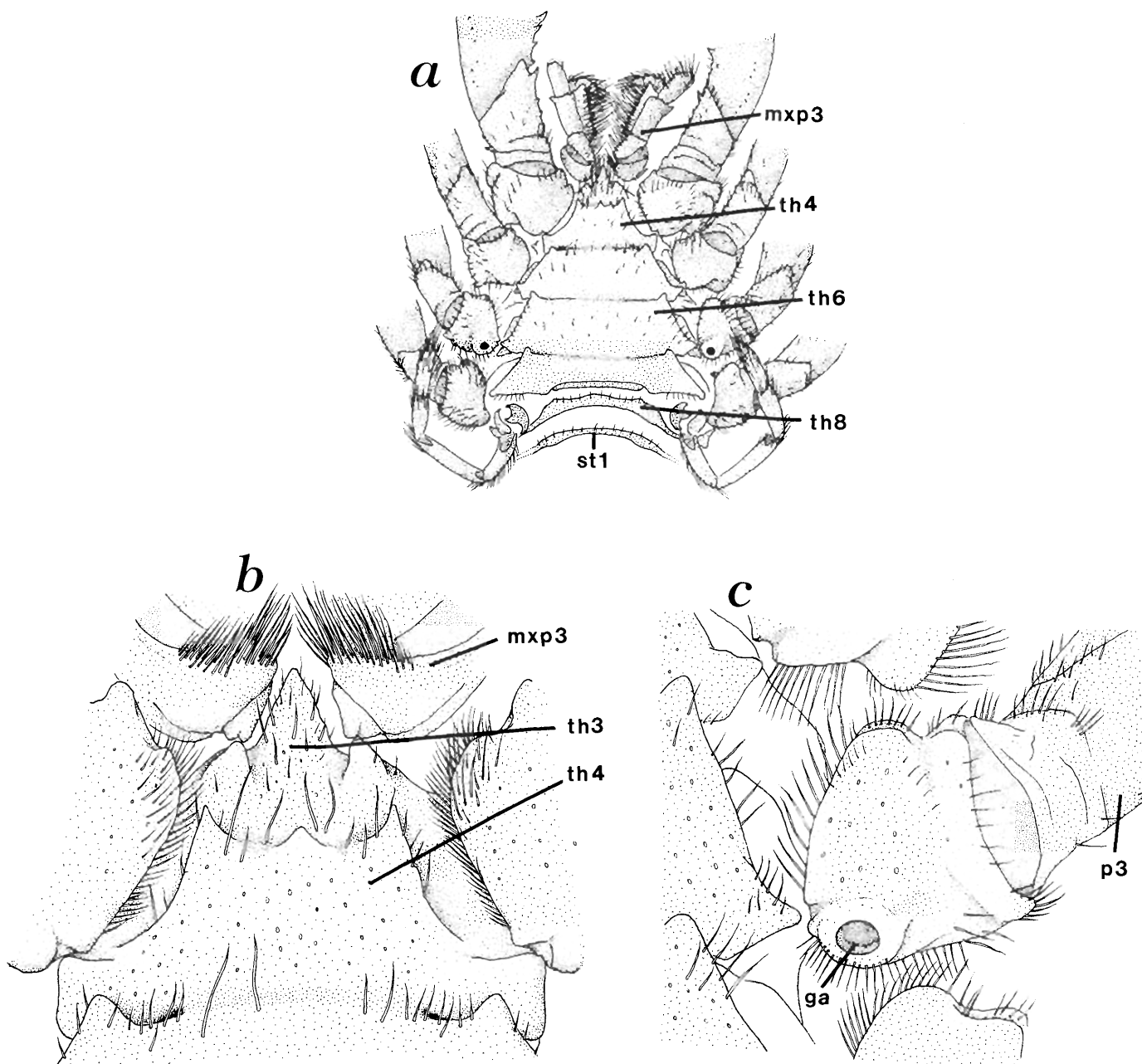
FIGURE 10.—Ventral view of thorax of *A. platensis: a,* ventral view of thorax showing last thoracic segment unfused and first abdominal sternum; *b,* high magnification of sternum of thoracic segment four showing median tubercle; *c,* high magnification of coxa of female third pereiopod showing genital aperture.

plate of the anterior somites by a narrow membranous band (Figures 10*a,* 16*b*).

### Pereiopods

The first pereiopods (chelipeds) are large chelate appendages. The second through the fourth are achelate and similar; the fifth are chelate and reduced. These three types of

pereiopods will be treated separately.

FIRST PEREIOPOD (Figures 2, 3, 11).—The first pereiopod is a large chelate appendage that varies in form among species. The cheliped is larger in males than in females, and almost always larger on the left side. Features of the cheliped have been used extensively as taxonomic characters, although it is known that many characters vary within a species and from
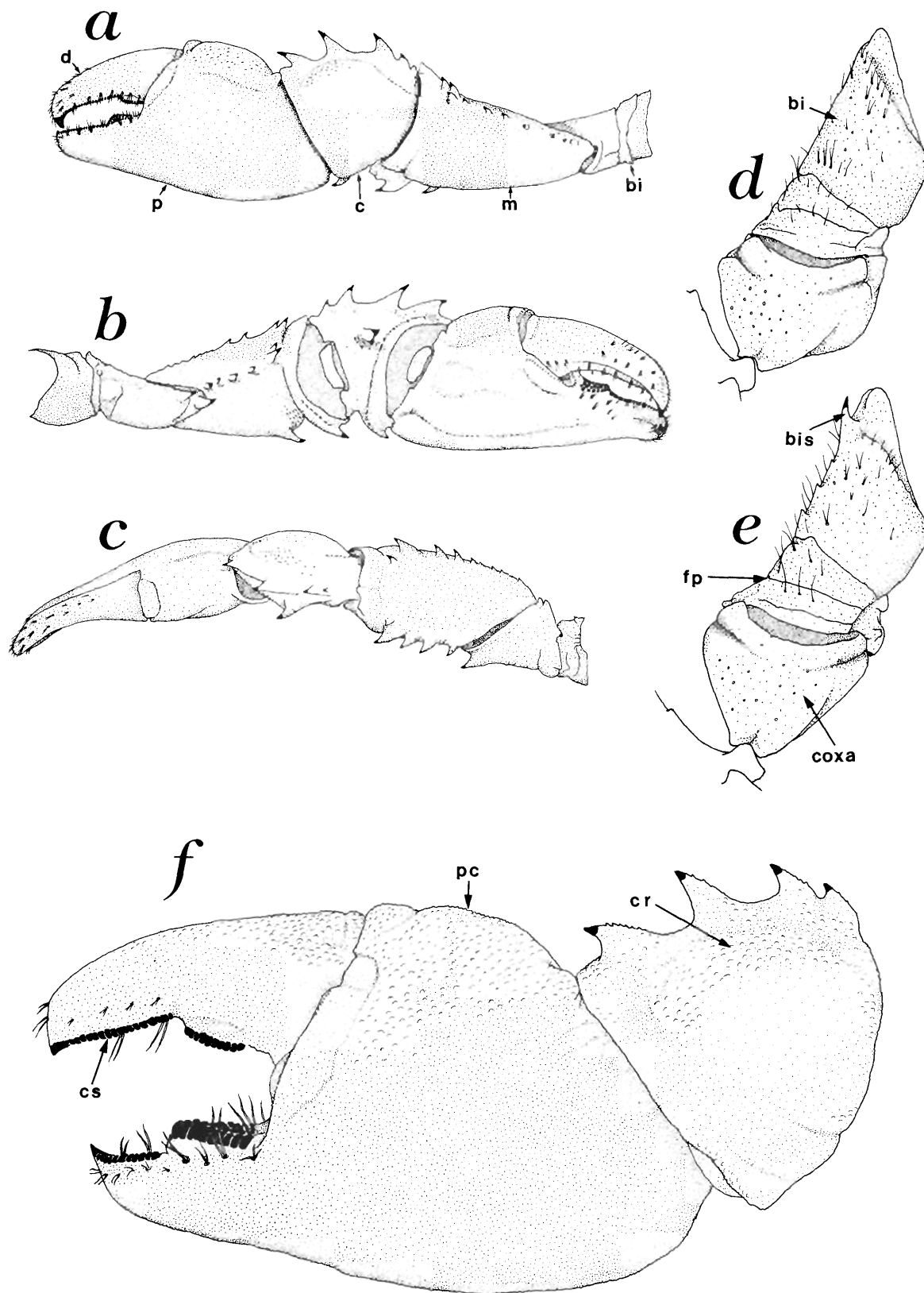
FIGURE 11.—Cheliped of aeglid crabs: *a*, lateral view of left (major) cheliped of *A. uruguayana; b*, mesial view of same; *c*, dorsomesial view of right (minor) cheliped of *A. uruguayana; d*, coxa and fused basi-ischium of *A. platensis; e*, coxa and fused basi-ischium of *A. uruguayana* (note distomesial spine); *f*, chela and carpus of male *A. platensis.*

side to side in one individual.

The dactylus (d) is typically short and heavy with the distal end curved inward. The outer surface is smooth or lightly granulate with scattered, stout, simple setae arising from circular depressions. The cutting margin is bordered with smooth, low, corneous scales (cs) or tubercles and may or may not have a lobular basal tooth; in *A. singularis* the cutting border of the dactylus is actually indented rather than produced basally. The dorsal border is usually smooth or has a slightly elevated ridge of tubercles; in many species (e.g., *A. rostrata, A. bahamondei, A. plana, A. camargoi, A. leptodactyla,* etc.) there may be a small, spiniform, dorsal tooth on the proximal ¼ of this segment.

The propodus (p) is large and inflated. The fixed finger has a row of corneous scales along the cutting edge and except for a few species (*A. humahuaca, A. jujuyana, A. plana, A. sanlorenzo, A. camargoi,* and *A. leptodactyla*) has a large basal tooth also covered with tubercles; this is often indistinct or absent on the minor (right) cheliped. Scattered simple setae arise from circular depressions on either side of the corneous border of the cutting edge. The dorsal border of the propodus may be nearly smooth (e.g., Figure 11) or it may be compressed and elevated into a palmar crest or lobe (pc; see also Figure 2). This lobe most often takes the form of a serrate or tuberculate ridge, as in *A. araucaniensis, A. manni, A. bahamondei, A. denticulata,* and many others, but it may be expanded into an excavated spoon-shaped structure. This condition, which is seen in *A. castro, A. odebrechtii* (both subspecies), and to a lesser degree in many other species, is best developed in the Brazilian *A. schmitti* (see Hobbs, 1979, and Figure 19). The lobe may be extremely variable within a species (e.g., see Hobbs, 1979). The approximation of the posterior edge of this palmar crest with the distal edge of the carpus can form a sinus termed by Ringuelet (1949a) the precrestal sinus (not illustrated). There is almost always a distinct dorsal groove just proximal to the articulation with the dactylus. Another groove extends proximally and ventrally from just below the distodorsal propodus border along the outer surface; this shallow groove appears to curve toward the upper margin of the fixed finger of the propodus. The ventral border of the propodus is usually smooth or tuberculate although in some species (e.g., *A. parana* and *A. lenitica*) the tubercles may give rise to small spines. The inner surface of the propodus (Figure 11b) may be smooth and slightly inflated or it may have a series of irregular longitudinal depressions (this condition illustrated). The posterior border of the inner surface of the propodus has a small, rectangular, detached sclerite that rests in the membranous area of the joint.

The carpus (c) is a short stout segment of variable form and ornamentation. The dorsal border typically bears a row of 4–5 heavy spines with corneous tips. These spines are typically of equal or subequal size, although there is considerable variation within a species (e.g., see Hobbs, 1979). Most often they increase in size distally to the subterminal (largest) spine. The

distalmost spine (termed the antero-internal lobe by Ringuelet, 1949a; carpal lobe of Schmitt, 1942b) is usually reduced, does not taper as sharply, and may be terminally rounded or broadly spinose (e.g., *A. jujuyana, A. n. neuquensis, A. affinis,* and *A. alacalufi*); often this terminal spine or tooth is separated from the remainder of the carpus by distinct grooves. The outer surface of the carpus is marked by a curved ridge of tubercles or small spines termed the carpal ridge (cr, Figure 11f). This ridge may be low and broad (illustrated) or it may be more sharply defined and bear corneous spines. Occasionally (e.g., *A. parana*) there may be a second row of spines ventral to the carpal ridge. Often the anterior edge of the carpal ridge merges with a shallow groove along the distal border of the outer surface. The ventral border of the carpus may be smooth or may bear 1–2 corneous spines (Figure 11a,b). The inner surface of the carpus almost always bears a single, sharp, heavy spine directed antero-mesially (Figure 11b,c). The posterior border of the inner surface of the carpus bears a subrectangular sinus in which rests a detached sclerite, similar to that seen in the propodus-carpus articulation (Figure 11b).

The merus (m) is heavy and triangular in cross section, with the dorsolateral and ventromesial edges armed with a row of heavy spines. The cheliped is slightly rotated inward so that the outer (dorsolateral) row of spines assumes a dorsal position and the smooth dorsomesial surface (see Figure 11c) is appressed to the pterygostomial region of the carapace (Figures 2 and 3). The ventrolateral border of the merus bears only one or two distal heavy spines rather than a row of spines (Figure 11b). The dorsal margin almost always bears a distinct transverse groove just proximal to the articulation with the carpus; this groove is connected to the distal border of the merus by a short longitudinal groove and usually is continued around the entire distal perimeter of the segment (Figure 11a–c). The ventromesial and lateral rows of spines terminate proximal to this groove.

The ischium and basis are fused into a basi-ischium (bi); this short segment articulates diagonally with the merus. The ventromesial border is often used as a taxonomic character; it may be nearly smooth, as in *A. platensis* (Figure 11d), or it may bear one to two distal basi-ischial spines (e.g., *A. uruguayana,* bis, Figure 11e). In some species (e.g., *A. jujuyana, A. parana, A. sanlorenzo,* and *A. prado*) the two basi-ischial spines may be widely separated, while other species may have a series of small spinules. Ringuelet (1948b, 1949a) has shown that at least in Argentine aeglids this character varies widely. The proximal end of the basi-ischium bears three indistinct lines, with the center line being a fracture plane (fp, Figure 11e) for autotomy of the cheliped.

The coxa is a heavy globose segment that articulates with the thoracic sternum by a produced, posteroventral, indented lobe (Figures 10, 11d,e).

The epipod is present as a reduced setose tubercle (ep, Figure 14b) loosely articulating with the coxa.

SECOND THROUGH FOURTH PEREIOPODS (Figure 12a–d).—
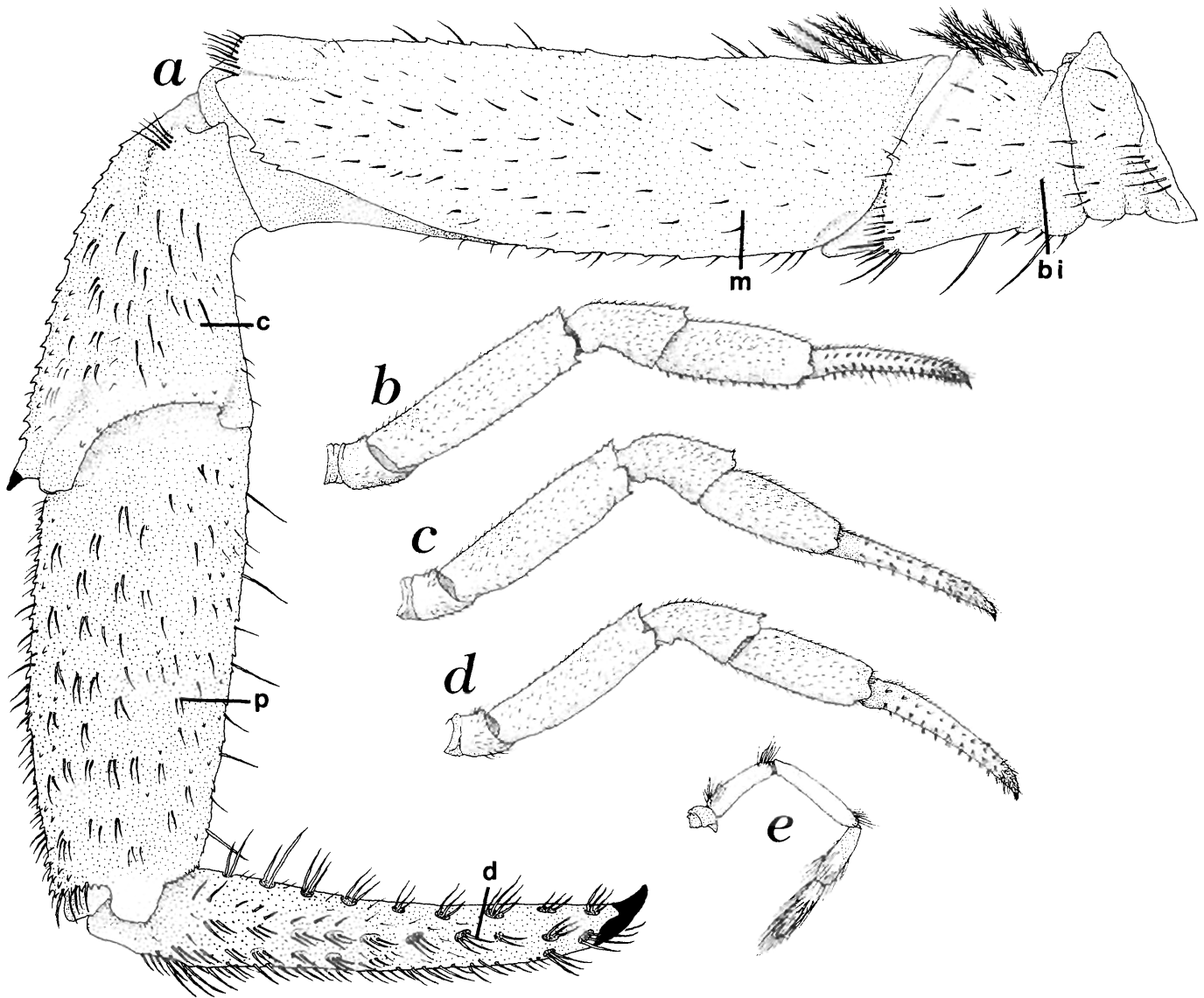
FIGURE 12.—Pereiopods 2 through 5, *A. platensis: a*, third pereiopod, high magnification; *b*, second pereiopod; *c*, third pereiopod; *d*, fourth pereiopod; *e*, fifth pereiopod.

The second, third, and fourth pereiopods are ambulatory and similar in form. The dactylus, propodus, carpus, and merus are slightly laterally compressed and the appendages are angled forward so that in dorsal view (Figure 2) the posterior face of the appendage faces upward.

The dactylus (d) is long and slender with a recurved cornified tip. The anterior and posterior surfaces have several longitudinal rows of small pits, each with several simple setae. Additional simple setae and occasional pappose setae are scattered between these rows. The dorsal (apparent anterior) edge of the segment bears a row of simple setae. The ventral border may bear, at least in some Chilean species, a short longitudinal row of short spines that may be homologous to the corneous scales of the fingers of the first and fifth pereiopods (Carlos Jara, pers. comm.).

The propodus (p) is shorter and broader than the dactylus. There are no rows of setose pits as on the dactylus. The dorsal border is sometimes minutely serrate or bears occasional small spinules. These small spinules may occur on the anterior and posterior surface of the segment and along the ventral border as well. The distolateral borders are slightly produced at the junction with the dactylus forming a rounded lobe. The entire segment is covered with scattered simple setae.

The carpus (c) is short and curved, and nearly always terminates in a sharp corneous spine on the dorsal border. Proximal to this terminal spine is a row of lesser spinules; these
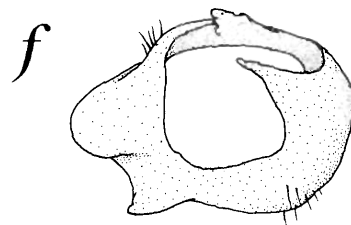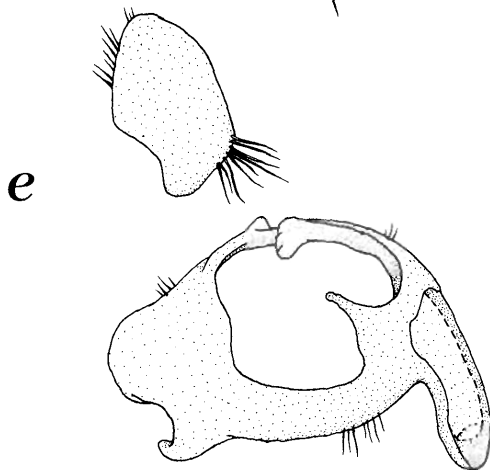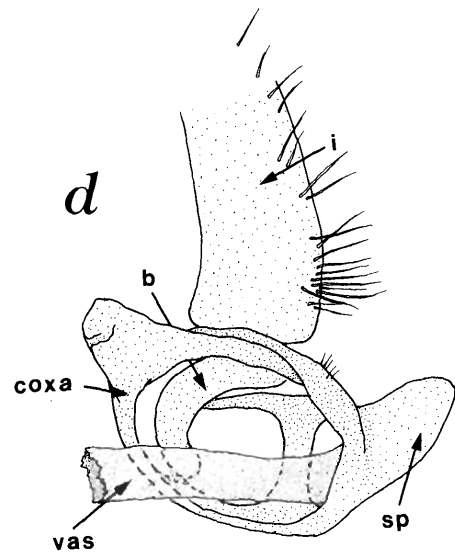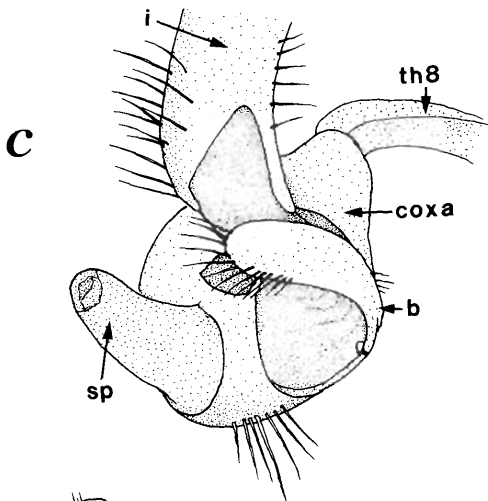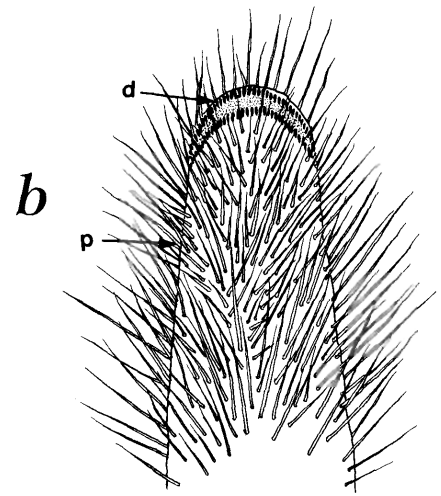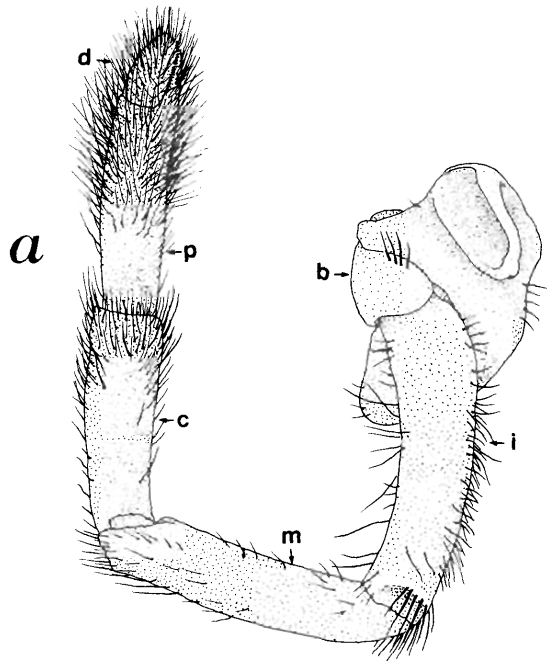
spinules occur also on the distolateral borders of the segment and occasionally on the anterior, posterior, and ventral surfaces. The dorsal border is often produced into a rounded lobe ventral to the terminal spine. The anterior and posterior surfaces bear scattered simple setae; often the dorsal and ventral borders have few simple setae.

The merus (m) is the longest segment and usually terminates in a small spine on the distal dorsal and ventral borders of the posterior surface (Figure 12b–d); these spines are not so apparent in frontal view (Figure 12a). The dorsal border may have a row of plumose setae (e.g., *A. jujuyana*) or bear few simple setae or a combination of setal types; this border in some species is minutely serrate. In a few species (e.g., *A. parana*, *A. sanlorenzo*, *A. lenitica*, and *A. plana*) the ventral border may bear a large subterminal spine or tooth. In *A. parana* and *A. maulensis* the dorsal border has a row of well-defined teeth, while in some species (e.g., *A. plana* and *A. camargoi*) the ventral border may have a row of small spines or teeth. The anterior and posterior surfaces bear scattered simple setae.

The fused basi-ischium (bi) is short and has numerous simple setae on the distal border, and typically few plumose setae on the dorsal border, in continuation of the line of plumose setae extending proximally from the merus. This segment is nearly cylindrical in cross section.

The coxa is similar to that seen in the first pereiopod; it is short and rather globose. The coxa of the third pereiopod in females bears the genital aperture (ga, Figure 10a,c) on the ventromesial surface; in males this coxa has no such aperture.

The epipod on pereiopods 2 and 3 is similar to that of the cheliped (ep, Figure 14b); the fourth and fifth pereiopods lack an epipod.

FIFTH PEREIOPOD (Figures 12e, 13).—The fifth pereiopod differs significantly from the other pereiopods in that it is greatly reduced and usually inserted beneath the posterior of the carapace. It functions in cleaning the branchiae, the abdominal sterna, the third and fourth pereiopods, the posterior dorsal surface of the carapace, and in females the pleopods and eggs (Martin and Felgenhauer, 1986). The dactylus (d) is minute and forms with the propodus a small chela (Figure 13a,b); this chela can not open very widely and may be nonfunctional. The borders of the chela have minute cornified teeth, somewhat similar to the scales on the cutting edges of the chelipeds but smaller and directed outward so that they make contact with the corresponding teeth on their lateral, not distal, borders. The dactylus bears several long, simple setae and compound-serrate setae; these setae coupled with those of the propodus form a stiff brush that probably functions in grooming more so than the chela itself. The propodus (p) is

more setose on the distal half and is cylindrical in cross section. It is subequal in length to the carpus, merus, and ischium. The carpus (c) is also setose on the distal half, less so on the proximal half, and articulates with the merus at a sharp angle. The merus (m) is much less setose than the propodus or carpus. The ischium (i) forms a right angle with the merus and, when in resting position, is almost parallel to the carpus. The ischium bears scattered long setae on the dorsal and ventral margins and is more flattened than any of the more distal segments. The basis (b) differs greatly from the basis of the anterior pereiopods in not being fused with the ischium; it articulates with the ischium and the coxa and has the form of a flattened curved bridge between the two (Figure 13c,d). The coxa differs in males and females. In males the coxa is a slightly dilated segment (the "pieza anular" of Lopretto, 1980b) with two dorsolateral and one ventromesial lobes. The larger of the two dorsolateral lobes (the "expansion cordiforme" of Lopretto) articulates with the eighth thoracic sternum (th8) and with a small plate called by Lopretto the precoxa; the smaller lateral lobe (the "expansion subcuadrangular" of Lopretto) articulates with the eighth thoracic sternum. The ventromesial lobe is a spoon-shaped process (sp) that supports the extended vas deferens (vas) and most likely assumes the function of the modifed first pleopods in other male anomurans. The vas deferens extends from the inside of the coxa to this supporting lobe and continues to the distal tip of the lobe, where it is encased in a thin membranous tube that forms the dorsal margin of the spoon-shaped lobe (Figure 13d,e). Lopretto (1980b) further describes these coxal lobes and subdivides them and the coxa into various areas, which she uses (1979, 1980a,b, 1981) to group various species of *Aegla* together and to distinguish among the Argentine species of the genus. In females (Figure 13f) the coxa lacks the spoon-shaped extension but is otherwise identical to the male coxa.

## BRANCHIAE

GILL FORMULA (Figure 14).—Aeglids have 26 gills, 13 per side. The anterior-most is a very small gill arising from the coxo-thoracic articulation of the third maxilliped; it is thus a small arthrobranch. None of the other maxillipeds has a gill. The first pereiopod has two arthrobranchs arranged serially; the anterior arthrobranch is the smaller of the two. The second pereiopod bears two serial arthrobranchs plus a small pleurobranch that arises from an oval opening in the pleural plate (Figure 14b,c); the pleurobranch lies between the anterior and posterior arthrobranch. The third and fourth pereiopods have the same gill complement as the second (two arthrobranchs flanking a small pleurobranch). The fifth pereiopod bears a single small pleurobranch.

GILL MORPHOLOGY (Figures 14a, 15).—The gills are very large foliose structures that completely fill the branchiostegal cavity (Figure 14a). They resemble trichobranchiate gills distally in that the gill filaments are long finger-like tubes;

FIGURE 13.—Fifth pereiopod of *A. uruguayana*: a, entire pereiopod; b, dactylus and propodus forming weak chela; c, male coxal region; d, male coxal region, inner view with soft tissue removed to show vas deferens; e, male basis (above) and coxa (below); f, female coxa.
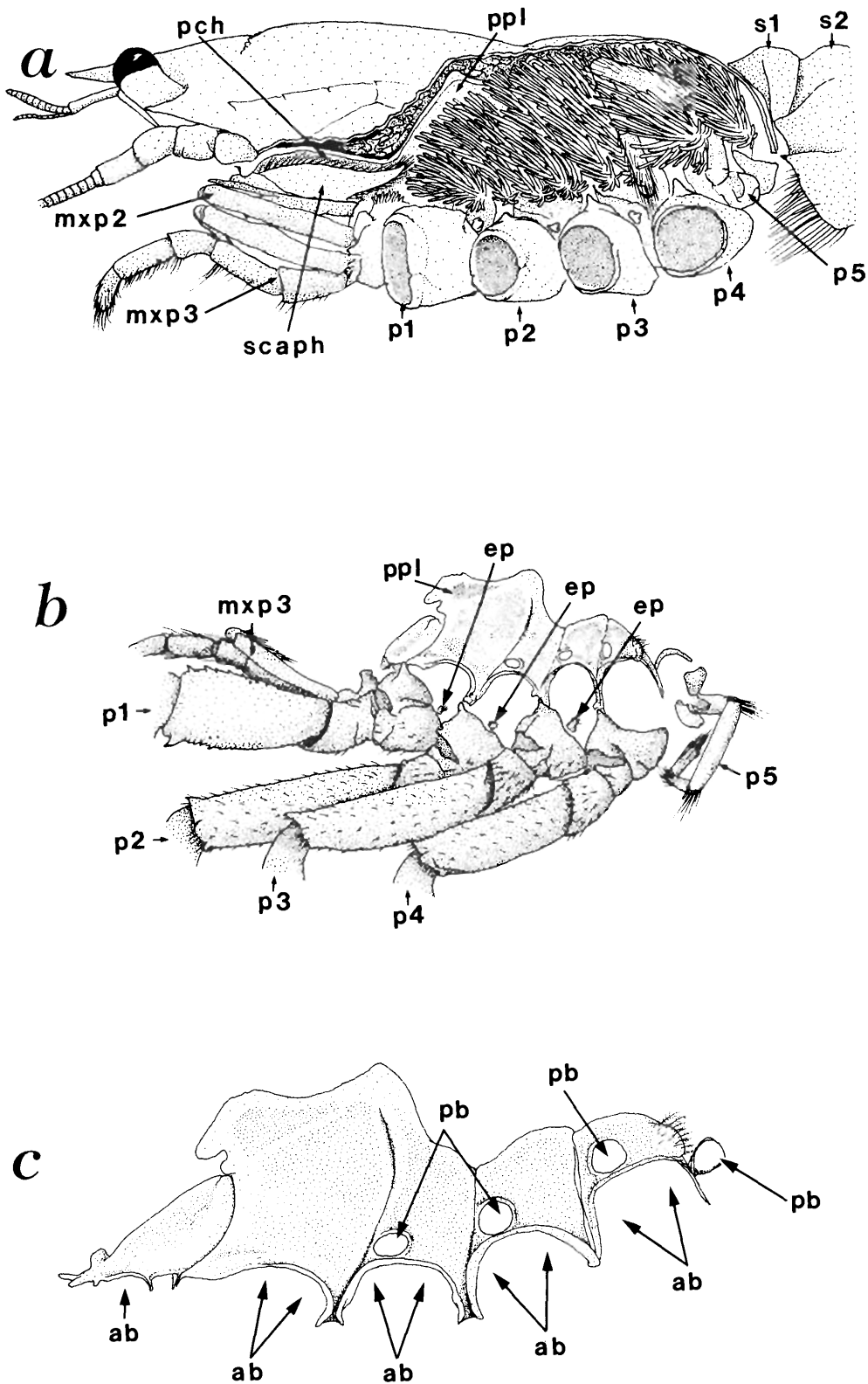
FIGURE 14.—Branchial area of *A. platensis: a,* lateral view of carapace with branchiostegite removed to show branchiae in situ; *b,* lateral view of pleural plate with pereiopods attached and with epipods of pereiopods 1–3 indicated; *c,* high magnification of pleural plate showing locations of the 9 arthrobranchs (ab) and 4 pleurobranchs (pb).
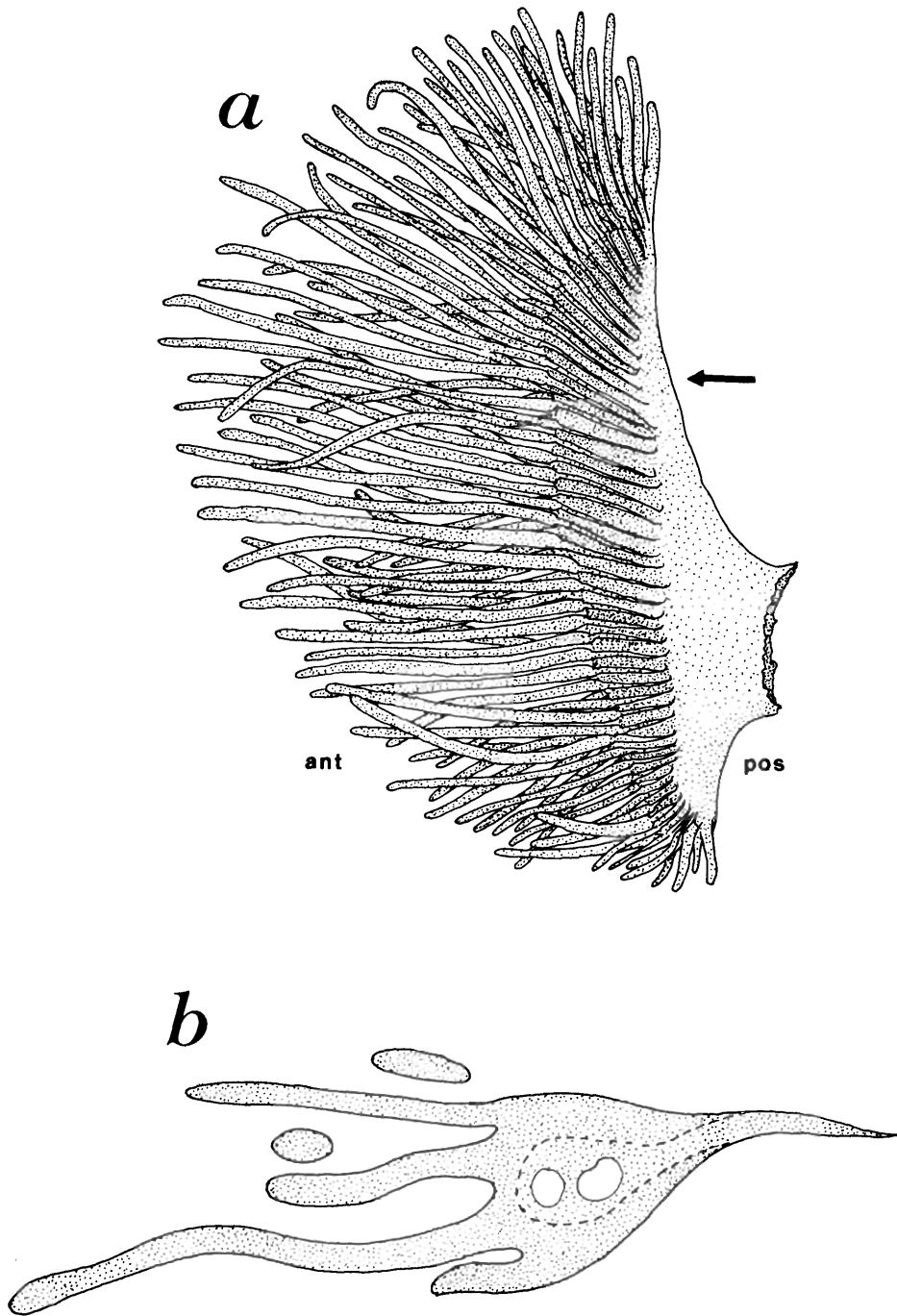
FIGURE 15.—Branchiae of *A. platensis: a,* anterior arthrobranch of pereiopod two; *b,* cross section of same at the level of arrow in a; dashed line indicates area of gill "axis."

these extend forward from the base of the gill. The proximal portion of the gill resembles that of a brachyuran phyllobranch in having plate-like lamellae extending out over the branchial axis (Figure 15a,b). These folds in the gill are apparently beyond the reach of the fifth pereiopod cleaning apparatus; they typically harbor an enormous number of stalked ciliate protozoans. The gills extend anterodorsally and slightly ventrally from their point of attachment to the body.

## ABDOMEN

The abdomen is well developed with six somites and a
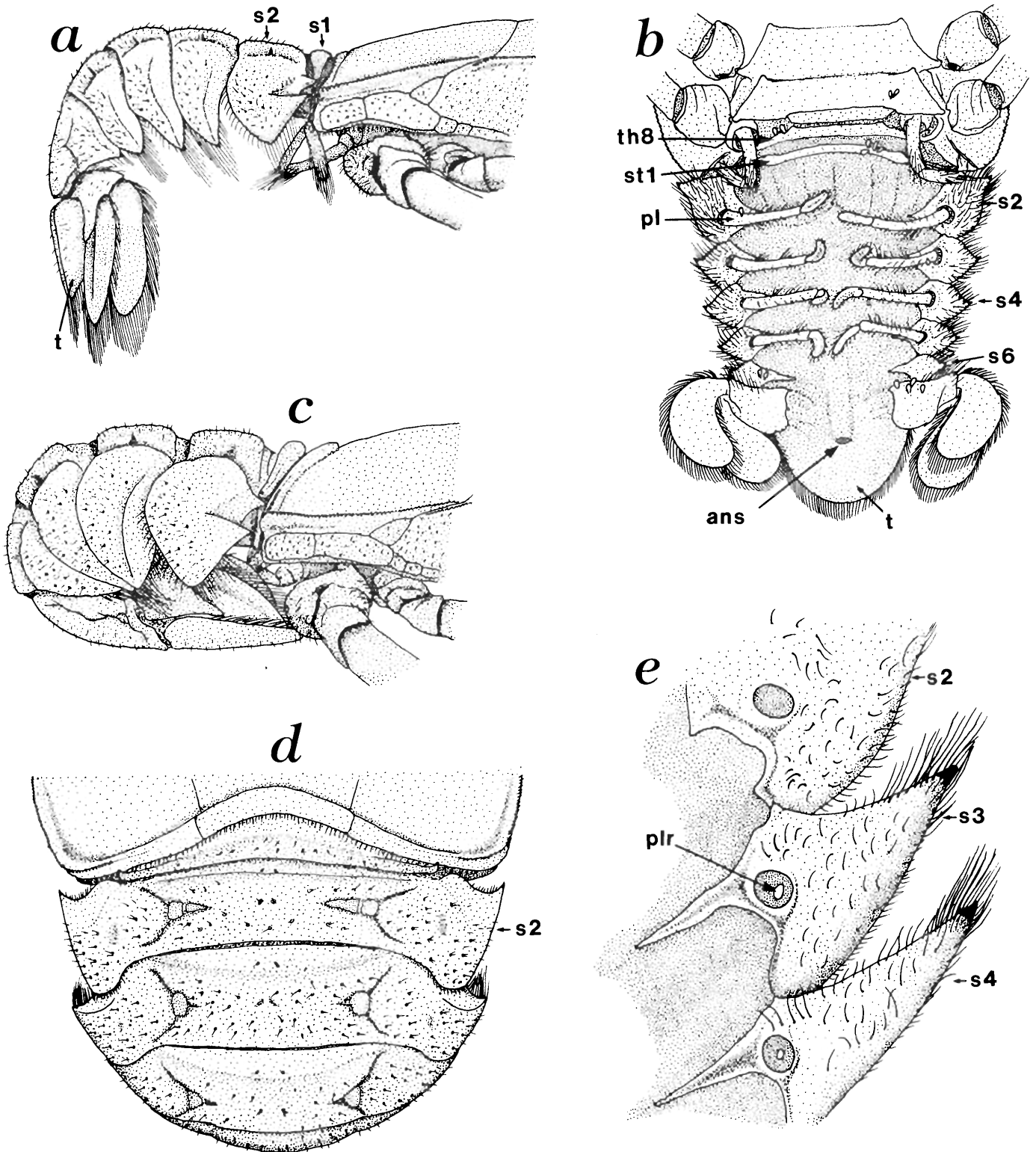
FIGURE 16.—Abdomen of *A. platensis* and (*c* only) *A. uruguayana: a,* lateral view of extended abdomen; *b,* ventral view of extended female abdomen showing functional pleopods (pl) on somites 2–5; *c,* lateral view of abdomen in normal flexed position; *d,* dorsal view of abdomen in flexed position; *e,* ventral view of abdominal somites 2–4 in male, showing pleopodal remnants (plr).

telson. The fifth and sixth somites and the telson and uropods are normally flexed forward beneath the anterior abdominal somites; the telson and uropods usually extend beneath the posterior thorax (Figures 3, 16c,d). The abdomen can be extended somewhat posteriorly during swimming (a caridoid reflex action similar to that seen in astacoid crayfishes) and grooming of the abdominal sterna and pleopods, but it never extends straight behind the thorax. The female abdomen is broader and shorter than that of the male, so much so that a dorsal view often will distinguish between sexes (e.g., see Jara, 1980b), and bears pleopods that the male abdomen lacks.

ABDOMINAL SOMITES (Figures 16, 18).—The first abdominal somite (s1) is reduced and largely covered by the posterior border of the carapace (Figure 16a,c,d); the anterior margin of the somite extends beneath the carapace beyond the posterior carapace groove. The first somite is the only abdominal somite to have a complete and well-calcified ventral sternum in the form of a rounded transverse bar (st1, Figures 10a, 16b). The lateral connections of this sternum to the reduced pleura of the somite are weak. The pleura are sharp and recurved anteriorly and dorsally. The dorsal surface of the somite is smooth with few small pits, most of which contain short simple setae; the posterodorsal surface slightly overlaps the anterior edge of the second somite.

The second somite (s2) is large with a well-developed tergum and pleura. The dorsal tergum rises sharply from beneath the first somite and then becomes slighty convex before descending sharply posteriorly over the third somite; its dorsal surface bears numerous small pits with short simple setae. The pleura (= epimera of many authors) are wide and fused to the tergum at a distinct boundary marked by a longitudinal groove. The medial portion of this groove extends onto the tergum as a triangular or subtriangular depression (Figure 16d). The posterolateral surfaces of the pleura bear numerous, small, setose pits similar to those on the tergum; these pits are absent along the anterolateral surface, which normally is hidden beneath the pleuron of the preceeding somite (compare Figures 16a and c). The boundary between these two regions of the lateral pleural surface is a low ridge. The pleuron of the second somite traditionally has been used as a systematic character. In most species the ventral border is produced into a rounded or acute and spine-tipped lobe. The anterior border of the pleuron may also be produced into a corneous spine (Figure 16a,c,d) or it may be nearly smooth (e.g., A. franca, A. jujuyana, A. odebrechtii (both subspecies), A. neuquensis (both subspecies), etc.). The development of the ventral border and anterior projection has been used as a taxonomic character. However, Ringuelet (1948b, 1949a) has shown variation in this character in Argentine species, even from one side to the other in a single individual. We have noticed considerable variation in the development of the anterior projection in A. platensis; while it is always acute it may curve ventrally or dorsally. The postero- and anteroventral borders of the second and subsequent somites bear long

pappose and simple setae. The sternum of the second and subsequent somites is reduced to a membranous covering of the abdominal muscle. The vestige of a sternum, a calcified extension of the pleuron, extends a short distance mesially as an acutely triangular projection (Figures 16b,e, 18a).

The third through fifth somites are similar to the second although not as large and without any anterior projection of the pleura. The anterolateral pleural border is instead smooth and slightly concave. The posterolateral pleural border is gently rounded or in some cases somewhat undulating. The membranous sternum, although greatly distended in the second somite to allow for a large muscle mass (see Figure 16b), is in the third and posterior somites nearly straight and flattened; these somites contain very little muscle (Figure 18a).

The sixth somite differs from the preceding ones; it terminates posteriorly in a flat border that articulates with the telson. The dorsal surface of the sixth somite bears deep posterolateral grooves that bifurcate into an anterior and posterior branch. The posterior branch leads to a shallow triangular depression in the posteromedial surface of the tergum (Figure 18c). The relative development of these grooves and depressions varies among and within species, and between sexes, although their presence is almost always discernible. The sternum of the sixth somite is reduced and represented by the same triangular calcified extension seen in the preceding somites.

PLEOPODS (Figures 16b,e, 17).—Females possess four pairs of well-developed functional pleopods. The first pair stems from the second abdominal somite; the last from somite 5 (pl, Figure 16b). The first pair is the smallest, the second and third largest and subequal in size, and the fourth is intermediate in size between the first and the second and third. The pleopods function much as in other reptant decapods in carrying the maturing eggs. In addition, they also function in maintaining the young after hatching. The aeglid hatchling stage (a miniature adult; there are no larval stages) is attached to the pleopods by thin filaments, as are the eggs. The young remain attached to the pleopods for an undetermined amount of time, after which the pleopods remain important in harboring the unattached young for up to five months after hatching (Burns, 1972). In the laboratory we observed much shorter periods of parental care (less than one month), but it is unclear what effect our artificial conditions might have had. Carlos Jara (pers. comm.) has made observations similar to ours in aquarium populations and also in the field.

The female pleopods (Figure 17) are basically two-segmented, although a small, weakly calcified, basal ring may represent a reduced third segment. They are not biramous. The distalmost segment is terminally rounded and bordered with numerous, long, simple setae. The anterior surface (Figure 17b–e) is slightly concave. In the first pleopod, this segment is oval and short, and curves slightly laterally away from the midline of the abdomen. In the succesive two pleopods this
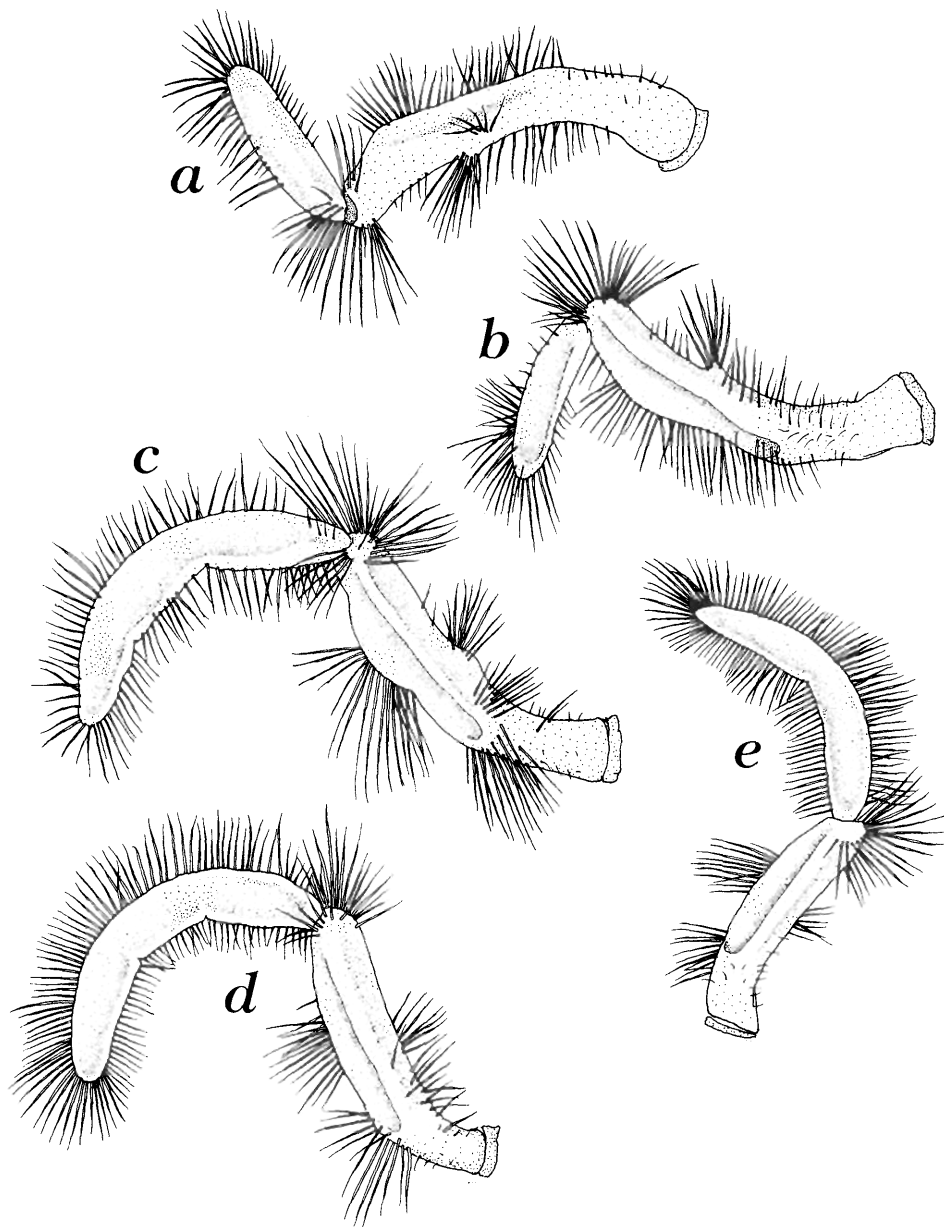
FIGURE 17.—Female pleopods of *A. platensis: a,* first pleopod (second abdominal somite), posterior view; *b,* same, anterior view; *c,* second pleopod, anterior view; *d,* third pleopod, anterior view; *e,* fourth pleopod, anterior view.

segment becomes progressively more elongate and curved; in the fourth pleopod this segment is longer than in the first but not as large or as curved as in pleopods 2 and 3. The proximal segment of all four pleopods is stout and curved mesially. The distal $^2/_3$ of the segment bears a long marginal groove on the lateral border. Numerous simple setae are located on the distal tip of the segment, on a small protuberance located about $^1/_2$ way along the length of the mesial border, and in two groups along the basal $^2/_3$ of the lateral border. Scattered, long, simple setae occur on the basal half of the segment.

The male pleopod is greatly reduced. On the first somite there is no indication of the presence of a pleopod, while in the posterior somites the pleopod may be represented by a small calcified knob, the pleopodal remnant (plr, Figure 16e). Dana's (1852) curious statement that male aeglids have a reduced pleopod of only two segments is therefore incorrect.

UROPODS (Figure 18b,c).—The sixth somite bears well-developed uropods (Figure 18b,c), which according to most workers (e.g., Glaessner, 1969) are modified pleopods. The basal segment of the branched uropods, termed a sympod (sym), is short, wide, and flattened, with a shallow distal groove on the dorsal (functional ventral) surface. Usually a
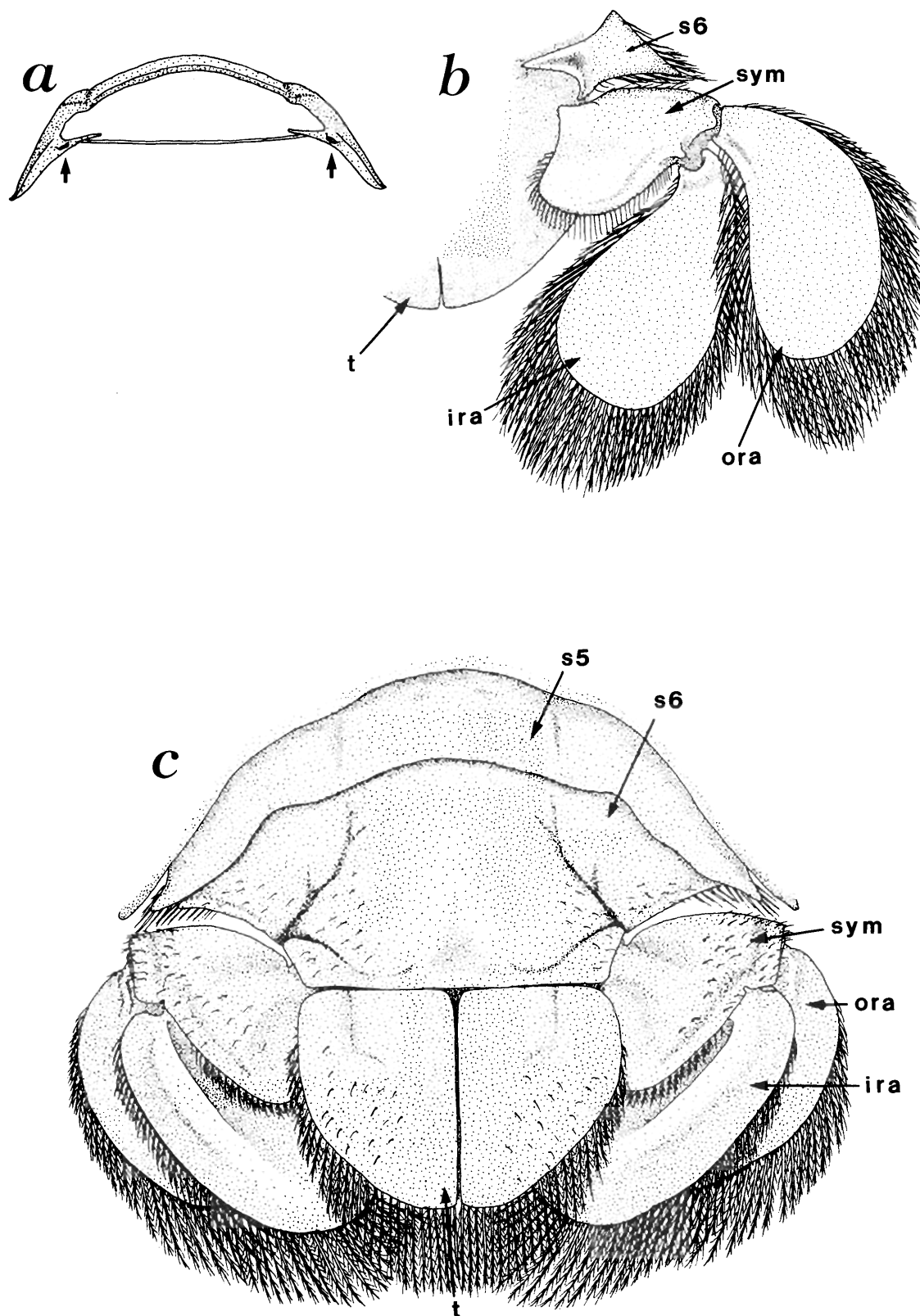
FIGURE 18.—Abdomen and telson of *A. uruguayana: a,* cross section through third abdominal somite, arrows indicate position of pleopod attachment; *b,* ventral view of telson and uropods; *c,* dorsal view of abdominal somites 5 and 6, telson, and uropods.

notch is present between the articulations of the inner (= dorsal) and outer (= ventral) rami. The posterior margin bears short plumose setae; the outer surface bears scattered, stout, simple, setae. The outer ramus (ora) and inner ramus (ira) are terminally rounded and slightly curved inward to function with the telson as a tailfan. The inner ramus has a slight medial ridge on its dorsal surface (Figure 18c). Both branches have numerous plumose setae on all borders. A border of short, small, movable spines is visible only in dorsal view under high magnification.

TELSON (Figure 18b,c).—The aeglid telson is a simple, broadly triangular, shield-like plate. It is typically divided by a single longitudinal suture (Figure 18c). This character has so often been associated with aeglids that several authors (e.g., Leach, 1821; Glaessner, 1969; Hobbs, Hobbs, and Daniel, 1977) use it as a distinguishing character of the family; indeed it is sometimes used in defining the superfamily Galatheoidea Samouelle (Glaessner, 1969). Although this condition is prevalent in aeglids, it is not a character shared by all members of the family. At least two species, *A. papudo* and *A. alacalufi,* have a telson with no longitudinal suture. In *A. alacalufi* there may be a small medial emargination on the posterior margin, but in *A. papudo* there is not (see Jara and López, 1981). As noted by Jara and López (1981), most authors have not mentioned the condition of the telson in other aeglid species, so the prevalence of this character (fused telson) is not known. The surface of the telson may be nearly smooth or granulate and with numerous, scattered, short, simple setae; in some specimens there may be shallow grooves or depressions. On the ventral surface of the telson, the anal aperture opens immediately posterior to a small, flat, subtriangular sclerite that may be a remnant of the sixth abdominal sternal plate.

## Discussion

The resemblance of the genus *Aegla* to members of the marine family Galatheidae is obvious. This resemblance is reflected in Latreille's (1818) original description of an aeglid as "*Galathea.*" Indeed, all subsequent workers have considered the Aeglidae part of the superfamily Galatheoidea, along with the families Galatheidae, Chirostylidae, and Porcellanidae (Figure 19). Although the galatheid genus *Munida* is illustrated in Figure 19, even closer similarities exist between aeglids and the galatheid genus *Munidopsis,* some species of which have shortened chelae and pereiopods creating an overall appearance much like *Aegla* (e.g., see Pequegnat and Pequegnat, 1970, figures 5-5, 5-8, 5-9). Characters shared by aeglids and galatheids include a well-developed rostrum, a large pyriform carapace wider posteriorly than anteriorly and with a distinct cervical groove, reduced chelate fifth pereiopod, subdivided telson (usually), and a dorso-ventral compression of the body (with exceptions among galatheids). These similarities no doubt precipitated Schmitt's (1942b:431) comment that the

nearest relatives of aeglids are probably among the galatheids. Almost certainly the other two families of galatheoids can be excused from ancestry or close relationship to aeglids; chirostylids are an aberrant, spindly, deep-water group usually associated with gorgonian corals, and porcellanids have undergone extreme brachyurization (Figure 19d) and do not closely resemble any of the other three galatheoid families.

The present investigation casts some doubt upon aeglid-galatheid affinities. First, the characters seeming to unite the two families are not shared apomorphies but are found in many other anomuran groups. A well-developed rostrum, a character used by Glaessner (1969) in defining the Galatheoidea, is in fact not shared by all galatheoids (porcellanids being the exception) but is common to lithodids, parapagurids, and thalassinoideans (sometimes considered anomurans; see Glaessner, 1969). Reduced chelate fifth pereiopods occur in nearly all of the Anomura and some Brachyura. A subdivided telson is known in some paguroids and coenobitoids (and is absent in some aeglids), and some dorso-ventral flattening of the cephalothorax and abdomen occurs in the Coenobitoidea, Paguroidea, and Hippoidea [see McLaughlin, 1983, for arguments for reuniting under one superfamily Paguroidea all families of hermit crabs]. A posteriorly-widened elongate carapace is not unique to the aeglids, galatheids, and chirostylids but is seen in lithodids, pomatochelids, pagurids, coenobitids, and parapagurids (see figures in Abele and Felgenhauer, 1982).

Second, and perhaps more important, is the occurrence in *Aegla* of several characters not found in any other members of the Galatheoidea. At least one of these characters, "eclosion from eggs," which is zoeal in galatheids but post-larval in aeglids, is likely coupled with the aeglid adaptation to a freshwater environment. Freshwater adaptation most likely does not explain the dorso-ventral compression of the body, as many decapod groups have invaded freshwater habitats without major modification of body form (e.g., cambarids, parastacids, atyids, pseudothelphusids, etc.). But by far the most striking character separating aeglids from galatheids is the presence in *Aegla* of weakly calcified lines that divide the carapace into discrete regions (Figure 2). Their presence is unexplained. Feldmann (1984) has observed, as have we, that these sutures increase somewhat the flexibility of the carapace; he then postulates a possible role in molting. We have observed several aeglids undergoing ecdysis and in no instance does the carapace split or widen along these lineae. This observation does not preclude the possibility of improved (faster or less traumatic) molting with a more flexible carapace, but does appear to lessen the advocated advantage these lineae might impart.

We have observed the function of some of the aeglid lineae in the laboratory. At certain times, occasionally during branchial grooming or aggressive encounters but often for no obvious reason, an aeglid will "inflate" the carapace with water and increase in apparent size. Involved are the linea aeglica

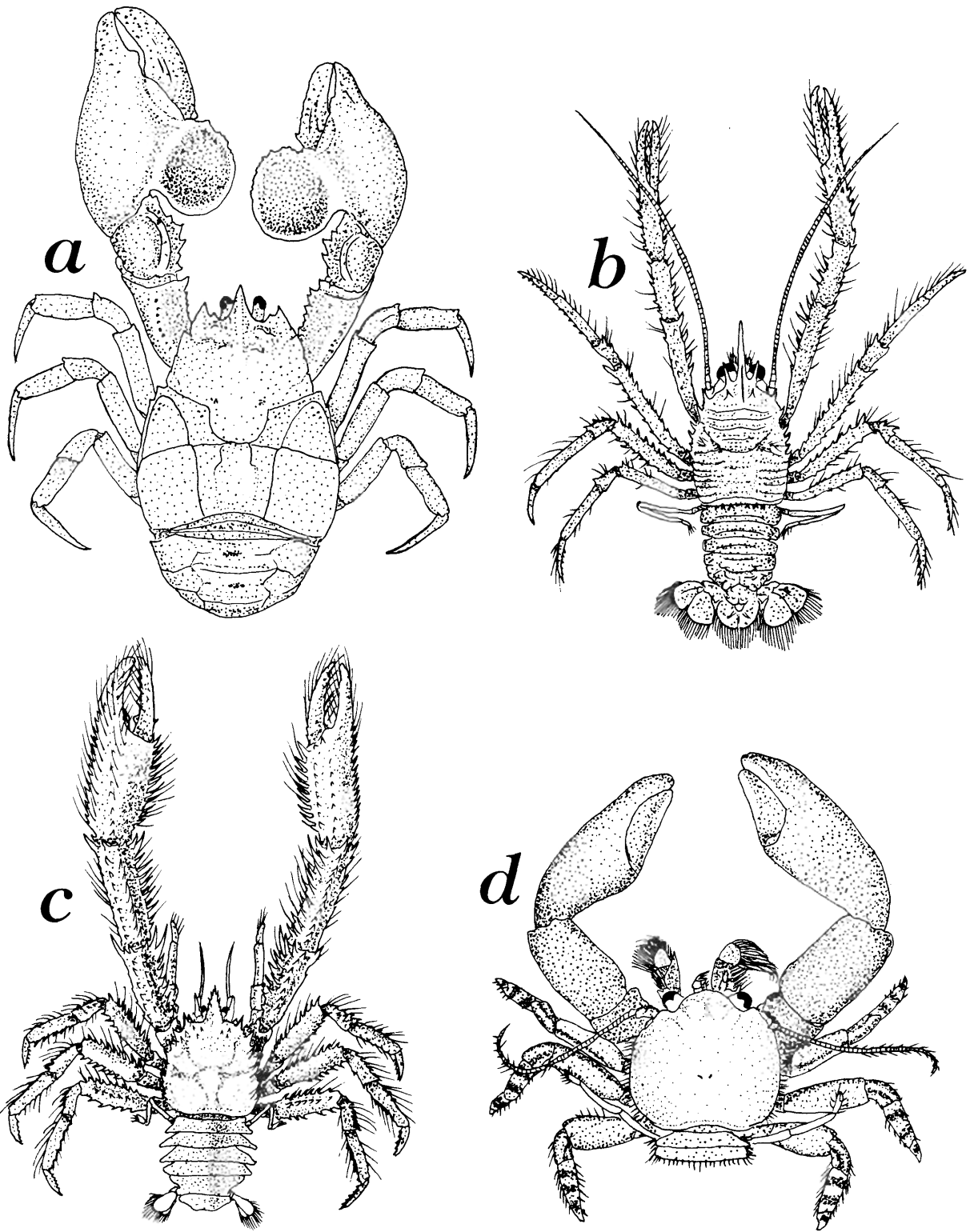FIGURE 19.—Representatives of the four families of the superfamily Galatheoidea Samouelle, 1819: *a, Aegla schmitti* Hobbs (Aeglidae) (after Hobbs III, 1979); *b, Munida curvipes* Henderson (Galatheidae) (after Benedict, 1902); *c, Uroptychus princeps* Benedict (Chirostylidae) (after Benedict, 1902); *d, Petrolisthes quadratus* Benedict, 1901 (Porcellanidae) (after Chace and Hobbs, 1969). Not drawn to scale.

posterioris, the posteroventral linea, and the posteroventral ossicles of the posterior carapace. The dorsum of the carapace does not change, at least not appreciably, but rather the lateral ventral regions rotate outward giving the impression of increased carapace height. This inflating is done usually when the aeglid is in a "standing" position with the thorax and abdomen not contacting the substrate. This observation, although interesting, does nothing to explain the presence of lineae across the pterygostomial, branchiostegal, and dorsal surfaces of the carapace. With this in mind, we turn to alternative explanations, i.e., possible phylogenetic significance of the aeglid lineae.

### GROOVES, SUTURES, AND LINEAE

Few decapod characters have received so much attention as have the external markings of the carapace. Yet our understanding of the significance of these features is poor. The various types of decapod carapace features (grooves, regions, spines, keels, and other sculptures) are discussed in Glaessner (1960, 1969). We shall limit our discussion to three terms employed in describing a linear furrow in the carapace: grooves, sutures, and lineae. "Groove" is used traditionally to describe infoldings or furrows of the carapace that do not extend through the carapace; i.e., they are irregularities rather than discontinuities of the carapace. Most common of such grooves is the cervical groove (cg, see Figures 2, 4a). Many authors, beginning perhaps with H. Milne Edwards (1851), Boas (1880), and Bouvier (1896), have erected classificatory schemes for the various grooves and often have attributed to them ontogenetic or phylogenetic importance. For example, H. Milne Edwards (1851), Huxley (1878), Glaessner (1960), and Secretan (1960) considered several of these grooves to represent ancestral somite boundaries (see discussion in Calman, 1909, and Glaessner, 1969). However, there is little agreement among students of decapod morphology about how much, if any, of the ancestral condition can be accurately interpreted from grooves in extant species. Various attempts to establish homologies of carapace grooves and some salient associated problems are discussed by Glaessner (1960, 1969). Adding to the uncertainty of meaning of these grooves is the excellent work of Albrecht (1981), which showed that, rather than being remnants of somite boundaries, some decapod carapace grooves are "mechanically induced secondary structures resulting from the attachment of different muscles to the carapace," reducing, of course, their value in reconstructing phylogenies.

Sutures and lineae differ markedly from grooves in that they are actual breaks in the calcification of the carapace. The terms often are used interchangeably (see McLaughlin, 1980, glossary), but because the common usage of "suture" often implies the joining of related parts (*The American Heritage Dictionary of the English Language*, 1980:1297) or is restricted to cirripeds (Moore and McCormick, 1969, glossary), we prefer

the Latin term "linea," which carries with it no such connotation. Lineae are much more consistent than are grooves in their form and occurrence in the Decapoda. For example, whereas grooves in the Brachyura are staggering in their diversity, all brachyurans possess a "pleural suture" (fide Glaessner, 1969; "pleural groove" of Pearson, 1908) that divides the pterygostomial region of the carapace and separates in molting. This same linea is known in all dromiid crabs as the linea dromica, and may be homologous to the linea homolica found in all the Homolidae.

In the Thalassinoidea there is a dorsal paired linea thalassinica extending from the anterior to the posterior border of the carapace in a more or less straight line. Its presence is only slightly less consistent than the above-mentioned lineae in that it is absent in the families Axiidae and Callianideidae (Abele and Felgenhauer, 1982) but is consistently present in the Axianassidae, Callianassidae, Laomediidae, Thalassinidae, and Upogebiidae.

The anomurans are supposedly characterized by the presence of a linea anomurica. This linea extends from the lateral margin of the antennal region in a fairly straight line posteriorly to the posterior border of the carapace. This linea anomurica is particularly obvious in the Galatheoidea—all galatheids, all chirostylids, and all porcellanids—but conspicuously absent in the aeglids. There is some confusion as to the true identity of the linea anomurica. Calman (1909) identified the linea anomurica with the linea dromica (as l. dromiidica) of dromiids and the "epimeral suture" of other Brachyura; Calman's figure 146 shows a *Callianassa* with both a linea thalassinica and a linea anomurica labeled. Yet according to Glaessner (1969) the linea thalassinica "may be comparable to the linea anomurica in Paguroidea, Galatheoidea (where it lies below the lateral margin), and Hippoidea," thus preventing the use of both terms in a single individual. In any case, the linea of galatheids is not at all similar to that of the pagurids, none of which possess the straight antenna-to-posterior-carapace linea of the galatheids.

Clearly, the homologies and even the terminology of the various decapod lineae are unresolved. We hope to examine the occurrence and ontogenetic development of these lineae in a future paper. The present paper serves to illustrate their infrequent previous use as a systematic character and their possible phylogenetic significance for the Anomura.

### ORIGIN OF *Aegla*

It has never been clear how much importance should be attributed to general morphological trends in the Decapoda. Convergence often obscures phyletic lineages and unites artificial groups having similar gross morphology (e.g., the now abandoned taxon *Macrura*). Yet the emerging pattern of lineae in decapod crustaceans is one of consistency. Where a

certain linea is present in a group, there are few or no exceptions. This makes more striking the uniqueness of the aeglids among the Galatheoidea, all of which, except *Aegla*, have a conspicuous linea anomurica. The complex system of lineae seen in *Aegla* (Figures 2–4) is not approached by any other member of that superfamily. By necessity our attention turns to non-galatheoid families to search for any carapace with similar subdivisions. We find that an almost identical system of uncalcified lines is seen amongst the hermit crabs.

We have not examined all families usually included under the heading "hermit crab" (see McLaughlin, 1983), but we have examined coenobitids, diogenids, and pagurids. In all three groups there is a linea, similar to the linea aeglica (Figure 4c), extending from the antennal region dorsally to an area that corresponds to the aeglid epibranchial tooth. This region, as in *Aegla*, is isolated by lineae from the remainder of the carapace. In both pagurids and coenobitids there is a pair of dorsal longitudinal lineae posterior to the cervical groove; these correspond to the dorsal longitudinal lineae of *Aegla*. The ventrolateral areas of the carapace of coenobitids, diogenids, and pagurids are subdivided into several loosely articulating ossicles, as in *Aegla*. In fact, for almost every linea found in *Aegla*, there is a correponding one found in the hermit crabs, so much so that the chance of these two groups (aeglids and hermits) being unrelated seems remote.

Our observations on this point are not new ones. Dana (1852) was aware of many such aeglid-hermit similarities and aeglid-galatheid differences and was apparently as amazed as we: "the transverse dorsal suture [our tdl, Figure 4a] of the carapax is strongly marked in the Paguridea and Aegleidea [sic], though faint or wholly wanting in the Galatheidea" (p. 429); also "it is not a little remarkable that the sutures [of *Aegla*] should be throughout almost identical with those of Pagurus described" (p. 431).

Evidence of similarity in carapace morphology, although strong, does not stand alone in uniting aeglids and hermit crabs. Aeglids tend to have an enlarged left chela, as do coenobitids; galatheids have symmetrical chelae. Some paguroids have trichobranchiate gills similar to those of *Aegla*, whereas to our knowledge all galatheids have phyllobranchiae. The chitinous teeth of the aeglid fifth pereiopod chela may be homologous to the sclerotized denticles of these appendages in hermits. Finally, although circumstantial, it may be significant that a large proportion of hermit crabs are supra-or intertidal and could easily become stranded in inland bodies of water during Cretaceous inundations and recedings. In contrast, most galatheids are subtidal or pelagic. We do not propose that aeglids stemmed from any such asymmetrical ancestor as the extant hermit crabs, but evidence for common ancestry seems convincing. We hope to follow this work with studies of a more traditional systematic nature.

# Appendix I

## Abbreviations and Lettering Used on the Figures

| | | | | |
|---|---|---|---|---|
| ab | arthrobranch | | lal | linea aeglica lateralis |
| ac | acicle (exopod of second antenna) | | lap | linea aeglica posterioris |
| aga | antennal gland aperture | | lav | linea aeglica ventralis |
| an1 | first antenna (antennule) | | lw | lateral wings of epistome |
| an1,f | foramen of first antenna | | | |
| an2 | second antenna | | m | merus |
| an2,f | foramen of second antenna | | ma | mesial articulation of mandible |
| ans | anus | | mbl | mandible |
| ar | articulation of mandible on maxillary bridge | | met | metastomal plate |
| as | anterolateral spine | | mh | marginal hinge of mandible |
| at | adductor testis ("tensor of branchial chamber roof") | | mr | marginal ridge of epistome (labral ridge, Snodgrass, 1952b) |
| | | | mth | mouth |
| b | basis of fifth pereiopod | | mxb | maxillary pleural bridge |
| bi | fused basi-ischium | | mx1 | first maxilla |
| bis | basi-ischial spine | | mx1,f | foramen of first maxilla |
| bl | bar linea | | mx2 | second maxilla (maxillule) |
| brl | branchial linea | | mx2,f | foramen of second maxilla |
| bs | basal segment of first antenna | | mxp1 | first maxilliped |
| | | | mxp1,f | foramen of first maxilliped |
| c | carpus | | mxp2 | second maxilliped |
| cd | crista dentata of third maxilliped | | mxp2,f | foramen of second maxilliped |
| cg | cervical groove | | mxp3 | third maxilliped |
| cor | cornea | | mxp3,f | foramen of third maxilliped |
| coxa | coxal segment (coxopodite) | | | |
| cr | carpal ridge of cheliped | | op | ocular plate |
| cs | corneous scales or tubercles of cheliped | | or | ocular ring (basal sclerites of eyestalk, Snodgrass, 1952b) |
| | | | ora | outer ramus of uropods |
| d | dactylus | | os | orbital spine |
| db | doublure of pterygostomial region of carapace | | | |
| de | distal endite | | p | propodus |
| dfl | dorsal flagellum of first antenna | | p(1–5) | pereiopod (1–5) |
| dll | dorsal longitudinal linea | | pb | pleurobranch |
| ds | distal segment of first antenna | | pc | palmar crest of cheliped |
| | | | pch | pumping chamber |
| en | endopod | | p1c | coxa of pereiopod 1 |
| ep | epipod (epipodite) | | pe | proximal endite |
| epg | epigastric prominence | | pg | paragnath |
| epst | epistome | | pgl | protogastric lobe |
| ept | epibranchial tooth | | pgp | posterior gastric pits |
| es | eyestalk | | pl | pleopod |
| es,f | foramen of eyestalk | | plp | palp of mandible |
| ex | exopod | | plr | remnant of male pleopod |
| | | | ppl | pleural plate |
| fl | flagellum | | ps | proximal segment of first antenna |
| fp | fracture plane | | ptg | pterygostomial groove in coxa of second antenna |
| | | | ptr | pterygostomial region of carapace |
| ga | genital aperture | | pvl | posteroventral linea |
| | | | pvp | posteroventral plate |
| i | ischium of fifth pereiopod | | | |
| ira | inner ramus of uropods | | r | rostrum |
| | | | | |
| la | linea aeglica | | s(1–6) | abdominal somite (1–6) |
| lab | labrum | | scaph | scaphognathite |
| lad | linea aeglica dorsalis | | sp | spoon-like lobe on coxa of male fifth pereiopod |

| | | | |
|---|---|---|---|
| srp | subrostral process | tdl | transverse dorsal linea |
| stl | sternum of first abdominal segment | th(1–8) | sternum of thoracic somite (1–8) |
| sym | sympod (basal segment of uropods) | | |
| | | vas | vas deferens |
| t | telson | vfl | ventral flagellum of first antenna |

# Appendix II

# List of the Known Species and Subspecies of the Aeglidae

(Most information is from the literature. All size measurements are of the cephalothorax,
inclusive of the rostrum. References are not exhaustive.)

## Museum Abbreviations for Type Depositions

| | | | |
|---|---|---|---|
| Acad. Nat. Sci. | Academy of Natural Sciences, Philadelphia, Pennsylvania, USA | MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA |
| AR | Collections of the Paleontology Section of the New Zealand Geological Survey, Lower Hutt, New Zealand | MFZB | Museu de Ciências Naturais da Fundação Zoo-Botânica do Estado do Rio Grande do Sul, Porto Alegre, Brazil |
| DZ.UFRGS | Departamento de Zoologia da Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil | MLP | Museo de La Plata, Buenos Aires, Argentina |
| Field Museum | Field Museum of Natural History, Chicago, Illinois, USA | MNHN | Museo Nacional de Historia Natural y Centro de Investigaciones Zoológicas de la Universidad de Chile |
| INICN | Sección Protozoología e Invertebrados del Instituto Nacional de Investigación de las Ciéncas Naturales, Buenos Aires, Argentina | MUZUC | Museo Zoológico, Universidad de Concepción, Chile |
| IZFML | Instituto de Zoología de la Fundación Miguel Lillo, Tucumán, Argentina | MZUSP | Museu de Zoológia da Universidade de São Paulo, Brazil |
| IZUA | Instituto de Zoología, Universidad Austral de Chile | NMG | Naturhistorisches Museum, Genf, Switzerland |
| MACN | Museo Argentino de Ciéncias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina | SMF | Senckenberg-Museum, Frankfurt, Germany |
| | | USNM | Collections in National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA |

## Annotated List of Species and Subspecies

### *Aegla abtao abtao* Schmitt, 1942a

Type-locality:  Abtao, Chile.

Type material:   Holotype (USNM 79079) is a 26.6 mm male, the largest of a lot of 5 males and 2 females collected in February, 1919.

Range:   Type-locality, "Falls of Petrohue," Chile, "El Valean" (= El Volcán; Haig, 1955:30), Santiago, Chile (Schmitt, 1942b) to Abtao, Province of Llanquihue, Chile. Bahamonde and López (1963:132) and Haig (1955:30) list additional records for Chile. Ringuelet (1960b:237) discusses geographic variation.

No. of specimens:   Described from 7 specimens (5 males, 2 females) collected in February, 1919. Two additional specimens, with slight differences from the type series, from the above two localities (one each). Many more specimens listed from Chile by Bahamonde and López (1963).

Size range:   11–28.0 mm.

Remarks:   Ringuelet (1948b) first recognized that *A. riolimayana* was a subspecies of *A. abtao* and erected the subspecies *A. a. riolimayana* for the former; the name *A. a. abtao* was used first in a later paper (Ringuelet, 1960b).

References:   Schmitt, 1942a:30, pl. 5: fig. 2; 1942b:510, fig. 63, pl. 28F,G.—Haig, 1955:30.—Ringuelet, 1960b:237.—Bahamonde and López, 1963:132.—Retamal, 1981:21, fig. 86.

### *Aegla abtao riolimayana* Schmitt, 1942b

Type-locality:   Rio Limay, boundary between the territories of Rio Negro and Neuquén, Argentina.

Type material:   Holotype (USNM 80025) is the largest of 5 males collected in November, 1903; it measures 23.5 mm.

Range:   Known from the Rio Limay in the vicinity of Lago Nahuel Huapi or from the lake itself (Schmitt, 1942b). Additional records are known from Argentina (Ringuelet, 1948b) (Lake Nahuel Huapi and vicinity, including Rio Limay, Rio Ñirihuau, Lago Frías, Lago Moreno, and Collon Cura) and Chile (Bahamonde and López, 1963). See also remarks under *A. abtao abtao*.

No. of specimens:   In addition to the five males that constitute the type series, Schmitt (1942b) was aware of about 25 other specimens from the same area, three of which belong to the Museo Argentino (MACN 9679, 2 females; MACN 8388, 1 male). Additional specimens were reported by Ringuelet (1948b, 37 specimens) and Bahamonde and López (1963).

Size range:   Males 8.5–24 mm; females 10–20.5 mm.

Remarks:   Schmitt (1942b) erected the species *A. riolimayana* and noted that it was very similar to *A. abtao,* differing only in the shape of the areola. Ringuelet (1948b) first considered the two forms to be subspecies of *A. abtao.* Lopretto (1979) lumped this species in the grouping "patagonico" along with *A. neuquensis neuquensis* on the basis of the fifth pereiopod. See also remarks under *A. abtao abtao* above.

References:   Schmitt, 1942b:513, fig. 64, pl. 28E.—Bahamonde and López, 1963:132.—Ringuelet, 1948b:319, pls. 7, 12 (as *A. riolimayana*).—Lopretto, 1979:9, figs. 5, 6, 8.—Retamal, 1981:21, fig. 84. Possibly *?A. abtao* of Schmitt (1942a).

### *Aegla affinis* Schmitt, 1942b (see *A. neuquensis affinis*)

### *Aegla alacalufi* Jara and López, 1981

Type-locality:   Brook at Puerto Henry, Madre de Dios Island (50°01'10"S,

75°18′45″W), Ultima Esperanza, Chile.

Type material: Holotype (IZUA C-471-1) is a 10.6 mm male collected in October, 1972. Allotype (IZUA C-471-2, a 9.5 mm female) and paratypes (IZUA C-471-3, MUZUC 16352, 2 males; IZUA C-471-4, C-471-5, MUZUC 16353, 4 females) with same collecting data.

Range: Known only from the type-locality.

No. of specimens: Jara and López (1981) mentioned only the 8 specimens in the type series.

Size range: 8.5–10.6 mm (Jara and López, 1981).

Remarks: This interesting species has no longitudinal suture along the midline of the telson, a character that Leach (1821) and Hobbs, Hobbs, and Daniel (1977) use as a generic (familial) character. Only one other species, *A. papudo,* also has an undivided telson plate; Jara and López (1981) tentatively suggest a relationship between the two species. Their record extended the known range of the aeglids about 400 km to the south.

Reference: Jara and López, 1981:88, fig. 1.

## *Aegla araucaniensis* Jara, 1980b

Type-locality: Arroyo Quinchaco, 6.5 km southwest of Paillaco, Valdivia Province, Chile.

Type material: Holotype (IZUA C-394-1) is a 22.9 mm male collected in November, 1975. Allotype (IZUA C-394-2, an ovigerous female) and paratypes (IZUA C-394-3 and 394-4, 2 males) with same locality data.

Range: Known only from the basin of the Rio Valdivia, Chile. (Collecting localities include the Rio Cruces, Rio Futa, and Rio Calle Calle within the Valdivia system.)

No. of specimens: Jara (1980b) examined 232 males, 192 females, and 113 juveniles (deposited in the IZUA) in addition to the type series.

Size range: Adult males 8.0–29.6 mm; females 8.0–20.4 mm; juveniles 4.3–10.5 mm (Jara, 1980b).

Remarks: This species is similar to *A. denticulata* and *A. rostrata* in the serrated carapace borders and in general carapace morphology.

Reference: Jara, 1980b:255, fig. 1.

## *Aegla bahamondei* Jara, 1982

Type-locality: Tucapel River, 5 km north of Cañete City, to the side of P-60-R national road (37°44′09″S, 73°22′53″W), Cordillera de Nahuel-buta, Chile.

Type material: Holotype (IZUA C-296) is a 20.8 mm male collected in December, 1974. Allotype (IZUA C-296, 18.9 mm female) and paratypes (IZUA C-296, 12 males and 8 females) with same collecting data.

Range: Known only from the type-locality and from Caramávida, 6 km north of type-locality in lowest part of Caramávida River, a tributary of the Tucapel (Jara, 1982).

No. of specimens: Jara (1982) listed only the 22 specimens in the type series.

Size range: 14.2–24.0 mm (Jara, 1982).

Remarks: This species is similar in many respects to *A. denticulata, A. rostrata,* and *A. singularis.* Jara (1982) stated that it is closely related to *A. rostrata.*

Reference: Jara, 1982:232, fig. 1.

## *Aegla camargoi* Buckup and Rossi, 1977

Type-locality: Rio Silveiras, Município de Bom Jesus, Rio Grande do Sul, Brazil.

Type material: Holotype (DZ.UFRGS 00119H) is a 15 mm male collected in October, 1975. Paratypes (DZ.UFRGS 00119P) comprise 5 males and 5 females from the same locality and date.

Range: Known only from the type-locality (Buckup and Rossi, 1977).

No. of specimens: Buckup and Rossi (1977) listed only the type series (above).

Size range: The holotype male is 15 mm; a typical female 17 mm.

Remarks: This species is similar to the sympatric *A. leptodactyla* and to *A. parana* with respect to spination on the ambulatory legs.

Reference: Buckup and Rossi, 1977:887, fig. 4.

## *Aegla castro* Schmitt, 1942b

Type-locality: Rio Iapó, Paraná, Brazil.

Type material: Holotype (USNM 80020) is a 28.5 mm male, the largest of a lot of "nearly 200" specimens. Paratypes (MCZ 12313, 1 male and 1 female) with same collection data.

Range: Known only from the general region of Castró, Paraná, Brazil, "chiefly in the Rio Iapó near the town, and for some distance up and down stream" (Schmitt, 1942b).

No. of specimens: Nearly 200, "about equally divided between males and females," collected in October, 1925.

Size range: Largest specimen is the male holotype, 28.5 mm.

Remarks: This species is very similar to *A. odebrechtii,* but differs in respect to spination of the dorsal anterior epimeral angles, rostral carina and carpal ridge.

Reference: Schmitt, 1942b:473, fig. 50, pl. 26F.

## *Aegla cavernicola* Türkay, 1972

Type-locality: Grutas das Areias, São Paulo, Brazil.

Type material: Holotype (NMG, no number given) is an ovigerous female of 15.0 mm collected in 1968.

Range: Known only from the type-locality.

No. of specimens: One known specimen (holotype).

Size range: Unknown; holotype is 15.0 mm.

Remarks: The cornea in this troglobitic species is tapered and more reduced than in any other species of *Aegla,* undoubtedly because of the habitat (taken from a freshwater basin with a slight current more than 300 m within the cave).

References: Türkay, 1972:415, fig. 1, pl. 1: figs. 1, 2.—Hobbs, Hobbs, and Daniel, 1977:142, fig. 66.

## *Aegla concepcionensis* Schmitt, 1942a

Type-locality: "Near Concepción, Chile" (Schmitt, 1942b).

Type material: Holotype (USNM 79078) is a 33.0 mm male collected in January, 1927; paratype (MCZ 12314) is a single male with same collection data; 3 additional specimens (MCZ 10481) known by Schmitt (1942b).

Range: Type-locality and Corral, Chile (Schmitt, 1942b); Rio Tronco, Province de Colchagua (Bahamonde and López, 1963); Chiloé Island, Chile (Haig, 1955).

No. of specimens: "About 30" (Schmitt, 1942a), collected in January, 1927; includes 3 specimens at MCZ (10481), and 2 males seen by Schmitt and presumably deposited in the USNM (Schmitt, 1942b:504). Additional specimens listed by Haig (1955) and Bahamonde and López (1963) (MNHN 2249, 2346).

Size range: Largest is a 33 mm male (holotype); most considerably smaller.

Remarks: This Pacific-form species is very similar to *A. laevis,* and similar to *A. papudo* and *A. affinis* in the lack of an orbital spine.

References: Schmitt, 1942a:26, pl. 5: fig. 1; 1942b:501, fig. 60, pl. 28A.—Haig, 1955:29.—Bahamonde and López, 1963:133.—Retamal, 1981:21, fig. 82.

## *Aegla denticulata* Nicolet, 1849

Type-locality: "Found in the republic of Chile;" neotype material from Osorno, Chile.

Type material: Neotype (USNM 80021) is a 27 mm male, in a lot of 10 males and 2 females.

Range: Osorno, Chile (Schmitt, 1942b); Rio Llollelhue, La Unión; Cocule, La Unión; Llancancura, en Rio Bueno; Rio Bueno (Bahamonde and López, 1963).

No. of specimens: Twelve (10 males, 2 females) known, collected in March, 1919. Additional specimens listed by Bahamonde and López (1963).

Size range: 14.5–31.0 mm (both males of Schmitt, 1942b).

Remarks: This remarkable species differs from all other aeglids in having a very long rostral carina extending along the carapace far posteriorly and

in having strong serrations along the anterolateral borders of the branchial region.

References: Nicolet, 1849:200; 1854, pl. 2: fig. 1.—Girard, 1855:255.—Rathbun, 1910:602.—Schmitt, 1942b:480, fig. 53, pl. 26c.—Bahamonde and López, 1963:133.—Retamal, 1981:20, fig 80.

### *Aegla franca* Schmitt, 1942b

Type-locality:  Franca, State of São Paulo, Brazil.

Type material:  Holotype (USNM 80019) is a 24.0 mm male.

Range:  Known from the type-locality and from Siambón, Departamento Tafí, Tucumán; Vipos, Tucumán; Tafí del Valle, Tucumán; Rio de la Quinta, El Suncho, Tucumán; Quebrada de Lules, Tucumán; Corralito, Departamento Trancas, Tucumán; Rio Cochuna, Tucumán; and Tacanas, Departamento Trancas, Tucumán, Argentina, south to the province of Catamarca, Argentina (Schmitt, 1942b; Ringuelet, 1949a; Williamson and Martinez Fontes, 1955).

No. of specimens:  10 males, collected in October, 1910, were known to Schmitt (1942b); Ringuelet (1949a:30) listed an additional 15 males, 6 females, and 9 juveniles from Tucumán, Argentina; and Williamson and Martinez Fontes (1955:59) reported 27 males and 7 females from the vicinity of La Chacra, Andalgalá, Catamarca, Argentina (INICN 7812).

Size range:  18.0–31.9 mm (Ringuelet, 1949a; Williamson and Martinez Fontes, 1955).

Remarks:  This is an Atlantic drainage species, but the rostrum is very similar to the "Pacific form" aeglids. Schmitt (1942b) considered this species and *A. jujuyana* possible transitional morphologies between "ridge-roofed" rostrums and rostrums that are longitudinally troughed or excavate on either side of the rostral carina (Pacific form).

References:  Schmitt, 1942b:476, fig. 51, pl. 26D.—Ringuelet, 1949a:30, figs. 1, 6, pls. 6, 7.—Williamson and Martinez Fontes, 1955:55.

### *Aegla franciscana* Buckup and Rossi, 1977

Type-locality:  São Francisco de Paula, Rio Grande do Sul, Brazil.

Type material:  Holotype (MFZB 00505H) is a 19 mm male. Paratypes (MFZB 00262P) comprise 3 males and 10 females; all type material collected in January, 1961.

Range:  Known only from the type-locality.

No. of specimens:  Buckup and Rossi (1977) mentioned only those specimens in the type series (above).

Size range:  Only the size of the male holotype (19 mm) given.

Remarks:  This species is similar to *A. plana* with respect to the carpal crest and shape of the carapace.

Reference:  Buckup and Rossi, 1977:890, fig. 6.

### *Aegla humahuaca* Schmitt, 1942b

Type-locality:  Humahuaca, Jujuy, Argentina.

Type material:  Holotype (MACN) is a 28.0 mm male, the largest of four males in that lot.

Range:  Known from the type-locality and from Tilcara, Jujuy; Rio Toro en El Gólgota, Salta; Rio San Antonio, San Antonio de los Cobres, Salta; and Rio Salado, Santiago del Estero; Argentina (Ringuelet, 1949a). Schmitt (1942b) noted the presence in the MACN of a fifth specimen lacking collecting data.

No. of specimens:  Four males, collection date not given, and one additional male (noted above) known to Schmitt; Ringuelet (1949a:25) listed an additional 11 males and 4 females from Argentina.

Size range:  17.5–30 mm (Schmitt, 1942b; Ringuelet, 1949a).

Remarks:  This species is very similar to *A. jujuyana,* but differs in the presence of a palmar crest and a bluntly ridged rostrum in *A. humahuaca.* The two species occur in the same general area ("scarcely more than 70 miles apart") but the areas differ substantially in the amount of annual rainfall received.

References:  Schmitt, 1942b:498, fig. 59, pl. 27D.—Ringuelet, 1949a:25, figs. 2c, 3e,f, 4e–g, 5c–e, pls. 4, 5.

### *Aegla intermedia* Girard, 1855

Type-locality:  "the upper affluents of the Rio de Maypu, 2,000 feet above the level of the sea, near Santiago" (Chile).

Type material:  Unknown; presumably lost.

Range:  Known only from the type-locality.

No. of specimens:  Girard (1855:254) mentioned "upwards of twenty-five specimens, including both sexes" upon which he based his description. No other specimens have been taken since that time.

Size range:  Unknown.

Remarks:  This species has not been collected since the original description in 1855. Schmitt (1942b) noted some similarities between *A. intermedia* as described by Girard and *A. castro* and *A. denticulata.*

References:  Girard, 1855:255.—Schmitt, 1942b:436, 448 (footnote).—Haig, 1955:28 (not *A. intermedia* of Moreira, 1901:23, which = *A. odebrechtii odebrechtii;* see Schmitt, 1942b:431).—Retamal,1982:21.

### *Aegla jujuyana* Schmitt, 1942b

Type-locality:  Rio Chico, Jujuy, Argentina.

Type material:  Holotype (MACN 16237) is the largest of three males collected in 1925.

Range:  Known only from the type-locality by Schmitt (1942b), it has since been reported from the Rio Grande en Reyes, in Tilcara, in the Rio Grande, and in Perico del Carmen, Jujuy, Argentina (Ringuelet, 1949a).

No. of specimens:  Described from three specimens; collection data not given. Ringuelet (1949a) recorded an additional male and female (MACN 16071) and 14 males and 8 females (MLP 74, 75, 77, 78) from Argentina.

Size range:  18.0–29.0 mm (Schmitt, 1942b); Ringuelet (1949a) gave a range of 18.5–28.4 mm for his additional specimens.

Remarks:  Although this species has an "Atlantic form" rostrum, Schmitt (1942b) felt that this species and *A. franca* were transitional between the two "forms" of aeglids. It resembles *A. humahuaca* except for the sharply carinated rostrum and absence of a palmar crest in *A. jujuyana.*

References:  Schmitt, 1942b:478, fig. 52, pl. 26E.—Ringuelet, 1949a:19, figs. 3a–c, 4a–d, 5a,b, 7a–g, pl. 3.

### *Aegla laevigata* (Latreille, 1818)

Incorrect translation of the French common name for *Aegla laevis,* according to Schmitt (1942b). The name appears in Milne Edwards and Lucas (1844:34).

### *Aegla laevis laevis* (Latreille, 1818)

Type-locality:  Neotype chosen from a lot collected "dans une riviere pres de St. Iago-de-Chile," collector and date unknown (Schmitt, 1942b).

Type material:  Neotype (MCZ 10479, incorrectly listed as 10478 in Schmitt, 1942b:507) is a 24 mm male, one of a lot (MCZ 12311) of 14 males and 17 females (12 ovigerous); paratype (MCZ 12310) is single male from same lot.

Range:  Talagante; El Monte; Isla de Maipo; Rio Maipo; from near Melipilla, Province of Santiago, Chile; probably common throughout most of Chile (see Bahamonde and López, 1963).

No. of specimens:  Described from a lot of 31 specimens; many more reported since (e.g., see Bahamonde and López, 1963:133).

Size range:  Largest reported is a 24.5 mm male.

Remarks:  This species is surrounded by much taxonomic confusion (see Schmitt, 1942b). Schmitt (1942b) recognized subspecies (*A. l. laevis* and *A. l. talcahuano*) but continued to refer to the original subspecies as *A. laevis* rather than *A. l. laevis.* Ecology of the species in El Monte, Chile, was described by Bahamonde and López (1961), and albinism was discussed by López (1959) and Bahamonde and Atria (1976). Live specimens of this species were returned to California by Burns (1972).

References:  Girard, 1855:255.—Rathbun, 1910:602.—Schmitt, 1942b:504, fig. 61, pl. 28D.—Haig, 1955:30.—Bahamonde and López, 1961:19; 1963:133.—Retamal, 1981:21, fig. 83. See Schmitt (1942b) for possible further references to, and specimens of, this species.

## *Aegla laevis talcahuano* Schmitt, 1942b

Type-locality: Talcahuano, Chile.

Type material: Holotype (MCZ 12312) is a 23.0 mm male taken from a lot of *A. papudo* (MCZ 10480) at the Museum of Comparative Zoology. Paratypes (MCZ 10483, 2 males) lack locality data.

Range: Known from the type-locality and from specimens without locality data (MCZ 10483) (Schmitt, 1942b); Rio Zamorano en Requegua; the vicinity of Santa Cruz; Constitución; Guaraculén near San Carlos; Itahue near Curico; Rio Ñuble, Chillán; Concepcion (Chile) (Bahamonde and López, 1963).

No. of specimens: Described from four specimens. Additional specimens listed by Bahamonde and López (1963).

Size range: 14.0–23.0 mm.

Remarks: Schmitt (1942b) was hesitant in proposing this subspecies as it differs only slightly from true *A. laevis laevis*.

References: Schmitt, 1942b:508, fig. 62, pl. 28B,C.—Haig, 1955:30.—Bahamonde and López, 1963:134.—Retamal, 1981:21, fig. 85.

## *Aegla lenitica* Buckup and Rossi, 1977

Type-locality: Banhado do Taim, Município de Rio Grande, Rio Grande do Sul, Brazil.

Type material: Holotype (DZ.UFRGS 00087H) is a 14 mm male collected in June, 1975. Paratypes consist of 10 males and 14 females from the same date and locality (DZ.UFRGS 00087P). Buckup and Rossi (1977) also mention one female specimen (MFZB 00269) in a different collection from the same area (Pelotas, Rio Grande do Sul).

Range: Known only from the Rio Grande do Sul, Brazil.

No. of specimens: Only 15 mentioned in the original description.

Size range: Male holotye is 14 mm; females up to 15 mm (Buckup and Rossi, 1977).

Remarks: This species is similar to the Uruguayan *A. prado* and the Argentine *A. singularis*, and also to *A. platensis* and *A. uruguayana*. Differences were noted by Buckup and Rossi (1977).

Reference: Buckup and Rossi, 1977:880, fig. 1.

## *Aegla leptodactyla* Buckup and Rossi, 1977

Type-locality: Rio Silveiras, Município de Bom Jesus, Rio Grande do Sul, Brazil.

Type material: Holotype (DZ.UFRGS 00117H) is a 16 mm male. Paratypes (DZ.UFRGS 00117P) comprise 3 males and 12 females; all type material collected in October, 1975.

Range: Known only from the type-locality.

No. of specimens: Buckup and Rossi (1977) mentioned only the type series (above).

Size range: Male holotype is 16 mm; "typical" female 22 mm.

Remarks: Buckup and Rossi (1977) noted the similarity between this species and *A. denticulata* from Chile. The species is distinguished from *A. denticulata* and from other species by the marked spination of the cheliped carpus, the strong convexity of the carapace, and the small size of the chelae.

Reference: Buckup and Rossi, 1977:888, fig. 5.

## *Aegla manni* Jara, 1980b

Type-locality: Arroyo Buenaventura (fundo Buenaventura), 13.5 km east of Valdivia (39°48'20"S, 73°09'49"W), Valdivia province, Chile.

Type material: Holotype (IZUA C-441) is a 24.9 mm male collected in March, 1977. Allotype (IZUA C-441, 18.3 mm female) and paratypes (IZUA C-441, 16 males and 2 females) with same collecting data.

Range: Known only from the type-locality.

No. of specimens: In addition to the type series, Jara (1980b) examined 34 males, 14 females and 1 juvenile from the type-locality (deposited in the IZUA).

Size range: Adult males 10.8–25.2 mm; females 12.0–18.7 mm; one 7.7 mm juvenile known (Jara, 1980b).

Remarks: The rostrum is similar to species having the Atlantic form of Schmitt (1942b). The species is similar to *A. maulensis* in many characters.

Reference: Jara, 1980b:259, fig. 2.

## *Aegla maulensis* Bahamonde and López, 1963

Type-locality: Laguna del Maule, Chile.

Type material: Holotype (MNHN 2011) is a female collected in April, 1956; paratypes (MNHN 2111, 2267, 2289) obtained from the stomach of a salmon (*Salmo gardnieri irideus*).

Range: Known only from the type-locality.

No. of specimens: Bahamonde and López (1963) listed only the holotype and the three paratypes listed above.

Size range: Unknown (sizes not given in original description).

Remarks: This species resembles *A. affinis*.

Reference: Bahamonde and López, 1963:135, pl. 1: figs. 1–6.—Retamal, 1981:21, fig. 87.

## *Aegla montana* Ringuelet, 1960b

Type-locality: El Sosneado, Province of Mendoza, northeast Argentina.

Type material: Holotype (MLP collections 86) is a 32.5 mm male. The paratype series consists of 4 males, same collection data.

Range: Known only from the type-locality.

No. of specimens: Ringuelet (1960b) listed only the five specimens listed above.

Size range: 21.2–37.0 mm.

Remarks: Ringuelet (1960b) noted similarities between this species and *A. neuquensis neuquensis*, *A. n. affinis*, and *A. squamosa* (originally described as *A. scamosa*).

References: Ringuelet, 1948b:323, pl. 8: figs. 3, 6–12, pl. 13 (as *Aegla* spec.); 1960b:231, fig. 1.—Lopretto, 1978b:57, figs. 1–3, 8.

## *Aegla neuquensis affinis* Schmitt, 1942b

Type-locality: Unknown; described from single male specimen found in a bottle in the Museo Argentino Ciéncias Naturales.

Type material: Holotype is a male (MACN 98170) and an unattached left cheliped (MACN 4186) (see Schmitt, 1942b:498).

Range: According to Ringuelet (1948b) this subspecies is found from the north of the Neuquén Territory to the Province of Salta, Argentina. Ringuelet (1949a) listed specimens from the northern territory of Neuquén and the Rio Arenales in Salta, Argentina, and Ringuelet (1960a) noted the presence of this subspecies in Tupiza, Bolivia.

No. of specimens: One male, found preserved (see above). Ringuelet (1948b, 1949a) listed additional material from the Rio Arenales in Salta and from Departamento Yavi, Jujuy, Argentina and Ringuelet (1960a) listed 44 males and 9 females from Bolivia.

Size range: 20.5–31.0 mm (Schmitt, 1942b; Ringuelet, 1949a).

Remarks: Schmitt (1942b) mentioned that this species and only one other, *A. papudo*, have the suture lines of the anterolateral angles of the cardiac region combine to form a "short, quite longitudinally oriented bar. In all other species except these two this short 'bar' is oriented so as to be very nearly transverse, or at least obliquely so." Ringuelet (1948b) first considered *A. affinis* a subspecies of *A. neuquensis*. Lopretto (1980a) placed this species in her "platensis" group along with *A. platensis*, *A. singularis*, and *A. uruguayana*.

References: Schmitt, 1942b:495, fig. 58, pl. 27F (as *A. affinis*).—Ringuelet, 1948b:312, pl. 8: figs. 1, 2, 4, 5, pl. 10; 1949a:34, figs. 3d, 5f, 7h–k, pl. 8; 1960a, fig. 1.—Lopretto, 1980a:37, figs. 1–3, 9.—Feldmann, 1984, fig. 6 (as *A. affinis*, photo of USNM 176807).

## *Aegla neuquensis neuquensis* Schmitt, 1942b

Type-locality: Arroyo, Territory of Neuquén, Argentina.

Type material: Holotype (USNM 80024) is the second largest (29.0 mm) male of a lot of 4 males and 1 female.

Range: Schmitt (1942b) mentioned a lot of 5 males and 1 female from another locality in the Neuquén Territory; specific site data were illegible. Ringuelet (1948b) noted its occurrence in the extreme southwest of Chubut (46°S Lat) and in the east of the Neuquén Territory, Rio Negro, near Pomona in the Choele-Choel zone, Argentina.

No. of specimens: Described from two lots containing a total of 9 males and 2 females, both collected in November, 1903. Ringuelet (1948b) listed over 100 specimens in 12 additional collections (MLP 67–70, 79–82, 85, 94, 96, 97) from Argentina.

Size range: 17.5 to "at least 30 mm" (Schmitt, 1942b). Ringuelet (1960a) reported sizes from 16.5 to 23.5 mm for the subspecies *A. n. affinis*.

Remarks: The species *A. neuquensis* was divided into two subspecies by Ringuelet (1948b). However, there is some confusion as to the status of the original *A. affinis*. According to Ringuelet (1948b:301), the holotype of *A. affinis* is actually an individual of *A. neuquensis* (MACN 25688), yet he recognizes both subspecies *A. n. neuquensis* and *A. n. affinis*. Lopretto (1979), in a study of the fifth pereiopod of Argentine aeglids, lumped this species with *A. abtao riolimayana* in the grouping "patagonico."

References: Schmitt, 1942b:493, fig. 57, pl. 27E (as *A. neuquensis*).—Ringuelet, 1948b:301, 311, pl. 9.—Lopretto, 1979:9, figs. 1–4, 7.

### *Aegla odebrechtii odebrechtii* Müller, 1876

Type-locality: Neotype from Santa Catharina, Brazil. Müller's holotype locality unknown.

Type material: Neotype (USNM 80022) is a 28 mm male collected in 1904.

Range: Known from Santa Catharina, Brazil.

No. of specimens: In addition to the single male neotype, Schmitt (1942b) was aware of only 8 other specimens also from Santa Catharina, and one "quite typical male belonging to the Academy of Natural Sciences of Philadelphia (no. 484, pt.)."

Size range: 13.5–28 mm.

Remarks: Schmitt (1942b) proposed a subspecies for one form of *A. odebrechtii* but continued to designate the original form *A. odebrechtii* rather than *A. o. odebrechtii*. This species is "the one east South American form that seems most to resemble those inhabiting the slopes of the Andes" (Schmitt, 1942b:489).

References: Schmitt, 1942b:487, fig. 55, pl. 27A.—Moreira, 1901:23 (as *A. intermedia* Girard).—Müller, 1876:13.

### *Aegla odebrechtii paulensis* Schmitt, 1942b

Type-locality: Alto da Serra do Cubatão, between Santos and São Paulo, Brazil.

Type material: Holotype is the second largest male of a lot of 4 males and 3 females, USNM 80023, collected in April, 1935.

Range: Known from the type-locality and from small streams and a pool in the "Reserva Forestal y Estación Biologica Experimental que el Departamento de Botanico de la Secretaria de Agricultura, Estado de São Paulo, tiene en Alto da Serra, fronte a Paranapiacaba" (23°47′S, 46°18′W) about 32 km from São Paulo, Brazil (López, 1965). Schmitt (1942b) listed questionable material from additional localities also in Brazil.

No. of specimens: Only the 7 specimens of the type series were known to Schmitt (1942b); other questionable material could not be definitely consigned to this subspecies. López (1965) examined 1,051 specimens in a study of the ecology of this species in Brazil.

Size range: López (1965) examined specimens from 1.6 mm up to 22.5 mm.

Remarks: This species is very similar to *A. o. odebrechtii*, so much so that Schmitt (1942b:492) stated: "It is possible that I have set up one form too many in naming this subspecies." López (1965) conducted a rather thorough study of the ecology of this species, and noted similarities in the biology of this species and *A. l. laevis*.

References: Schmitt, 1942b:490, fig. 56, pl. 27B.—López, 1960:37; 1965:301.—Luederwaldt, 1919:431.

### *Aegla papudo* Schmitt, 1942b

Type-locality: Papudo, Chile.

Type material: Holotype (Field Museum 2285) is the largest male (26.0 mm) of a lot of 14 males and 6 females (1 ovigerous). Paratypes exist at the Field Museum (2286) and MCZ (10480).

Range: Known from the 20 original specimens from Papudo and from 4 specimens from Talcahuano, Chile (MCZ 10480). Schmitt (1942b) listed an additional specimen possibly belonging to this species from the Rio Mapocho, near Talagante, Santiago, Chile, and two additional dried specimens in the Academy of Natural Science, Philadelphia. Known also in Chile from Illapel; San Alfonso, near Zapallar; Putaendo; Rio Aconcagua, near Llayllay; Ocoa (Bahamonde and López, 1963) and from Viña del Mar, Parque Vergara (Haig, 1955).

No. of specimens: Described from the 20 listed above. Bahamonde and López (1963:134) and Haig (1955:28) listed additional specimens.

Size range: Up to 26.0 mm. Two other specimens measuring 30 and 31 mm were found dried at the Acad. Nat. Sci., Philadelphia (No. 484, part).

Remarks: This species is the only one besides *A. affinis* to exhibit a longitudinally oriented (rather than transverse) bar at the anterolateral borders of the cardiac region.

References: Schmitt, 1942b:483, fig. 54, pl. 27c.—Haig, 1955:28, fig. 5.—Bahamonde and López, 1963:134.—Retamal, 1981:21, fig. 81.

### *Aegla parana* Schmitt, 1942b

Type-locality: Rio Negro, Paraná, Brazil.

Type material: Holotype (USNM 80016) is a large (44 mm) male, the largest of "several" collected at Rio Negro on 21 October 1925. One male paratype (MCZ 12316) taken from same lot.

Range: Known only from the type-locality.

No. of specimens: Schmitt (1942b) did not give exact numbers but noted that he secured "a modest number of specimens" during October 1925.

Size range: Schmitt (1942b:461) noted that the 44 mm holotype is the "largest individual *Aegla* I have ever seen."

Remarks: This species resembles *A. sanlorenzo* in having two fairly long and strong spines on the ventral margin of the cheliped ischium (these are the only two species to have this). It is distinguished from all other species in having a serrate margin on the anterior (dorsal) margin of the pereiopods.

Reference: Schmitt, 1942b:458, figs. 42, 43, pl. 25A.

### *Aegla perobae* Hebling and Rodrigues, 1977

Type-locality: Gruta da Peroba, São Pedro, State of São Paulo, Brazil.

Type material: Holotype (MZUSP 4005) is a male of about 24 mm; paratypes (MZUSP 4006) comprise 12 males and 4 females.

Range: Known only from the type-locality.

No. of specimens: Hebling and Rodrigues (1977) mentioned 2,113 specimens examined; these formed the basis of an ecological study by Rodrigues and Hebling (1978).

Size range: Attains a maximum of 25 mm (males).

Remarks: Hebling and Rodrigues (1977) used rostral morphology to distinguish this species from *A. parana*, *A. platensis*, *A. castro*, and *A. franco*. The rostrum is similar to the Pacific form rostrum of Schmitt (1942b), and the species is smaller than the four cited above. Comparisons with other Brazilian species are given by Hebling and Rodrigues (1977).

References: Hebling and Rodrigues, 1977:289, fig. 1.—Rodrigues and Hebling, 1978:383, figs. 1, 2.

### *Aegla plana* Buckup and Rossi, 1977

Type-locality: Arroyo D. Pedro, on the border between the townships of São Francisco de Paula and Tainhas, Rio Grande do Sul, Brazil.

Type material: Holotype (DZ.UFRGS 00086H) is a male collected in January, 1961. Paratypes (DZ.UFRGS 00086P) consist of one male and 6 females collected on the same date.

Range: Known only from the type-locality.

No. of specimens: Buckup and Rossi (1977) mention only the type series above.

Size range: An "exemplar maior, macho" was 20 mm.

Remarks: This species, somewhat similar to *A. franciscana*, is characterized

by a carapace that is smooth and lacking epigastric prominences.

Reference: Buckup and Rossi, 1977:883, fig. 2.

## Aegla platensis Schmitt, 1942b

Type-locality: "Isla Flores" [? Tigre, Buenos Aires, Argentina] (Schmitt, 1942b). Ringuelet (1949a) listed the same locality as belonging to Departamento Canelones, Uruguay.

Type material: Holotype (USNM 80018) is the largest male ("slightly over 38 mm") from a lot of 2 males and 2 females collected on 4 May 1887.

Range: A widely occuring species. Schmitt (1942b) listed it from Buenos Aires, "nearby Tigre," and (possibly) Tucumán, Argentina; the Prado Park, Arroyo Miguelete, Montevideo and Bahia de Colonia, Uruguay; and Rio Grande do Sul, Brazil. Ringuelet (1949a) listed additional localities for northwest Argentina. Ringuelet (1960b) extended the known range into Paraguay, and Buckup and Rossi (1977) listed additional records for the state of Rio Grande do Sul, Brazil.

No. of specimens: Type series consists of 4 specimens collected in May, 1887. Many other specimens collected since that time (e.g., see Buckup and Rossi, 1977; Ringuelet, 1949a, 1960b).

Size range: Attaining a length "of about 39 mm" (Schmitt, 1942b). Ringuelet (1949a) records a range of 20.3 to 37.4 mm.

Remarks: This species closely resembles A. uruguayana. Characters that separate the two include a long slender rostrum and a ventral ischial spine on the cheliped of A. uruguayana. There may be some doubt as to the distinctness of the species. Lopretto (1980a) established a "platensis" group of aeglids that included this species and A. neuquensis affinis, A. singularis, and A. uruguayana (based on fifth pereiopod morphology).

References: Schmitt, 1942b:464, figs. 45, 46, pl. 25c.—Buckup and Rossi, 1977:880.—Ringuelet, 1949a:7, figs. 5i, 7g, pl. 1; 1960b:235, fig. 2.—Lopretto, 1980a:37, figs. 4–8.

## Aegla prado Schmitt, 1942b

Type-locality: A "small tributary of the Arroyo Miguelete" in the Prado Park, Montevideo, Uruguay.

Type material: Holotype (USNM 80017) is "one of the larger of a sizable lot of specimens" collected at the type-locality on 1 December 1925. Holotype is the second largest male (25 mm). One male and one female paratype (MCZ 12317) from the same lot.

Range: Schmitt (1942b) listed only the type-locality and the Arroyo Malvin, Uruguay ("19 females, of which 16 were ovigerous").

No. of specimens: Schmitt (1942b) did not give exact numbers but instead described the type series as a "sizable lot of specimens" that included a "considerable number of juveniles." In addition, 19 females were known to him from the Arroyo Malvin.

Size range: The largest male in the type series is 25.5 mm (Schmitt, 1942b); the largest female 21 mm. The juveniles are listed as "between 10 and 15 mm long."

Remarks: Schmitt (1942b) noted the similarity between this species and A. uruguayana. He reported that specimens of A. prado are always dark colored, even after preservation, whereas specimens of A. uruguayana are very light colored. Other differences noted involve relative development of sternal and ischial spines.

Reference: Schmitt, 1942b:470, figs. 48, 49, pl. 26A,B.

## Aegla riolimayana Schmitt, 1942b (see A. abtao riolimayana)

## Aegla rostrata Jara, 1977

Type-locality: Eastern extreme of Lake Riñihue, approximately 1 km southeast of the mouth of the Rio San Pedro (39°46'30"S, 72°26'30"W), Valdivia River Basin, Valdivia Province, Chile (Jara, 1977).

Type material: Holotype (IZUA 226-2C) is a 40.5 mm male collected on 10 February 1974. Allotype is a 35.0 mm female. Paratype series (MNHN D-10720, D-10721, and IZUA 266-3C) consists of 13 males and 14 females.

Range: Known from Lakes Riñihue, Villarica, Pellaifa, Panguipulli, Calafquén, and Rio Huanahue and Rio Calle Calle, Valdivia Basin (Province of Valdivia), Chile.

No. of specimens: In addition to the type series, Jara (1977) listed 62 specimens examined.

Size range: Type series range is given as 18.3 to 41.6 mm (Jara, 1977).

Remarks: This species is very similar to A. denticulata in the serrated lateral borders of the branchial region of the carapace, but differs in lacking the elongate rostral carina of A. denticulata.

References: Jara, 1977:166, fig. 1.—Thomasson, 1963:129 (as A. denticulata.)

## Aegla sanlorenzo Schmitt, 1942b

Type-locality: Rio San Lorenzo, Salta, Argentina. Ringuelet (1949a) listed the same locality (Rio San Lorenzo) but placed it in Jujuy rather than Salta, Argentina.

Type material: Holotype (MACN 7099) is a single damaged male of 29 mm collected in the Rio San Lorenzo; no date given.

Range: Known from the type-locality (Schmitt, 1942b); it has since been reported from the Arroyo Paco, Urundel, and Vado Hondo, Orán, both in Salta, Argentina (Ringuelet, 1949a).

No. of specimens: Schmitt (1942b) was aware of only the single damaged 29 mm male; Ringuelet (1949a) listed an additional 7 males and 8 females from Argentina (IZFML collections).

Size range: 18.1–29.7 mm (Ringuelet, 1949a).

Remarks: Schmitt (1942b) noted that the species is "certainly more nearly related to A. parana than to A. uruguayana, which it superficially resembles." It is distinguished from either species by the presence of a strong ventral spine on the ambulatory pereiopods (only one of which was intact, however, on Schmitt's specimen).

References: Schmitt, 1942b:461, fig. 44, pl. 25B.—Ringuelet, 1949a:13, figs. 2a,b, 4h–k, 5g,h, pl. 2.

## Aegla scamosa Ringuelet, 1948b

Type-locality: Fray Luis Beltrán, Mendoza, Argentina.

Type material: Ringuelet (1948b) listed as cotypes 19 males and 24 females (MLP 87).

Range: From Viluco in Mendoza south to San Juan in Zonda, corresponding to the Rio Desaguadero drainage (Ringuelet, 1948b). Localities listed are Viluco, Uspallata, Chacras de Coria, Fray Luis Beltrán, and Zonda. .

No. of specimens: Ringuelet (1948b) listed 61 specimens including the type series.

Size range: 20.0–41.0 mm (Ringuelet, 1948b).

Remarks: Ringuelet (1948b) felt that this species was similar to A. neuquensis. Aegla squamosa, a replacement name used by Ringuelet (1960b:234, footnote) and several subsequent authors (e.g., Lopretto, 1978b), is an unjustified emendation (see A. squamosa).

References: Ringuelet, 1948b:315, fig. 2, pls. 6, 11.—MacDonagh, 1945:333, pls. 1, 2 (as Aegla spec.).—Lopretto, 1978b:62, figs. 4–7, 9. Ringuelet (1948b) also listed "Species I" in Schmitt (in prep.); we have not seen this manuscript.

## Aegla schmitti Hobbs III, 1979

Type-locality: "Da dazenda Natal Cecone" (ranch of Mr. Natal Cecone), Curitiba, Brazil.

Type material: Holotype (USNM 171276) is a 31.4 mm male. Paratype series contains 19 males and 1 ovigerous female (USNM); one male paratype deposited in each of MFZB (Porto Alegre, Brazil) and Museu National, Rio de Janeiro, Brazil.

Range: Known only from the type-locality and from Rio Bariguy, on the outskirts of Curitiba, Paraná, Brazil (Hobbs III, 1979).

No. of specimens: Including the holotype and all paratypes, 23 specimens are known.

Size range: 24.8–38.0 mm.

Remarks: This distinctive species was culled from a large collection of aeglids amassed by W. Schmitt in anticipation of a revision of his 1942b

monograph (see Hobbs III, 1979). It differs from all other known species in having large spooned lobes on the palm of the cheliped.

Reference:   Hobbs III, 1979:982, figs. 1, 2.

## *Aegla serrana* Buckup and Rossi, 1977

Type-locality:   Barragem do Salto, Município de São Francisco de Paula, Rio Grande do Sul, Brazil.

Type material:   Holotype (MFZB 00506H) is a male collected in November, 1962. Paratypes (MFZB 00309P, 00270, 00261, 00260; DZ.UFRGS 00090, 00091) consist of an additonal 11 males and 5 females.

Range:   Known from various localities in the state of Rio Grande do Sul, Brazil (see Buckup and Rossi, 1977).

No. of specimens:   Buckup and Rossi (1977) mentioned only the specimens of the type series (above).

Size range:   Male holotype is 26 mm; another large male was 40 mm.

Remarks:   A distinctive species, *A. serrana*, has a short rostrum and rounded anterolateral margins of the cephalothorax. The orbital spine is greatly reduced. It resembles somewhat *A. neuquensis*.

Reference:   Buckup and Rossi, 1977:885, fig. 3.

## *Aegla singularis* Ringuelet, 1948a

Type-locality:   Pindapoy, Territorio de Misiones, Argentina.

Type material:   4 males and 4 females listed as cotypes by Ringuelet (1948a) (MLP collections 147, 148, and 149), collected in January and May, 1943.

Range:   Known from the type-locality and from the area of San Ignacio, near Alto Paraná, northeast Argentina.

No. of specimens:   Ringuelet (1948a:208) mentioned only 4 males and 4 females, including the type series.

Size range:   Up to 20.2 mm (Ringuelet, 1948a).

Remarks:   This species is very similar to *A. denticulata* but does not have the rostral carina extending as far posteriorly as in *A. denticulata*. Lopretto (1980a) included this species in her "platensis" group of aeglids along with *A. neuquensis affinis*, *A. platensis*, and *A. uruguayana*, based on characters of the fifth pereiopod.

References:   Ringuelet, 1948a:204, pls. 1, 2.—Lopretto, 1980a:37, figs. 10, 16–18.

## *Aegla spectabilis* Jara, 1986

Type-locality:   Chol Chol River, under bridge on outskirts of Chol Chol, 29 km northwest of Temuco (38°36'S, 72°51'W), Chile.

Type material:   Holotype (IZUA C-637) is a 19.5 mm female collected 21 December 1982. Paratype (IZUA C-633) is a 15.0 mm young female from the Perquenco River at Galvarino town, 27 km north of Chol Chol (38°25'S, 72°47'W), Chile, collected 22 December 1982.

Range:   Known only from the type-locality and from Galvarino, 27 km north of the type-locality, in the Perquenco River, a tributary of the Chol Chol River, both on the eastern slope of the Nahuelbuta Range, Chile.

No. of specimens:   Only the 2 females listed above are known.

Size range:   15.0–19.5 mm.

Remarks:   This truly remarkable species resembles *A. rostrata* and *A. denticulata* but is even more spinose and has a spine on the external face of the cheliped carpus. Jara (1986) discusses increased spinulation as an apomorphic character in this group.

Reference:   Jara, 1986:34, fig. 1.

## *Aegla squamosa* Ringuelet, 1948b

Unjustified emendation, according to Article 33(b) of the International Code of Zoological Nomenclature (third edition), of *A. scamosa* Ringuelet, 1948b, used by Ringuelet (1960b:234, footnote), Lopretto (1978b), and others.

## *Aegla strinatii* Türkay, 1972

Type-locality:   Gruta da Tapagem, São Paulo, Brazil.

Type material:   Holotype (NMG, no number given) is a male of 18.0 mm. Paratypes consist of NMG (no number given; 2 males and 1 female) and SMF 5688 (2 males).

Range:   Known only from the type-locality.

No. of specimens:   Known from the 6 specimens noted above.

Size range:   Not given by Türkay (1972); holotype is 18.0 mm.

Remarks:   This species, similar morphologically to *A. franca*, was found near the mouth of a cave, but shows no obvious adaptations to a spelean environment (Hobbs, Hobbs, and Daniel, 1977).

References:   Türkay, 1972:417, pl. 1: figs. 3, 4.—Hobbs, Hobbs, and Daniel, 1977:150.

## *Aegla uruguayana* Schmitt, 1942b

Type-locality:   14 kilometers northeast of San Carlos, Uruguay.

Type material:   Holotype (Field Museum 2287) is a 33.3 mm male in a lot of 2 males and 4 females (these paratypes are catalogued as Field Museum 2288) collected in October, 1936. Three male and two female paratypes exist at MCZ (10478), from Maldonado, Uruguay.

Range:   Widely distributed on both sides of the La Plata river; eastward at least as far as Punta del Este, Uruguay, south and westward to Buenos Aires, Isla Flores, Belgrano, and Luján, Province of Buenos Aires, Argentina; north and westward to Paysandu, Uruguay; and Concordia and Paraná, Entre Rios, Argentina (Schmitt, 1942b). Schmitt listed some additional questionable material from other areas, and Ringuelet (1948b) described 6 individuals from Mendoza, Argentina.

No. of specimens:   Schmitt (1942b) was aware of specimens from the above localities and several other specimens of doubtful determination or bearing questionable locality data; he probably had a fairly large series at his disposal. Ringuelet (1948b) listed 6 specimens from Argentina.

Size range:   Up to 33.3 mm (holotype male).

Remarks:   This Atlantic form species is characterized by a long slender rostrum. It is similar to *A. prado* and *A. platensis* in many respects. Lopretto (1980a) placed this species in her "platensis" group along with *A. platensis*, *A. neuquensis affinis*, and *A. singularis*, based on the fifth pereiopod.

References:   Schmitt, 1942b:467, fig. 47, pl. 25D.—Vaz-Ferreira, Gary, and Vaz-Ferreira, 1945:1.—Ringuelet, 1948b:324, fig. 1, pl. 14.

## *Haumuriaegla glaessneri* Feldmann, 1984

Type-locality:   Cheviot, North Canterbury, New Zealand.

Type material:   Holotype (AR915) and paratypes (AR909-926) are in the collections of the Paleontological Section of the New Zealand Geological Survey, Lower Hutt, New Zealand. All are incomplete fossils.

Range:   Known only from the type-locality.

No. of specimens:   Eighteen fragmentary specimens (see Feldmann, 1984) collected from 1934–1980.

Remarks:   The earliest known representative of the Aeglidae, this species differs considerably from other aeglids. The lineae are "only slightly developed" and the collection is from marine sediments. Feldmann noted that "it is reasonable to conclude that this new species might form the basis for definition of a new family of anomurans" but refrained from doing so. Interestingly the rostrum is carinate and of the "Atlantic form" of Schmitt (1942b), although the find suggests an Indo-Pacific origin for the group.

Reference:   Feldmann, 1984:379, figs. 1–5, 7.