

TREATISE ON ZOOLOGY – ANATOMY, TAXONOMY, BIOLOGY

THE CRUSTACEA

COMPLEMENTARY TO THE VOLUMES TRANSLATED FROM THE FRENCH OF THE

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DECAPODA: ASTACIDEA P.P. (ENOPLOMETOPOIDEA, NEPHROPOIDEA),
GLYPHEIDEA, AXIIDEA, GEBIIDEA, and ANOMURA

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INFRAORDERS AXIIDEA DE SAINT LAURENT,
1979 AND GEBIIDEA DE SAINT LAURENT, 1979
(FORMERLY KNOWN COLLECTIVELY AS
THALASSINIDEA)¹⁾

BY

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AND CHRISTOPHER C. TUDGE

Contents. – **Introduction and definition** – Remarks – Diagnoses. **External morphology** – General habitus – Cephalothorax – Pleon – Appendages. **Internal morphology** – Nervous, neuromuscular, and neurosensory organization – Digestive system – Circulatory and respiratory systems – Excretory and osmoregulatory systems – Genital apparatus and reproduction. **Development and larvae** – Brooding and larval development. **Ecology and ethology** – Habitats – Depth distribution – Role in food chains – Burrows – Behavior – Bioturbation – Symbionts. **Economic importance** – Impacts as “pests” – Importance as “fisheries”. **Phylogeny and biogeography** – Phylogeny – Biogeography. **Systematics. Acknowledgements. Bibliography.**

INTRODUCTION AND DEFINITION

Remarks

Formerly treated together as the “**thalassinideans**”, the infraorders **Gebiidea** and **Axiidea** represent two distinctly separate groups of decapods that have converged morphologically and ecologically as **burrowing forms**. They are commonly known as **mud lobsters** (hard and heavily calcified, often pigmented and ornamented with spines and tubercles), and **mud** or **ghost shrimps** (more soft and delicate, comparatively unpigmented and unornamented). They live in marine, mostly soft-bottom sediments of primarily intertidal or subtidal (<200 m) areas and rarely range into the deep sea. They occur in most oceans and

¹⁾ Manuscript concluded 5 July 2010.

seas, except for high latitude polar seas, and exhibit their greatest diversity in tropical to temperate regions (Dworschak, 2005).

Over the history of treating these groups together under the name Thalassinidea, they were for a period regarded as members of Anomura, but it is now widely accepted that they instead represent two independent lineages positioned in reptant decapod phylogeny basally to both Anomura and Brachyura (cf. Bracken et al., 2009, 2010). The common name “thalassinidean” is derived from their former grouping together in the taxon Thalassinidea, and this derivative common name may see continued use for reference to these lineages in combination. Given a large body of literature that addresses “thalassinideans” as a single group, this is unavoidable in even our own treatments that follow, and we have sometimes resorted simply to comparative treatments by family instead of drawing distinctions by infraorder. This should not be taken to perpetuate recognition of a monophyletic grouping deserving taxonomic rank, or some indication of closest phylogenetic proximity. Instead, thalassinideans now appear to represent two major, well-separated **clades**, sometimes considered as superfamilies or, as herein adopted, separate **infraorders** (*sensu* Robles et al., 2009).

Recent phylogenetic hypotheses based on a combination of morphological and molecular datasets support partitioning of 12 to 15 families between these two infraorders, though debate continues as to family versus subfamily rankings in several cases (see findings and reviews by Sakai, 2005a; Sakai & Sawada, 2006; Tsang et al., 2008a, b; Bracken et al., 2009, 2010; De Grave et al., 2009; Felder & Robles, 2009; Robles et al., 2009). **Gebiidea** encompasses the widely recognized families Axianassidae, Laomediidae, Thalassinidae, and Upogebiidae. In turn, **Axiidea** is partitioned at minimum into Axiidae, Callianassidae, Callianideidae, Ctenochelidae, Micheleidae, and Strahlaxiidae. Potentially adding to this list, the axiidean families Eiconaxiidae and Calocarididae have been regarded as separate from Axiidae, but preliminary molecular studies do not support their continued independent recognition, or treatment of Thomassiniidae independent of Callianideidae. Furthermore, Gourretiidae (*sensu* Sakai, 1999a) was proposed for family rank independent of the axiidean family Ctenochelidae, but merit of that separation cannot yet be supported by phylogenetic analyses; a confused subsequent application of this family name (Sakai, 2004, 2005a) also leaves its status in question (see Dworschak, 2007b; Poore, 2008b).

The sparse **fossil record** for this group is essentially a series of major chelae, especially for the callianassids (Roberts, 1964; Swen et al., 2001; Schweitzer et al., 2005), and possible trace fossils of burrows (Glaessner, 1969; Dworschak & Rodrigues, 1997; Swen et al., 2001), as well as some coprolites (Mehling, 2004) extending back to the Lower Jurassic (~180 mya) (Burkenroad, 1963; Glaessner, 1969; Briggs et al., 1993). Individual families for which there are plausible fossil evidence and trace fossils include Thalassinidae (cf. Bennett, 1968), Upogebiidae, Axiidae, Laomediidae (cf. Glaessner, 1969), Axianassidae (cf. Dworschak & Rodrigues, 1997), and Callianassidae (cf. Swen et al., 2001; Schweitzer et al., 2005). A limited dataset for **molecular clock** estimates (Porter et al., 2005) reported a possible divergence time of “thalassinideans” from other reptant decapods at about the mid-Carboniferous (325 mya), though this estimate must apply to only

axiideans as their five representatives were all callianassids. A subsequent more robust molecular phylogenetic analysis, calibrated to the fossil record (Bracken et al., 2010), has alternatively estimated independent **radiation** of Gebiidea to have occurred within the Carboniferous (309 mya) and radiation of Axiidea within the Permian (255 mya).

Diagnoses

The infraorder Gebiidea de Saint Laurent, 1979a is characterized by having the first pereopod chelate or subchelate (on rare occurrences, almost simple); and exhibiting the second pereopod as either subchelate, or simple.

The infraorder Axiidea de Saint Laurent, 1979a possesses a chelate first and second pereopod.

EXTERNAL MORPHOLOGY

General habitus

The **habitus** (fig. 69.1) ranges from lobster-like with a well-calcified exoskeleton (Thalassinidae and Axiidae) to weakly calcified elongated forms (Callianassidae) that show strong adaptations to a **burrowing lifestyle**. The **size** of adult shrimp ranges from about 1.5 cm (Thomassiniidae and many Callianassidae) to over 35 cm (Thalassinidae).

Cephalothorax

In most axiideans and gebiideans, the **carapace** (figs. 69.2, 69.3) is as wide as high or slightly higher than wide (laterally compressed), especially in Calocarididae. An exception is the laomediid genus *Naushonia*, which is dorsoventrally compressed.

The median **rostrum** is usually dorsoventrally flattened to some degree, especially when it is well developed. If well developed, it can overreach the **eyestalks**, and is sometimes spined terminally or laterally, with lateral edges continuing posteriorly in Axiidae, Strahlaxiidae, Calocarididae, and Eiconaxiidae. The rostrum of Laomediidae and some Micheleidae (*Marcusiaxius* and *Meticonaxius*) is simply triangular and shorter. In Upogebiidae, the rostrum is broad and has lateral gastric ridges that are usually protruding forward. Some upogebiid species have one or more infrarostral spines (*Austino-gebia* and *Gebiacantha*). In Callianassidae, Callianideidae, some Micheleidae (*Tethisea*), Thomassiniidae, and most Ctenochelidae, the rostrum is very reduced, triangular, and shorter than the eyestalks. There may be secondarily a spike-like rostrum in some genera (*Corallianassa* and *Glypturus*).

The front of the carapace shows lateral spines with a carina continuing posteriorly in *Thalassina*, **lateral spines** without a carina in Laomediidae and some Callianassidae, and blunt lobes in *Michelea*, *Callianidea*, and most Callianassidae. A median rostral carina

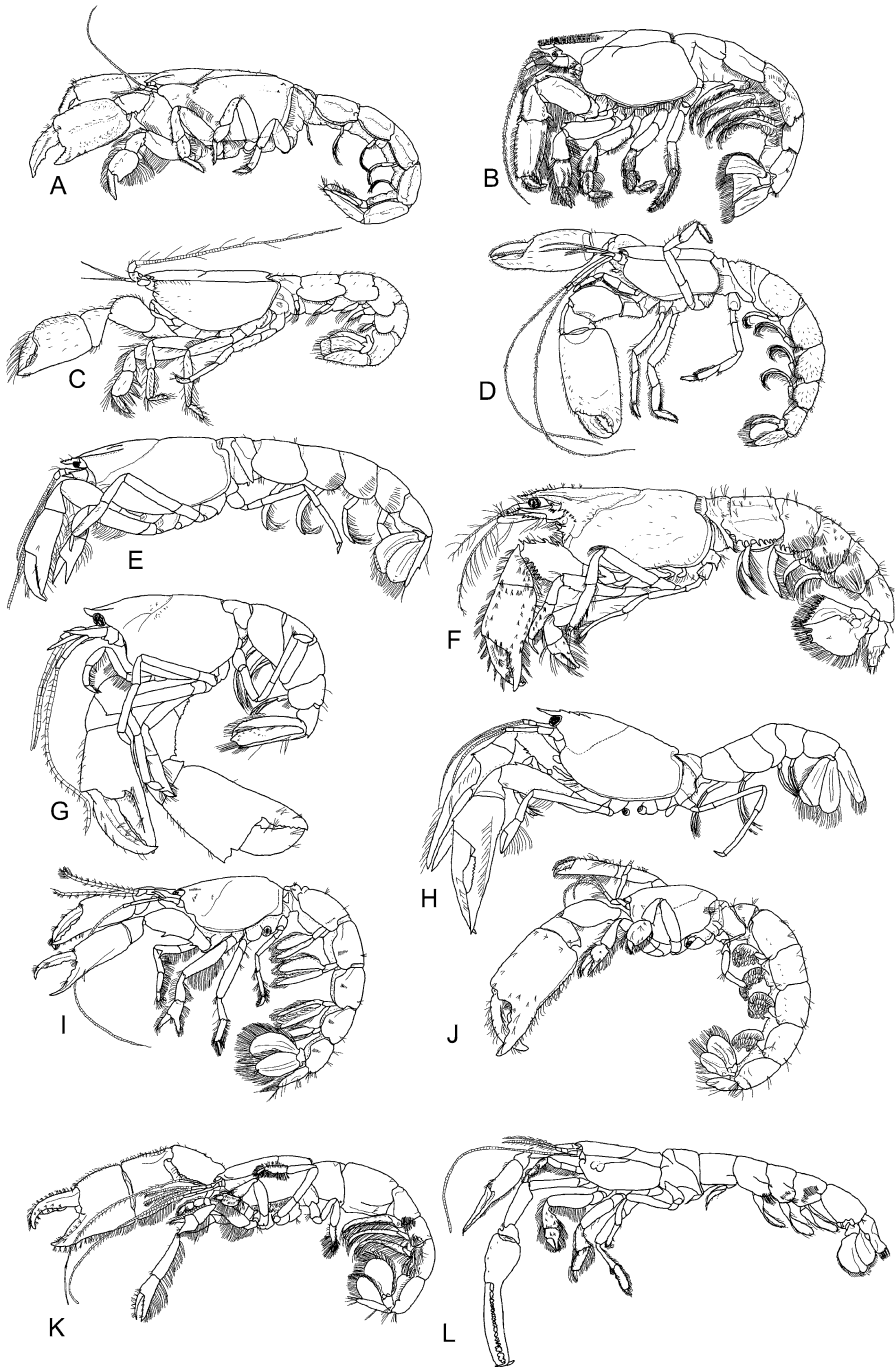


Fig. 69.1. ²)Habitus: A, *Thalassinoma anomala* (Herbst, 1804) [modified from Sakai, 1992b, fig. 2A]; B, *Upogebia affinis* (Say, 1818) [modified from Williams, 1993, fig. 14a]; C, *Laomedea healyi* Yaldwyn & Wear, 1972 [modified from Yaldwyn & Wear, 1972, fig. 1]; D, *Axianassa intermedia*

in the anterior region is present in some Ctenochelidae. The genus *Naushonia* has a long median dorsal carina, together with variable numbers of lateral and sublateral carinae.

The **linea thalassinica** (lt in figs. 69.2 and 69.3) is a longitudinal, hinge-like seam that flexes the **branchiostegite** from the thoracic wall. It is straight and runs the entire length of the carapace in Thalassinidae, Laomediidae, Axianassidae, Callianassidae, and Ctenochelidae. In Upogebiidae, the anterolateral margin of the cephalothorax is oblique, the branchiostegal sclerite is some distance posterior to the ocular spine, and the thoracic sternites are very short. As a consequence the linea thalassinica is depressed anteriorly to the point where the **cervical groove** meets it (Poore, 1994). In several upogebiids, the linea thalassinica either fails to reach the posterior or anterolateral margin, or is not detectable at all. A linea thalassinica is either lacking, or is very short in Callianideidae, and complete (*Mictaxius*) or incomplete (*Thomassinia* and *Crosniera*) in Thomassiniidae. Generally no linea thalassinica occurs in Axiidae, Strahlaxiidae, Calocarididae, and Micheleidae.

A **cervical groove** (cg in figs. 69.2 and 69.3), either straight or running curved anterolaterally, is present in most genera. It starts dorsally in the first third of the cephalothorax in Thalassinidae, in the posterior third in Callianassidae, and about mid-length in all other families. One to two additional transverse sutures posterior to the cervical groove are present dorsally in *Thalassina* and some Callianassidae (*Eucalliix* and *Bathycalliix*) and can continue onto the branchiostegite.

In most Callianassidae, a “**dorsal oval**” (do in figs. 69.2L, M and 69.3J, K) is present, an area bounded posteriorly by the cervical groove, and delimited anteriorly by a transverse groove behind the rostrum (Schmitt, 1935). A distinct swelling, the **cardiac prominence** close to the posterior border of the carapace, occurs in most Ctenochelidae and some Callianassidae.

At the anteroventral border an anterior **branchiostegal lobe** (a free lobe of the carapace enclosing the mouthparts anterolaterally) is more or less developed in all genera. The anterolateral surface of the branchiostegite may have either oblique rows of spines (*Thalassina*), or setal rows in Micheleidae, Callianideidae, and Thomassiniidae. In Callianassidae and Ctenochelidae a prominent tubercle, the **hepatic boss** (hp in figs. 69.3J-M) occurs on the anterior third of the carapace ventrally to the linea thalassinica. This is

Schmitt, 1924 [modified from Kensley & Heard, 1990, fig. 1]; E, *Axius stirhynchus* Leach, 1815 [modified from Ngoc-Ho, 2003, fig. 1A]; F, *Neaxius acanthus* (A. Milne-Edwards, 1878) [modified from Tirmizi, 1983, fig. 1A]; G, *Eiconaxius hakuhou* Sakai & Ohta, 2005 [modified from Sakai & Ohta, 2005, fig. 6A]; H, *Calocaris macandreae* Bell, 1853 [modified from Ngoc-Ho, 2003, fig. 7A]; I, *Michelea pillsburyi* Kensley & Heard, 1991 [modified from Kensley & Heard, 1991, fig. 18]; J, *Callianidea tya* H. Milne-Edwards, 1837 [modified from Sakai, 1992b, fig. 3A]; K, *Callianassa subterranea* (Montagu, 1808) [modified from Manning & Felder, 1991, fig. 8a]; L, *Ctenocheles balssi* Kishinouye, 1926 [modified from Matsuzawa & Hayashi, 1997, fig. 2].

²⁾ In this caption with habitus figures, all authorities and dates of species names are given, whereas in subsequent captions only names at first mention are provided with author and date; all authors and dates can be seen in the Appendix with the names of genera and species alphabetically arranged.

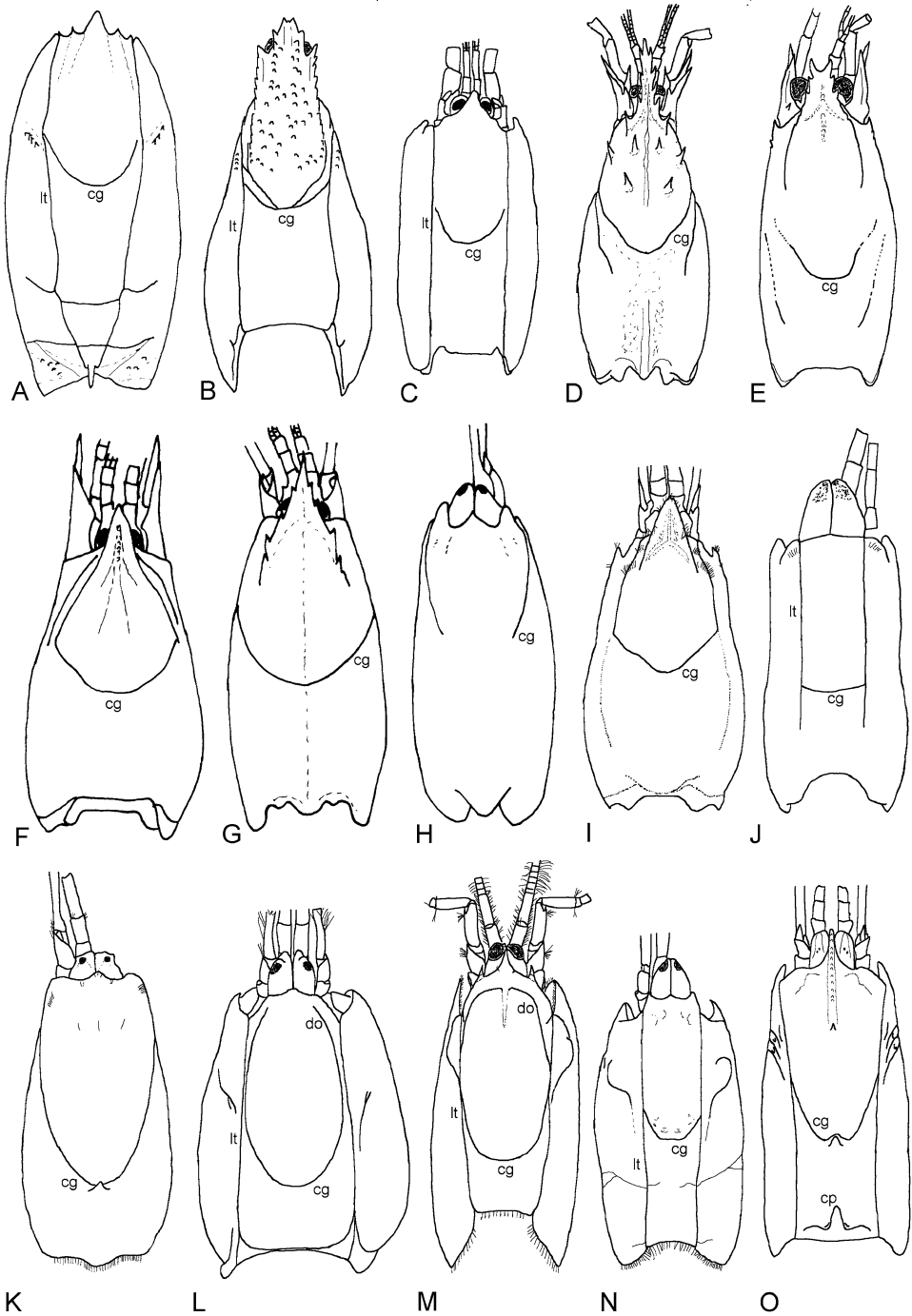


Fig. 69.2. Cephalothorax, dorsal aspect: A, *Thalassina krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 2B]; B, *Upogebia deltaura* (Leach, 1815) [modified from LeLoeuff &

the insertion of a transverse muscle that upon contraction allows flushing of the branchial chamber.

The posterior border of the cephalothorax has a **median concavity** and a prominent **dorsomedian process** in Thalassinidae and is straight or slightly convex in the other families. In Axiidae, Eiconaxiidae, Micheleidae, Thomassiniidae, and Callianideidae, the posterior margin is similar and tripartite. On each side of the median convexity is a strong **posterolateral lobe** whose margin is strengthened by a smooth ridge on which the anterolateral lobes of the first pleomere ride. The medial portion may be strongly depressed posteriorly in Micheleidae, to enclose the mid-anterior sclerite of the pleomere (Poore, 1994).

Pleon

The **pleon** is longer than the cephalothorax in most genera (fig. 69.1). In callianassids the pleon is especially elongated, up to 4 times as long as the cephalothorax. The first **pleomere** is usually the shortest, the second pleomere the longest followed in length by the sixth. The **pleura** are acutely angled in many Axiidae, Eiconaxiidae, and Calocarididae, especially that of the first pleomere. The pleura are rounded in most other families, sometimes with teeth on their lower border. The first pleomeres in the callianassid genera *Corallianassa* and *Callichirus* are very soft and elongate. In Callianassidae, the pleura of the third to fifth pleomeres bear **setal tufts** above the insertion of the pleopods. In *Callichirus*, these pleomeres show a distinct pattern of plates and setal tufts dorsally that are assumed to be connected to **tegumental glands** (Manning & Felder, 1986). Micheleidae, Thomassiniidae, and Callianideidae have various arrangements of **setal rows** on the pleomeres (Kensley & Heard, 1991; Poore, 1997).

The **telson** is elongate in *Thalassina* (fig. 69.4A) and of various shapes in Upogebiidae (oval, rectangular, or square). A special case is found in *Pomatogebia*, where the telson widens distally and forms an **operculum** together with the uropods and a dense fringe of setae on the posterior margin of the fourth pleomere (fig. 69.4C). A typical rhomboid telson occurs in Strahlaxiidae with several transverse carinae (fig. 69.4G). The telson of the other families is mostly oval to rectangular with rounded edges, and lateral borders

Intes, 1974, fig. 19b]; C, *Laomedia paucispinosa* [modified from Ngoc-Ho, 1997, fig. 2B]; D, *Calaxius acutirostris* [modified from Sakai & de Saint Laurent, 1989, fig. 25A]; E, *Calocaris macandreae* Bell, 1853 [modified from Ngoc-Ho, 2003, fig. 6A]; F, *Neaxius frankeae* [modified from Lemaitre & Ramos, 1992, fig. 1b]; G, *Eiconaxius hakuhou* [modified from Sakai & Ohta, 2005, fig. 7A]; H, *Michelea novaecaledoniae* [modified from Poore, 1997, fig. 22A]; I, *Mictaxius dentatus* [modified from Lin, 2006, fig. 1B]; J, *Thomassinia gebioides* de Saint Laurent, 1979 [modified from Poore, 1997, fig. 38A]; K, *Callianidea typa* [modified from Poore, 1997, fig. 1B]; L, *Rayllianassa amboinensis* (De Man, 1888) [modified from Sakai, 1984, fig. 1C]; M, *Corallianassa hartmeyeri* (Schmitt, 1935) [modified from Manning & Chace, 1990, fig. 19a]; N, *Eucalliax aequimana* (Baker, 1907) [modified from Sakai, 1999b, fig. 31a]; O, *Ctenocheles serrifrons* LeLoeuff & Intès, 1974 [modified from LeLoeuff & Intès, 1974, fig. 3a]. Abbreviations: cg, cervical groove; cp, cardiac prominence; do, dorsal oval; lt, linea thalassinica.

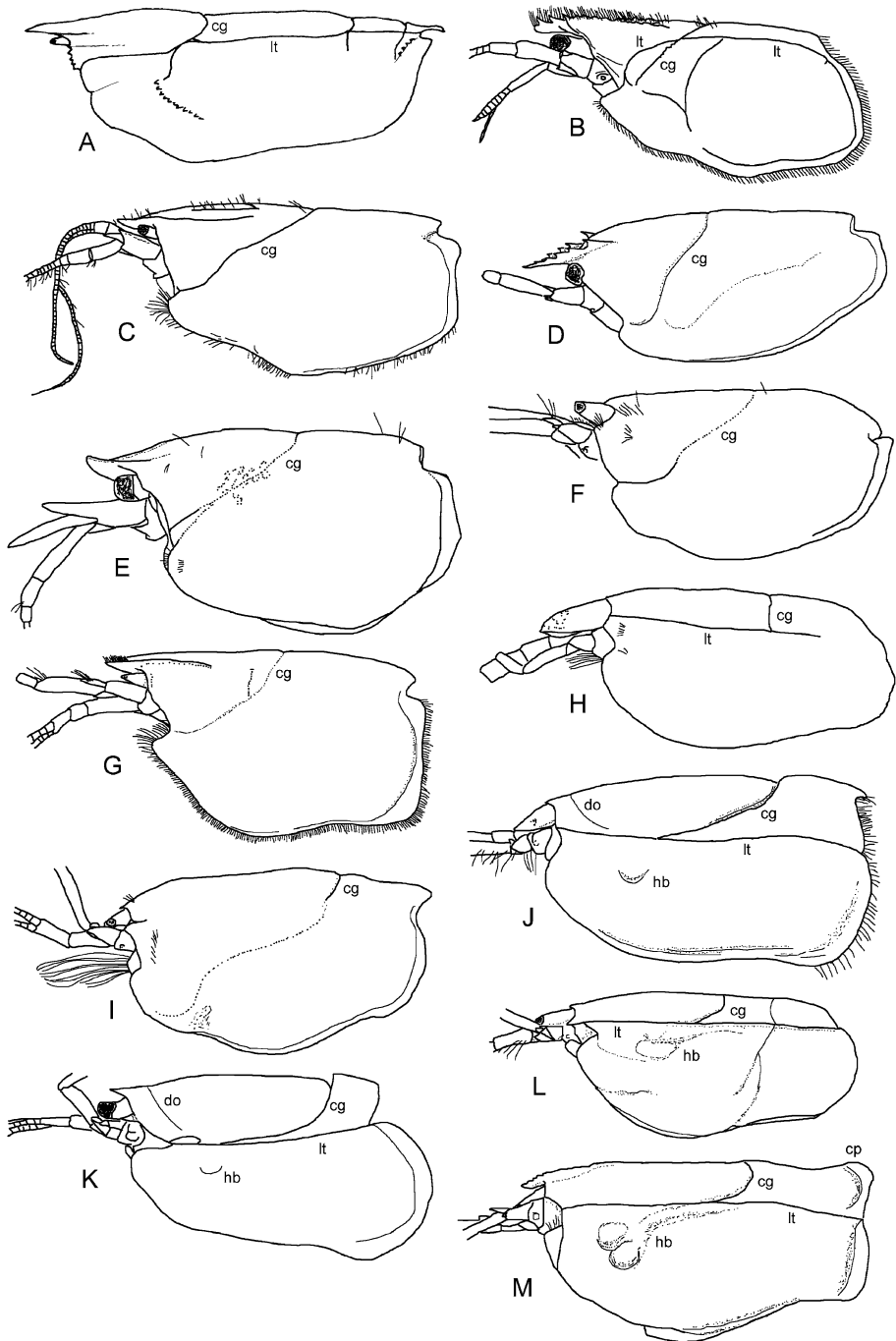


Fig. 69.3. Cephalothorax, lateral aspect: A, *Thalassinoma anomala* [modified from Sankolli, 1970, fig. 3a]; B, *Upogebia deltaura* [modified from LeLoeuff & Intès, 1974, fig. 19a]; C, *Axius stirhynchus*

and dorsal surface sometimes with spines in Axiidae, Eiconaxiidae, and Calocarididae. A great diversity in telson shapes occurs also in Callianassidae (broadly or elongately oval, trapezoid, trapezoidal, or broadly rectangular; fig. 69.4M-O), sometimes with a terminal median spine.

Appendages

CEPHALON

Antennule. – The antennule (fig. 69.5) consists of a **peduncle** with 3 articles and paired **flagella**. The basal article of the peduncle has a prominent **statocyst**. The antennular peduncles as well as the **flagellum** are shorter than those of the antennae in most families. In some Callianassidae, the antennular peduncles are much longer and heavier than the antennal peduncles and show a dense setation ventrally. The antennular flagella are usually longer than the peduncle, except in some species of Callianassidae and Upogebiidae. The flagella are usually of the same length, except in Laomediidae and Axianassidae where the dorsal one is much longer than the ventral one. The dorsal flagellum is thicker than the ventral one and bears **aesthetascs** on the ventral face proximally.

Antenna. – The antenna (fig. 69.6) of most genera consists typically of a **peduncle** and a **flagellum**. The peduncle consists of 5 articles of which the basal two represent the **protopod** and the 3 distal ones the **endopod**. In Callianassidae, the basis and ischium are very short and triangular, appear fused, and the two proximal articles are rather elongate compared to those in the other families. In Upogebiidae, the basis and ischium appear fused. The **exopod** is represented by the **scaphocerite**. This is developed as a broad, denticulate scale only in the laomediid genus *Naushonia*. In the other genera it is a narrow, spinous process (Axiidae and Axianassidae), sometimes denticulate (Strahlaxiidae), or reduced to a tiny scale (Upogebiidae, Laomediidae, Calocarididae, Callianassidae, and Ctenochelidae). The flagellum is usually longer than the carapace.

Labrum. – The labrum is rarely mentioned in species descriptions of axiideans and gebiideans. Nickell et al. (1998) in a SEM study on setal structures described the labrum as a lobe-like structure that covers the buccal space, has a median keel, and is approximately trapezium-shaped in *Callianassa subterranea* (Montagu, 1808). A similar labrum occurs in *Upogebia stellata* (Montagu, 1808). In *Jaxea nocturna* Nardo, 1847, it is shield-shaped and keeled along the outer midline, while its inner face has two central ridges forming an almost closed channel leading to the esophagus.

[modified from Sakai & de Saint Laurent, 1989, fig. 7A]; D, *Ambiaxius japonicus* [modified from Kensley, 1996b, fig. 11A]; E, *Eiconaxius hakuhou* [modified from Sakai & Ohta, 2005, fig. 6B]; F, *Michelea novaecaledoniae* [modified from Poore, 1997, fig. 22B]; G, *Marcusiaxius colpos* [modified from Kensley & Heard, 1991, fig. 7A]; H, *Thomassinia gebioides* [modified from Poore, 1997, fig. 38B]; I, *Callianidea laevicauda* Gill, 1859 [modified from Kensley & Heard, 1991, fig. 3A]; J, *Callianassa subterranea* [modified from Sakai, 2005b, fig. 5B]; K, *Corallianassa xutha* [modified from Manning, 1988, fig. 3a]; L, *Eucalliax aequimana* [modified from Sakai, 1999b, fig. 31b]; M, *Ctenocheles balsi* [modified from Sakai, 1999a, fig. 1a]. Abbreviations: cg, cervical groove; cp, cardiac prominence; do, dorsal oval; hb, hepatic boss; lt, linea thalassinica.

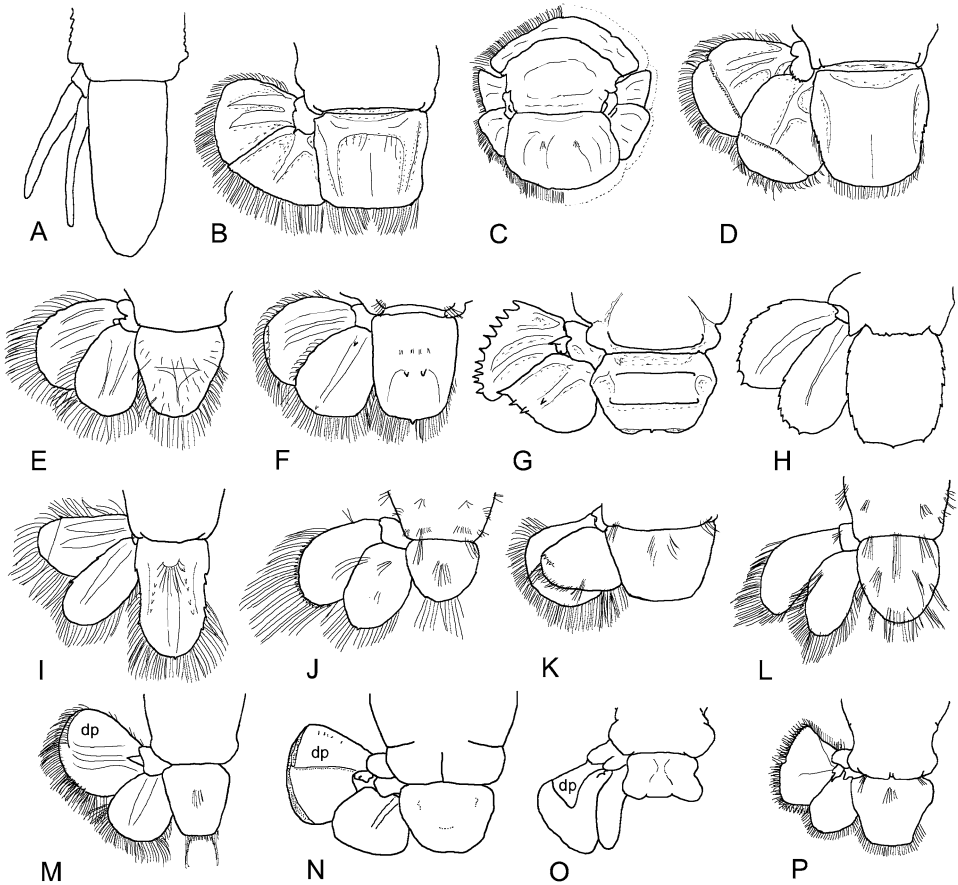


Fig. 69.4. Telson and left uropod: A, *Thalassinia anomala* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 2F]; B, *Upogebia deltaura* [modified from Ngoc-Ho, 2003, fig. 26C]; C, *Pomatogebia rugosa* (Lockington, 1878) [modified from Williams, 1986, fig. 21o]; D, *Laomedea healyi* [modified from Ngoc-Ho, 1997, fig. 6B]; E, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 3A]; F, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1E]; G, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7J]; H, *Eiconaxius cristagalli* (Faxon, 1893) [modified from Kensley, 1996b, fig. 7D]; I, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6M]; J, *Michelea leura* (Poore & Griffin, 1979) [modified from Poore, 1997, fig. 17F]; K, *Thomassinia gebioides* [modified from Poore, 1997, fig. 36N]; L, *Callianidea tyra* [modified from Ngoc-Ho, 2003, fig. 9F]; M, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9F]; N, *Neocallichirus grandimana* [modified from Manning, 1987, fig. 2g]; O, *Callichirus adamas* (Kensley, 1974) [modified from de Saint Laurent & LeLoeuff, 1979, fig. 17a]; P, *Ctenocheles holthuisi* [modified from Rodrigues, 1978, fig. 21]. Abbreviation: dp, dorsal plate.

Mandible. – The **molar process** in axiideans and gebiideans is weakly developed, consisting of a ridge, usually smooth (Axiidae and Eiconaxiidae), and sometimes with a median spine perpendicular to the **incisor process** (fig. 69.7D, G-K, N). The incisor process may be thin and weakly calcified with a smooth distal border (Axiidae, Eiconaxiidae, and

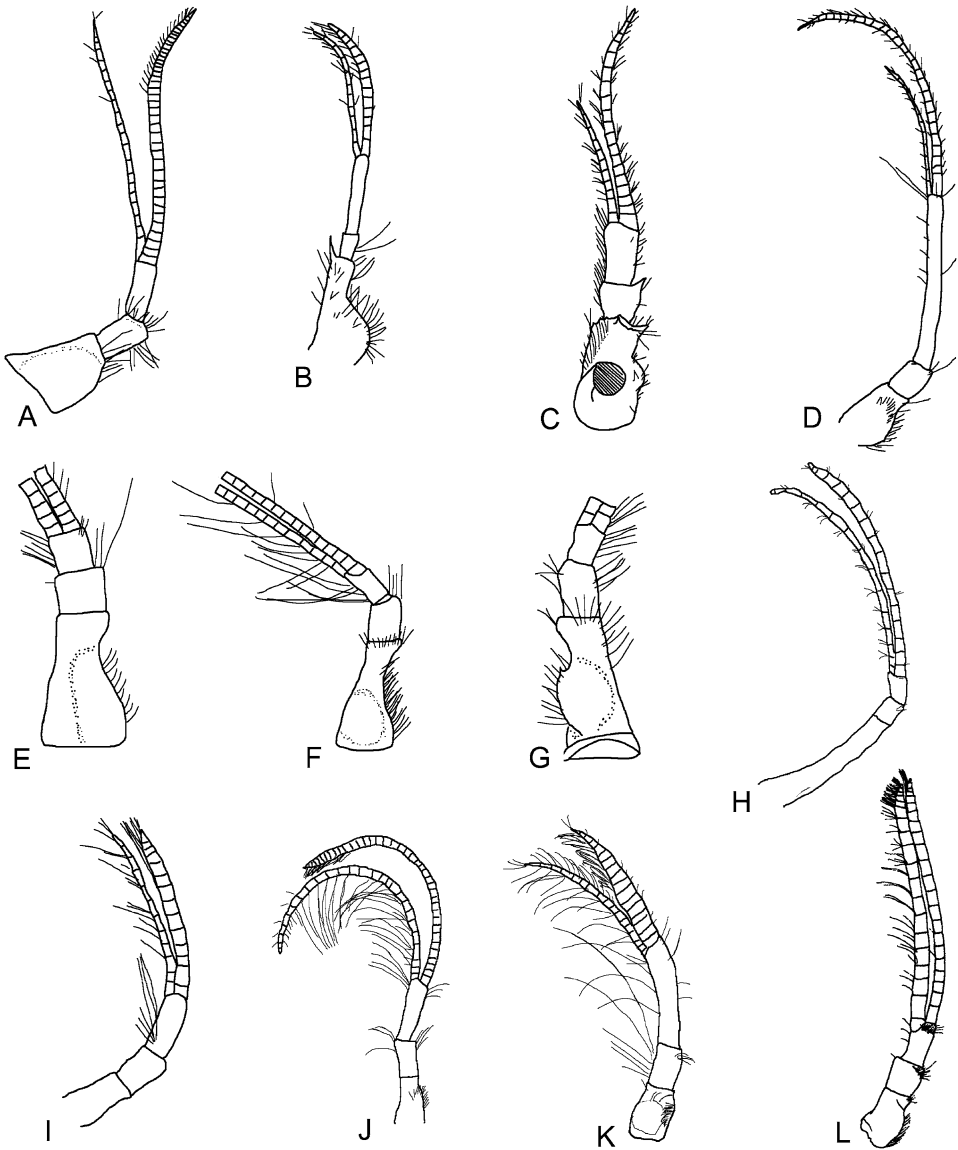


Fig. 69.5. Antennule: A, *Thalassinia krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3A]; B, *Gebiacantha acutispina* [modified from de Saint-Laurent & Ngoc-Ho, 1979, fig. 9]; C, *Naushonia carinata* [modified from Dworschak et al., 2006b, fig. 3g]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2B]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1J]; F, *Neaxius mclaughlinae* [modified from Ngoc-Ho, 2006, fig. 2A]; G, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6F]; H, *Michelea leura* [modified from Poore, 1997, fig. 19A]; I, *Thomassinia gebioides* [modified from Poore, 1997, fig. 36C]; J, *Callianidea typa* [modified from Poore, 1997, fig. 3A]; K, *Rayllianassa amboinensis* [modified from Ngoc-Ho, 1991, fig. 1a]; L, *Gourretia coolibah* Poore & Griffin, 1979 [modified from Dworschak, 2009, fig. 5).

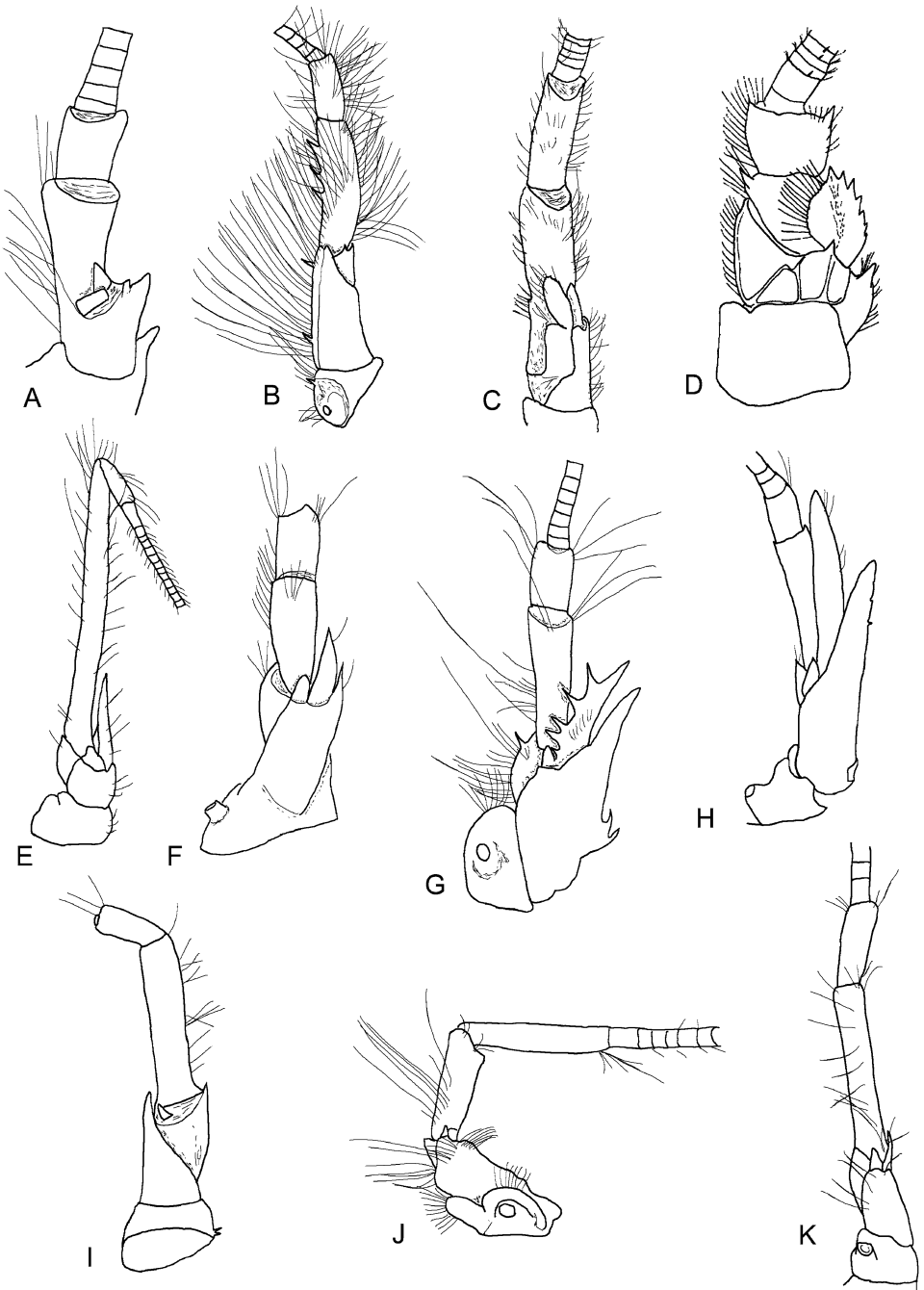


Fig. 69.6. Antenna: A, *Thalassina anomala* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3B2]; B, *Gebiacantha talismani* (Bouvier, 1915) [modified from Ngoc-Ho, 2003, fig. 24D]; C, *Laomedea astacina* [modified from Ngoc-Ho, 1997, fig. 1H]; D, *Naushonia carinata* [modified

Calocarididae) to more heavily calcified and showing strong teeth on the distal border (Callianassidae). Some Upogebiidae show a large mesio-anterior pointed tooth on the incisor process (fig. 69.7B). The mandibular **palp** usually has three articles and is curved mesially between incisor and molar process. In some Laomediidae, i.e., *Naushonia*, the proximal two articles may be fused.

First maxilla. – The first maxilla (**maxillula**) is a thin, foliose appendage (fig. 69.8), consisting of an **endite**, separated into a wide proximal lobe and an elongated distal lobe, and a bi-articulated palp (endopod). There is no significant variation with regard to this appendage.

Second maxilla. – The second maxilla (fig. 69.9) consists of a proximal and a distal endite, both deeply bilobed, a median palp (endopod) and a large exopod (**scaphognathite**) with a distal (anterior) and a proximal (posterior) lobe. The proximal lobe has several long (as long as, or exceeding, the total length of the scaphognathite) setae in Thalassinidae and Laomediidae, one long seta (or two setae in rare cases) in Axiidae, Strahlaxiidae (*Strahlaxius*), Eiconaxiidae, Calocarididae, Callianideidae, Micheleidae, and Thomassiniidae. No setae are present on the shortened, rounded proximal lobe in Callianassidae, Ctenochelidae, Strahlaxiidae (*Neaxius*), and Upogebiidae.

THORAX

First maxilliped. – The first maxilliped (fig. 69.10) is a **foliose appendage** and consists of a proximal and a distal endite, an endopod, and an exopod. An **epipod** is missing in Thalassinidae, absent or reduced in Upogebiidae, and present in all other families. The endopod is simple and thin in Thalassinidae, Upogebiidae, Axiidae, Strahlaxiidae, Eiconaxiidae, Calocarididae, and Thomassiniidae, very short in Micheleidae, and reduced to a bud in most Callianassidae. The endopod is expanded in Laomediidae, especially in *Naushonia*, and in Axianassidae. The exopod is simple, slender, or expanded, but restricted to a basal article in *Thalassina*, Upogebiidae, Strahlaxiidae, Micheleidae, Thomassiniidae, Callianideidae, Callianassidae, and Ctenochelidae. One or two more articles, and/or a flagellum, are present in the exopod of the Laomediidae, Axianassidae, Axiidae, Eiconaxiidae, and Calocarididae.

Second maxilliped. – The second maxilliped (fig. 69.11) is a **pediform appendage**, consisting of an endopod with 5 articles and an exopod. The merus is the longest article of the endopod. The carpus may show a dorsodistal expansion in Laomediidae, Axianassidae, and Strahlaxiidae. The exopod is well developed, as long as, or longer than, the endopod in Thalassinidae, Upogebiidae, Laomediidae, Axianassidae, Axiidae, Strahlaxiidae, Eiconaxiidae, and Calocarididae, with a long basal article and one or two proximal

from Dworschak et al., 2006b, fig. 3h]; E, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2C]; F, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1K]; G, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 6D]; H, *Eiconaxius farreae* (Ortmann, 1891) [modified from Sakai & Ohta, 2005, fig. 1C]; I, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6G]; J, *Lepidophthalmus tridentatus* (Von Martens, 1868) [modified from Dworschak, 2007a, fig. 10]; K, *Ctenocheles serrifrons* [modified from LeLoeuff & Intès, 1974, fig. 3e].

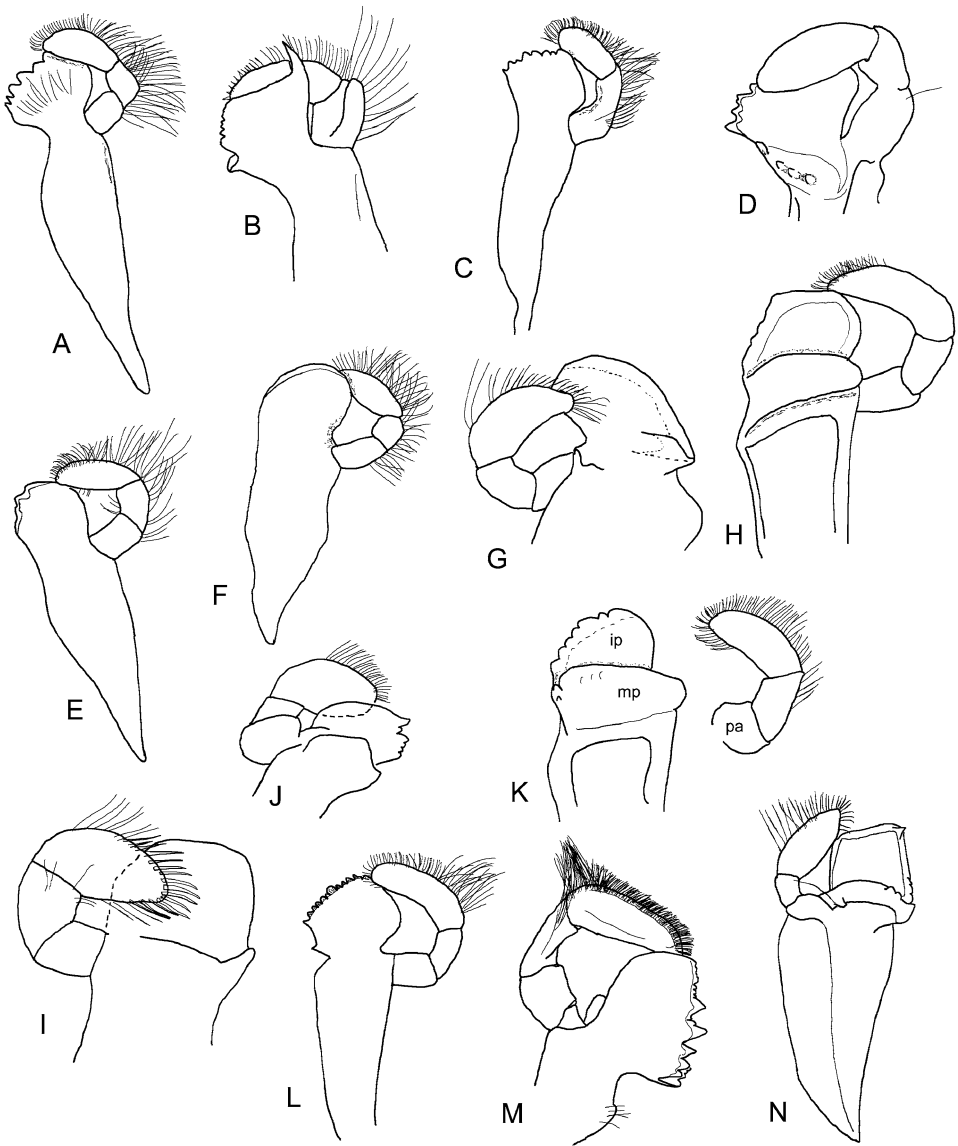


Fig. 69.7. Mandible: A, *Thalassina krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3C]; B, *Upogebia deltaura* [modified from LeLoeuff & Intès, 1974, fig. 19m]; C, *Laomedea astacina* [modified from Ngoc-Ho, 1997, fig. 1B]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2E]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1H]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7i]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5A]; H, *Calocaris caribbaeus* [modified from Kensley, 1996a, fig. 5F]; I, *Michelea leura* [modified from Poore, 1997, fig. 19C]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37A]; K, *Callianidea laevicauda* [modified from Kensley & Heard, 1991, fig. 4B, C]; L, *Callianassa subterranea* (Montagu, 1808) [modified from Ngoc-Ho, 2003,

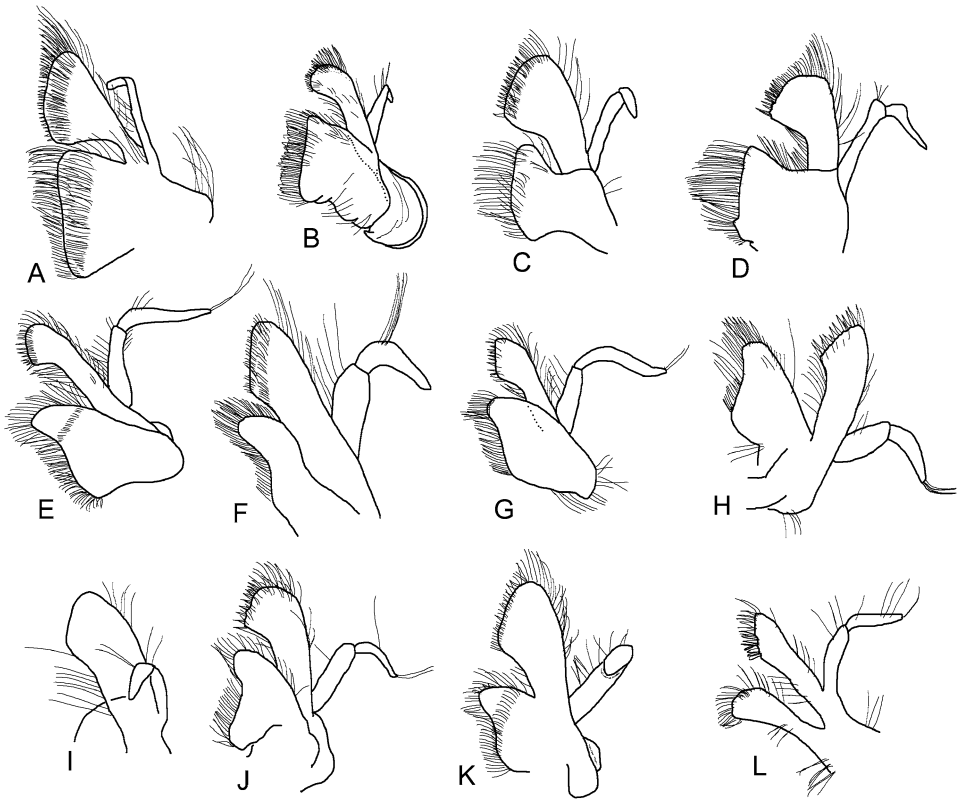


Fig. 69.8. First maxilla: A, *Thalassina krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3D]; B, *Upogebia acanthura* [modified from Williams, 1993, fig. 6d]; C, *Laomedea paucispinosa* [modified from Ngoc-Ho, 1997, fig. 3C]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2F]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1F]; F, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5B]; G, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6N]; H, *Michelea leura* [modified from Poore, 1997, fig. 19D]; I, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37B]; J, *Callianidea typa* [modified from Sakai, 1992b, fig. 4B]; K, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 10A]; L, *Ctenocheles serrifrons* [modified from LeLoeuff & Intès, 1974, fig. 3k].

articles or a flagellum. The exopod is shorter than the endopod in Thomassinidae, Callianideidae, Callianassidae, Ctenochelidae, and Micheleidae, where in the last it may be reduced to a bud (*Michelea*).

Third maxilliped. – The third maxilliped (fig. 69.12) is generally a **pediform appendage** consisting of an endopod with 5 articles, the merus being the longest, and an exopod that is usually shorter than the endopod and flagellate distally. All axianassids and

fig. 9M]; M, *Neocallichirus cacahuate* [modified from Felder & Manning, 1995, fig. 2a]; N, *Ctenocheles serrifrons* [modified from LeLoeuff & Intès, 1974, fig. 3l]. Legends: A-C, E, F, L, M, in lateral view, D, G-K, N, in mesial view; ip, incisor process, mp, molar process; pa, mandibular palp.

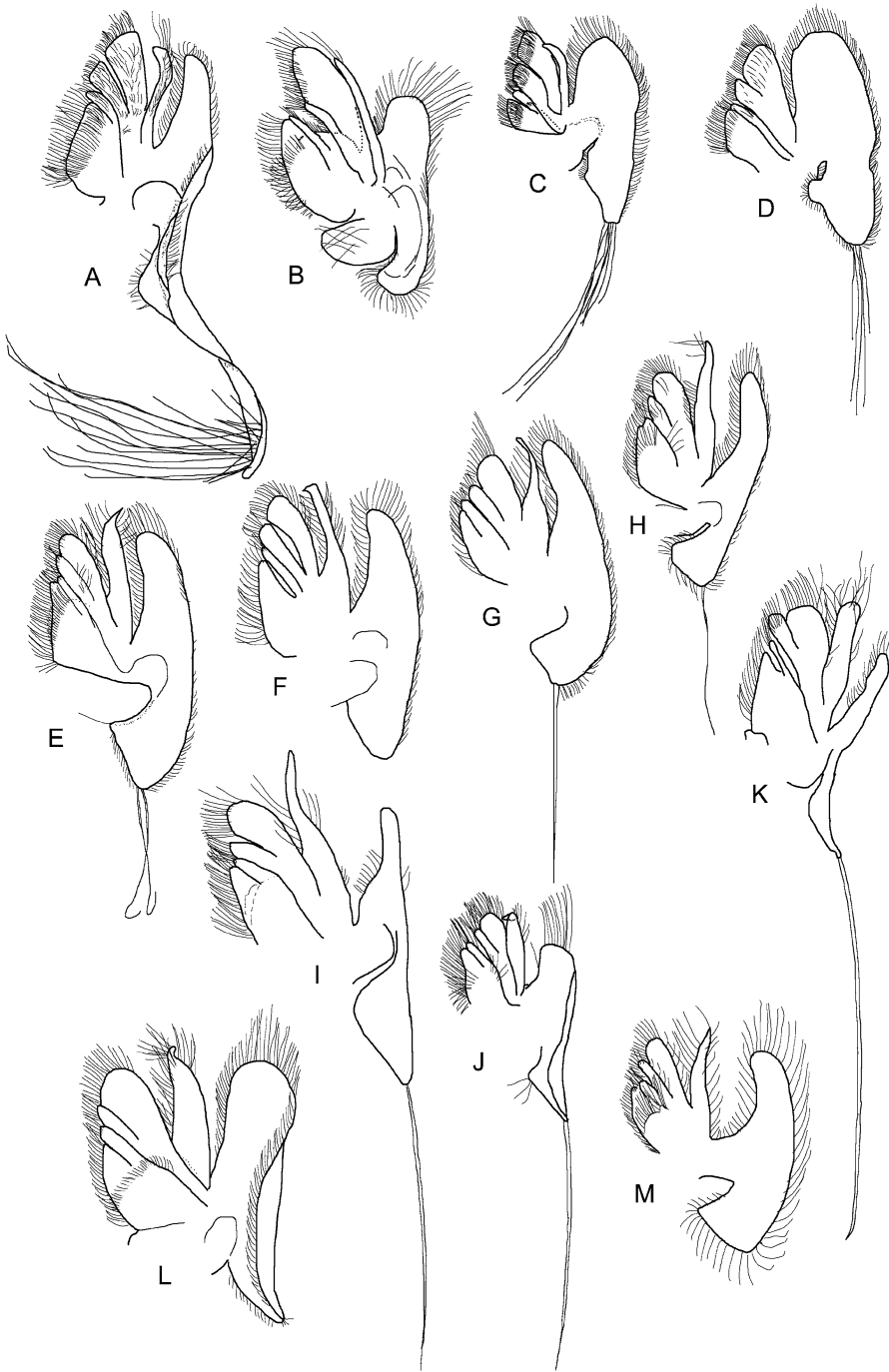


Fig. 69.9. Second maxilla: A, *Thalassinia krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3F]; B, *Upogebia acanthura* [modified from Williams, 1993, fig. 6e]; C,

most callianassids lack the exopod with the exception of reduced to vestigial ones in the genera *Calliixina* and *Lepidophthalmus*. Among the Ctenochelidae only *Gourretia* has an exopod, while it is lacking in *Ctenocheles* and *Dawsonius*. In *Thomassinia* and many Callianassidae, the ischium-merus is expanded and can be as long as high (**operculiform**). One or several strong spines on the lower distal border of the merus are usually present in all Axiidae, Strahlaxiidae, Calocarididae, and in a few Callianassidae (*Calliapagurops*). The propodus is usually slender, but may be broadly expanded in several genera of Callianassidae, whereas the dactylus is broadly rounded in *Thomassinia* and some callianassids (*Calliix*, *Eucalliix*, and *Calliixina*). On the mesial face of the ischium is a row of denticles (sometimes ridged) and the denticles become larger distally, often projecting above the ischium-merus junction. This row of teeth, the **crista dentata** (fig. 69.12M) is present in most genera, but is often reduced or lacking in micheleids and in a few callianassids. Upogebiidae generally lack the crista dentata except for one genus, *Acutigebia*.

First pereopod. – The first pereopod (figs. 69.13 and 69.14) is **chelate** or **subchelate** in all Axiidea and Gebiidea. In all families except Thomassiniidae, Callianideidae, Callianassidae, and Ctenochelidae, the ischium is much shorter than the merus and fused with the latter (Thalassinidae), or it can be flexed at the ischium-merus junction by only 10° (Upogebiidae and Strahlaxiidae). In Callianassidae, an angle of more than 70° can be reached between flexed and extended at the ischium-merus articulation. The carpus is triangular or is cup-shaped and is usually much shorter than the merus and the propodus, except in many Callianassidae.

Thalassinidae, Axianassidae, Axiidae, Strahlaxiidae, Eiconaxiidae, and Thomassiniidae have slightly **unequal chelipeds**, whereas the chelipeds do not differ between sides in Upogebiidae, Laomediidae, Micheleidae, and Calocarididae. A strong **heterochely** occurs in Callianideidae, Callianassidae, and Ctenochelidae. In upogebiids, the chelipeds are stout in the chelate forms, more slender and spiny when subchelate. An unusual first pereopod occurs in *Gebiacantha laurentae* Ngoc-Ho, 1989 where carpus and propodus are fused and show a deep excavation and numerous spines (fig. 69.13D). In Laomediidae the first pereopods are stout and heavy (*Laomedia*), elongate (*Jaxea*), or flattened dorsoventrally (*Naushonia*). The **chelae** are stout and heavy in Strahlaxiidae, Eiconaxiidae, and most Axiidae. In the latter family, there occur also elongate, often very spiny chelae (*Acanthaxius*), whereas Calocarididae have chelae with long fingers. The chelae of Callianassidae are ventrally flattened, and the upper border of the carpus is expanded mesially in some major chelipeds thus forming a shield for the carapace when held flexed

Laomedia paucispinosa [modified from Ngoc-Ho, 1997, fig. 3D]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2G]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1G]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 6C]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5C]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 7B]; I, *Michelea leura* [modified from Poore, 1997, fig. 19E]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37C]; K, *Callianidea typa* [modified from Sakai, 1992b, fig. 4C]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 10B]; M, *Ctenocheles serrifrons* [modified from LeLoeuff & Intès, 1974, fig. 3j].

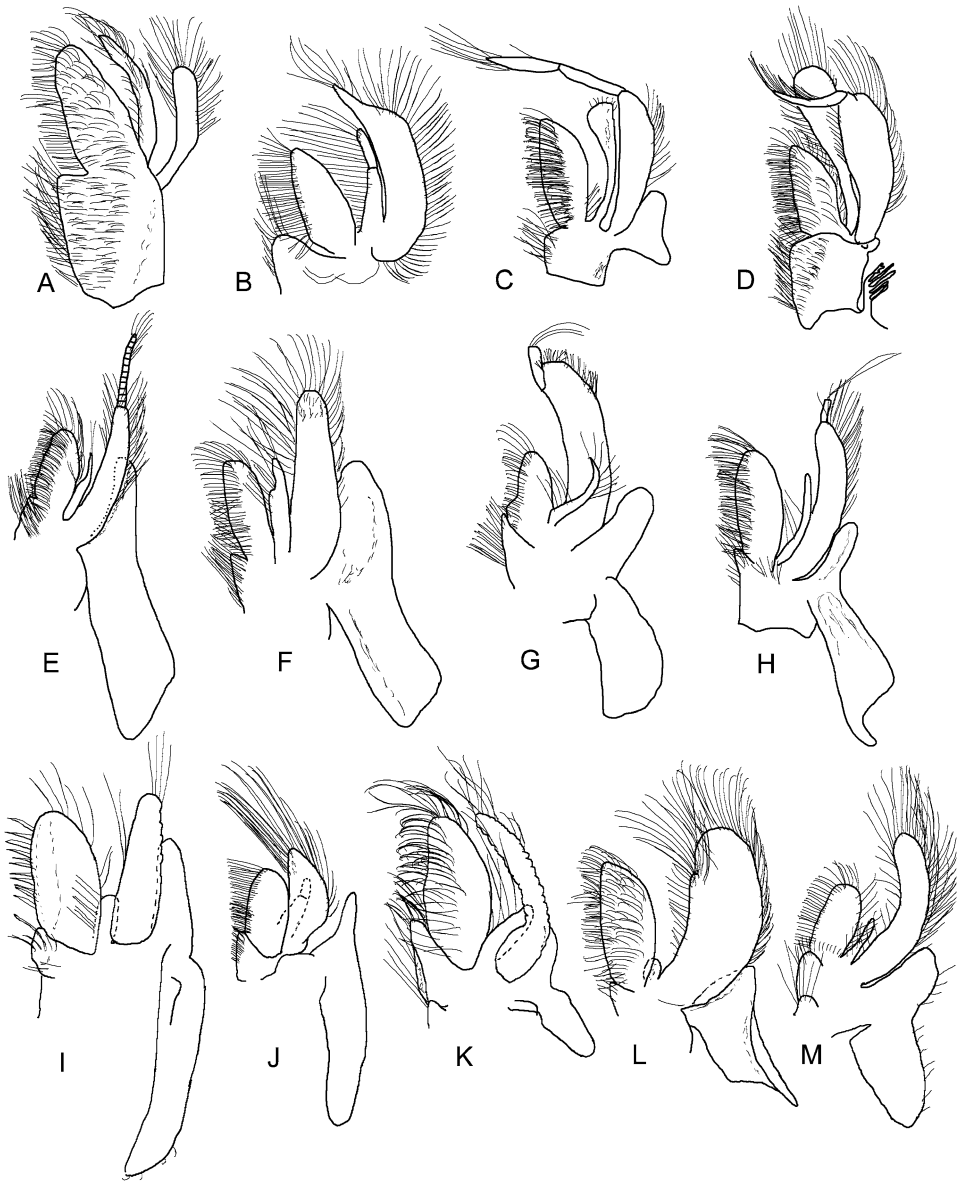


Fig. 69.10. First maxilliped: A, *Thalassina kremphi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3E]; B, *Upogebia acanthura* [modified from Williams, 1993, fig. 6f]; C, *Laomedina paucispinosa* [modified from Ngoc-Ho, 1997, fig. 3F]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2H]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2A]; F, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5D]; G, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7E]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6B]; I, *Michelea leura* [modified from Poore, 1997, fig. 19F]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37E]; K, *Callianidea typa* [modified from Sakai, 1992b, fig. 4D]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 10C]; M, *Ctenocheles serrifrons* [modified from LeLoeuff & Intès, 1974, fig. 3i].

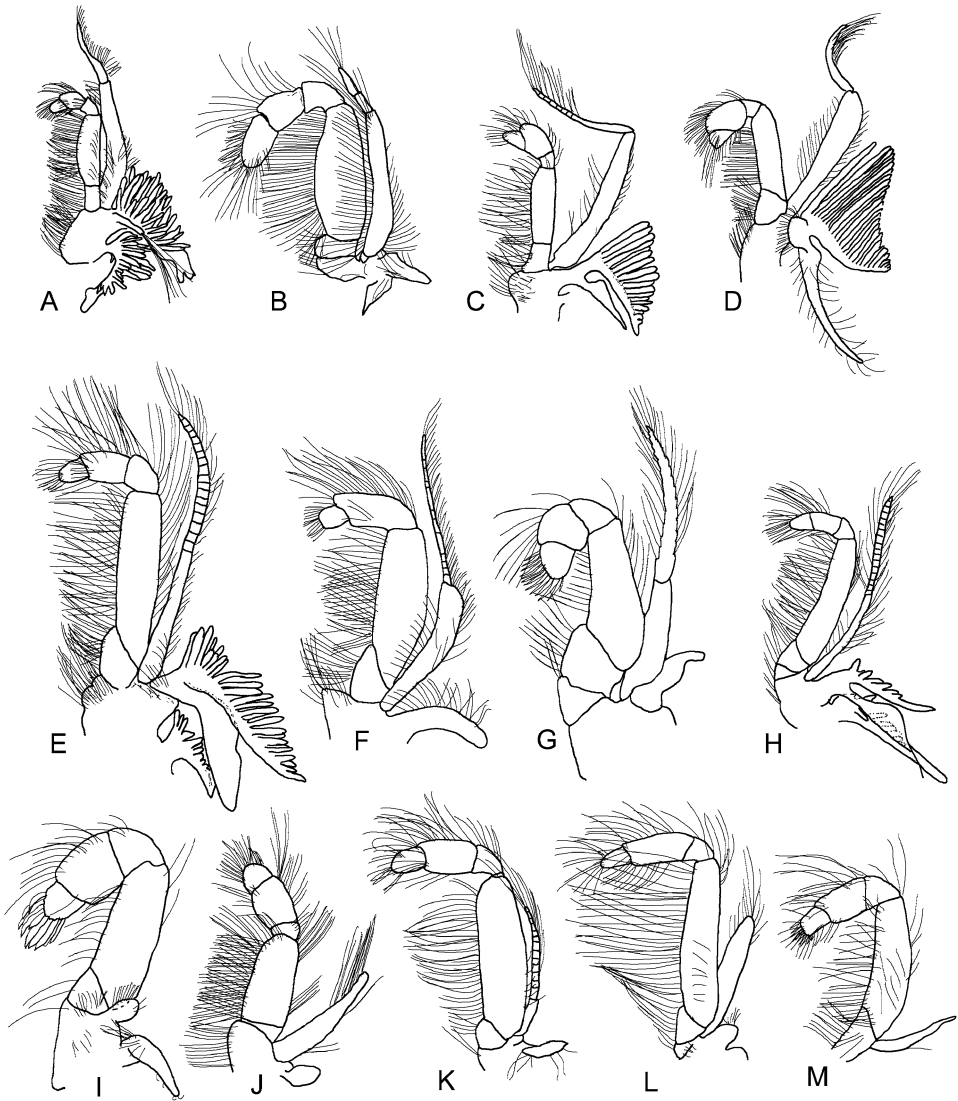


Fig. 69.11. Second maxilliped: A, *Thalassinia krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 4B]; B, *Upogebia acanthura* [modified from Williams, 1993, fig. 6g]; C, *Laomedea paucispinosa* [modified from Ngoc-Ho, 1997, fig. 3G]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2I]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2B]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7F]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5E]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6C]; I, *Michelea leura* [modified from Poore, 1997, fig. 19G]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37G]; K, *Callianidea typa* [modified from Sakai, 1992b, fig. 4E]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 10D]; M, *Ctenocheles serrifrons* [modified from LeLoeuff & Intès, 1974, fig. 3h].

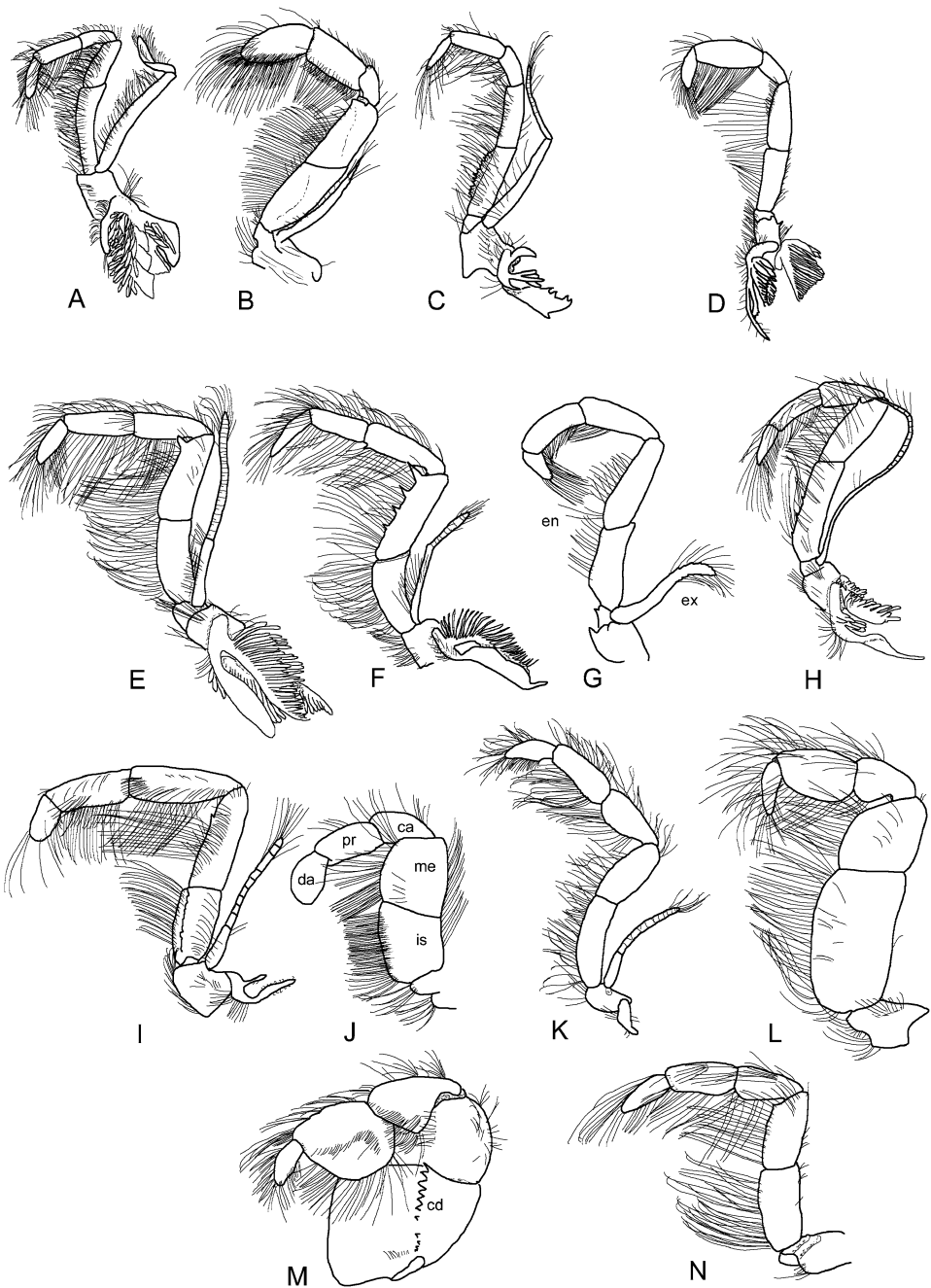


Fig. 69.12. Third maxilliped: A, *Thalassinia krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 4C]; B, *Upogebia acanthura* [modified from Williams, 1993, fig. 6h]; C, *Laomedea paucispinosa* [modified from Ngoc-Ho, 1997, fig. 3H]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 2J]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2C];

(*Callianassa ceramica* Fulton & Grant, 1906 and *Callianassa filholi* A. Milne-Edwards, 1878). All articles of the major cheliped in males of the callianassid genus *Callichirus* are extremely elongate (fig. 69.14C). The major cheliped of *Ctenocheles* is pectinate, having a bulbous propodus and very long and slender toothed fingers (fig. 69.14E).

Second pereopod. – The second pereopod is subchelate in Thalassinidae (fig. 69.15A), simple in Upogebiidae, Laomediidae, and Axianassidae (fig. 69.15B-D). It is, however, fully chelate in all families of Axiiidea (fig. 69.15E-M), providing a **diagnostic character** for separation of the infraorders. The lower border bears a row of setae on ischium to propodus in all families. This was previously considered a **synapomorphic character** supporting **monophyly** of the Thalassinidea in the phylogenetic study based on morphology by Poore (1994), but must now be regarded as a **convergent adaptation**. This setal row forms a **basket** between the flexed opposing second pereopods and is used in **burrowing** for lifting sediment. However, in Calocarididae the setation is sparse and is restricted to a few short setae only on the propodus in Eiconaxiidae. In Upogebiidae, the setae are very long and occur in two rows and form, together with the setae of the first pereopods, a basket that is used for the interception of particles in **suspension feeding**. The chelae (when present) are used to initially loosen the sediment or working sediment into the burrow wall.

Third pereopod. – This appendage (fig. 69.16) is pediform, slender in Calocarididae and Laomediidae, and broadened in Thomassiniidae. There is great variation in the shape of the propodus, which can be linear, triangular, or rounded, especially in Callianassidae, where the propodus is often expanded proximally and appears heeled (fig. 69.16M). Here, it is used like a trowel to loosen sediment or to plaster and smooth the burrow wall (Dworschak, 1998).

Fourth pereopod. – The fourth pereopod (fig. 69.17) is very similar to the third pereopod, except in Micheleidae, Thomassiniidae, Callianideidae, Callianassidae, and Ctenochelidae where the propodus is more slender than that of the third pereopod. In Upogebiidae, some Micheleidae, Callianideidae, and Thomassiniidae the coxa of the fourth pereopod is immobile (Poore, 1994). This appendage is mainly used for **walking** (the ischium-merus held upwards and the distal articles extended forwards within the burrow) and **grooming**, especially of the dorsal face of cephalothorax and antennae.

Fifth pereopod. – The fifth pereopod, whose base is usually not covered by the carapace, is similar to the fourth pereopod, but usually shorter and more slender (fig. 69.18). The dactylus is unguulate in *Thalassina*, Laomediidae, and Axianassidae, rounded in Eiconaxiidae and Thomassiniidae, and simple in Calocarididae. A subchela is formed with

F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7G]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5F]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6D]; I, *Michelea leura* [modified from Poore, 1997, fig. 19H, I]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37H]; K, *Callianidea typa* [modified from Sakai, 1992b, fig. 4F]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9D]; M, *Corallianassa collaroy* [modified from Sakai, 1992a, fig. 1c]; N, *Ctenocheles balssi* [modified from Sakai, 1999a, fig. 2a]. All except M in lateral view; en, endopod; ex, exopod; is, ischium; me, merus; ca, carpus; pr, propodus; da, dactylus; cd, crista dentata.

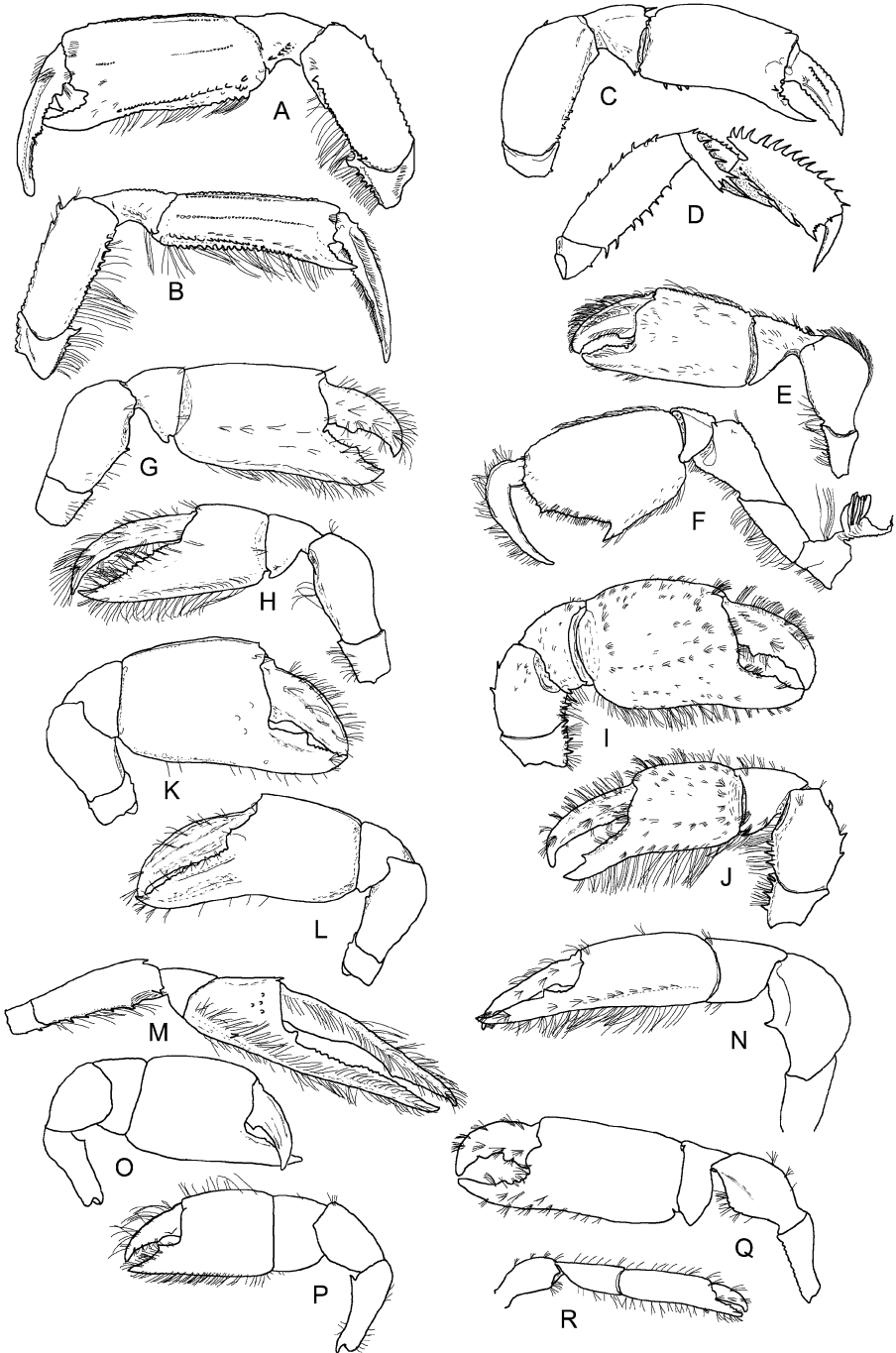


Fig. 69.13. Pereiopod 1 (major/minor): A, B, *Thalassina emerii* Bell, 1844 [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 6A, B]; C, *Upogebia deltaura* [modified from Ngoc-Ho, 2003,

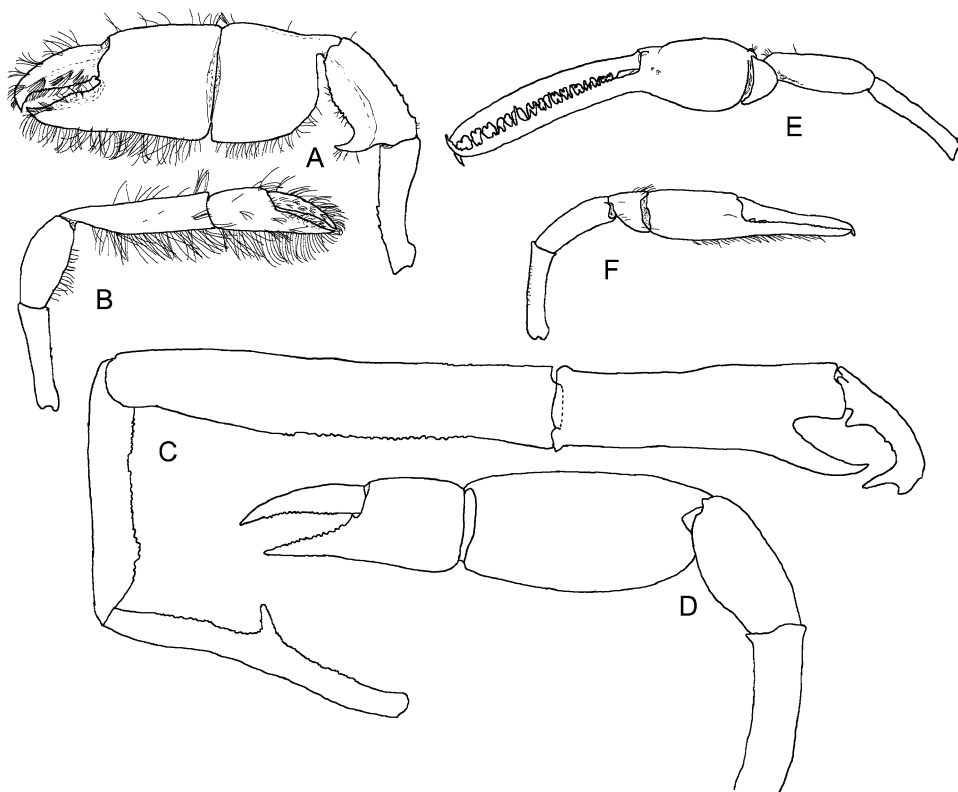


Fig. 69.14. Pereiopod 1 (major/minor): A, B, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9B, C]; C, D, *Callinectes islagrande* [modified from Manning & Felder, 1986, fig. 2c, d]; E, F, *Ctenocheles balssi* [modified from Sakai, 1999a, fig. 2b, c].

the simple dactylus and the ventrodistal protrusion of the propodus in Upogebiidae, Axiidae, Strahlaxiidae, Micheleidae, Callianideidae, Callianassidae, and Ctenochelidae. This appendage is very flexible in callianassids and upogebiids and used for **grooming**, as it can reach almost every location of the body including the **gill chamber** (Batang & Suzuki, 2003). In Thalassinidae and Laomediidae, the fifth pereopod is not used for cleaning of the gills (Batang & Suzuki, 1999; Batang et al., 2001). In these families, grooming of the

fig. 23A); D, *Gebiacantha laurentae* Ngoc-Ho, 1989 [modified from Ngoc-Ho, 1994, fig. 1B]; E, *Laomedia astacina* [modified from Ngoc-Ho, 1997, fig. 1D]; F, *Naushonia carinata* [modified from Dworschak et al., 2006b, fig. 5a]; G, H, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1B, C]; I, J, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 6E, F]; K, L, *Eiconaxius farrae* [modified from Sakai & Ohta, 2005, fig. 2A, B]; M, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6H]; N, *Marcusiaxius lemoscastroi* Carvalho & Rodrigues, 1973 [modified from Kensley & Heard, 1991, fig. 10A]; O, P, *Thomassinia gebioides* [modified from Poore, 1997, fig. 36E, F]; Q, R, *Callianidea laevicauda* [modified from Kensley & Heard, 1991, fig. 3D, E].

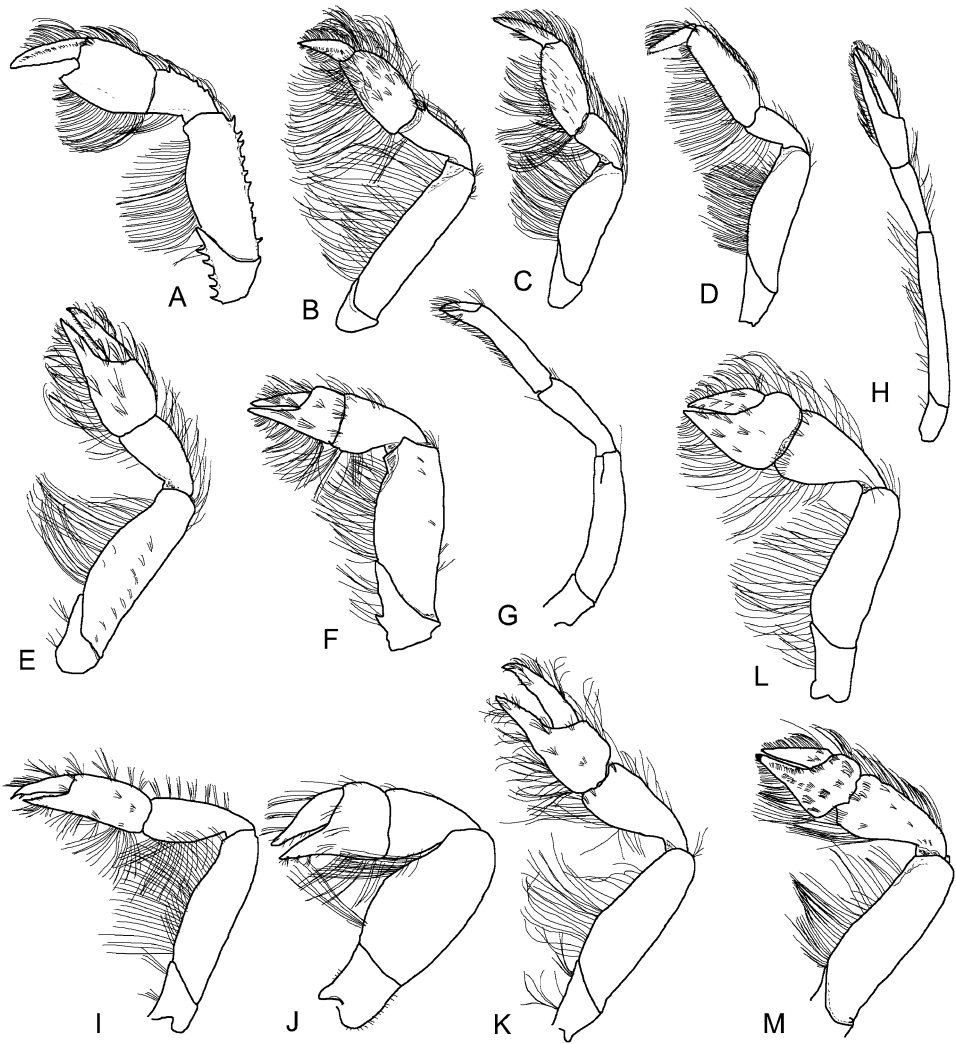


Fig. 69.15. Second pereiopod: A, *Thalassinia spinosa* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 10E]; B, *Upogebia deltaura* [modified from Ngoc-Ho, 2003, fig. 27B]; C, *Laomedea astacina* [modified from Ngoc-Ho, 1997, fig. 1F]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 3D]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2H]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7A]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5I]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6I]; I, *Michelea leura* [modified from Poore, 1997, fig. 18C]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 36G]; K, *Callianidea tyta* [modified from Sakai, 1992b, fig. 5A]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9I]; M, *Ctenocheles balsi* [modified from Sakai, 1999a, fig. 2d].

gills is passive, with **setiferous epipods** and **setobranchs**. In addition, the fifth pereiopod is used for walking, extended backwards and pushing the shrimp forward in its burrow.

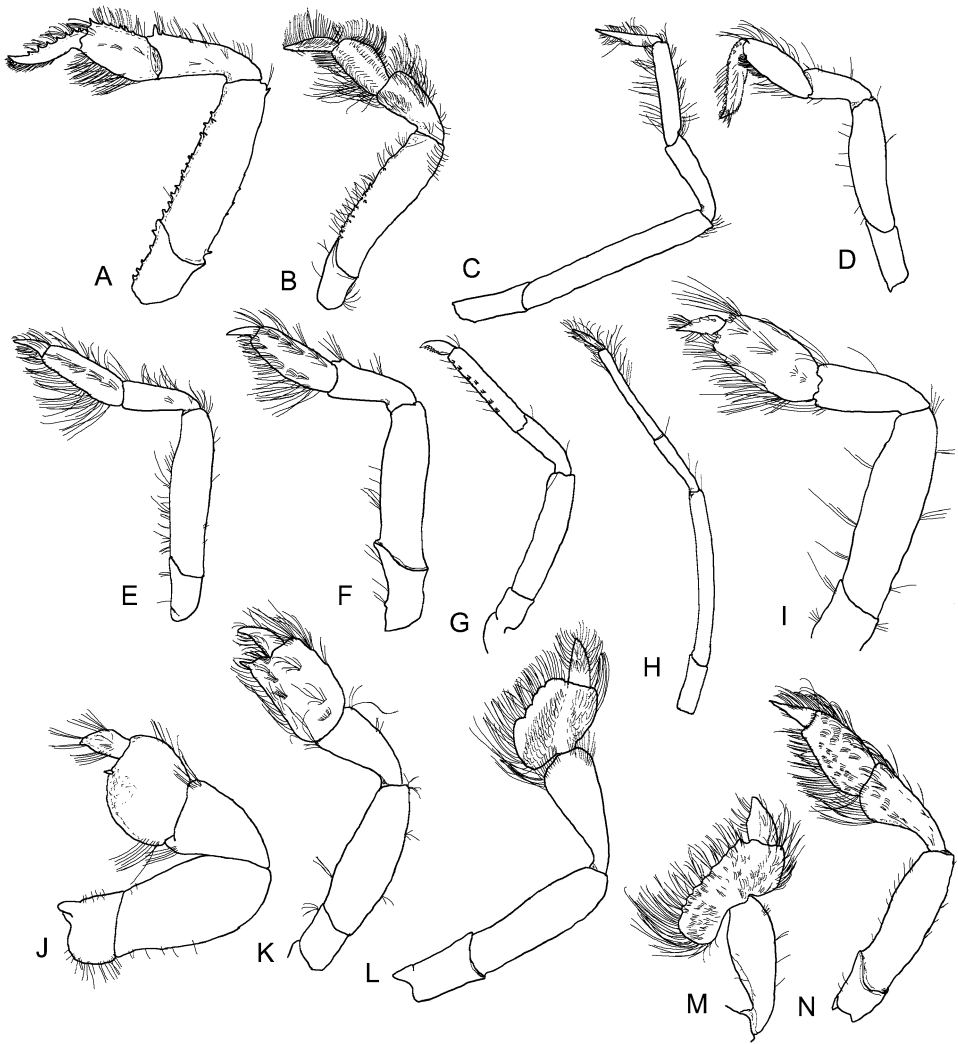


Fig. 69.16. Third pereopod: A, *Thalassina anomala* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 5E]; B, *Upogebia deltaura* [modified from Ngoc-Ho, 2003, fig. 27B]; C, *Jaxea nocturna* [modified from Ngoc-Ho, 2003, fig. 23F]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 3E]; E, *Axius stirrhynchus* [modified from Ngoc-Ho, 2003, fig. 2I]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7B]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5J]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6J]; I, *Michelea leura* [modified from Poore, 1997, fig. 18E]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 36I]; K, *Callianidea tya* [modified from Sakai, 1992b, fig. 5B]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9J]; M, *Neocallichirus audax* (De Man, 1911) [modified from Sakai, 1999b, fig. 21d]; N, *Ctenocheles balsi* [modified from Sakai, 1999a, fig. 2e].

PLEON

First pleopod. – The first pleopod is **sexually dimorphic**. It is lacking in **males** of Upogebiidae, Laomediidae, Strahlaxiidae, Eiconaxiidae, and in numerous Callianassidae. In

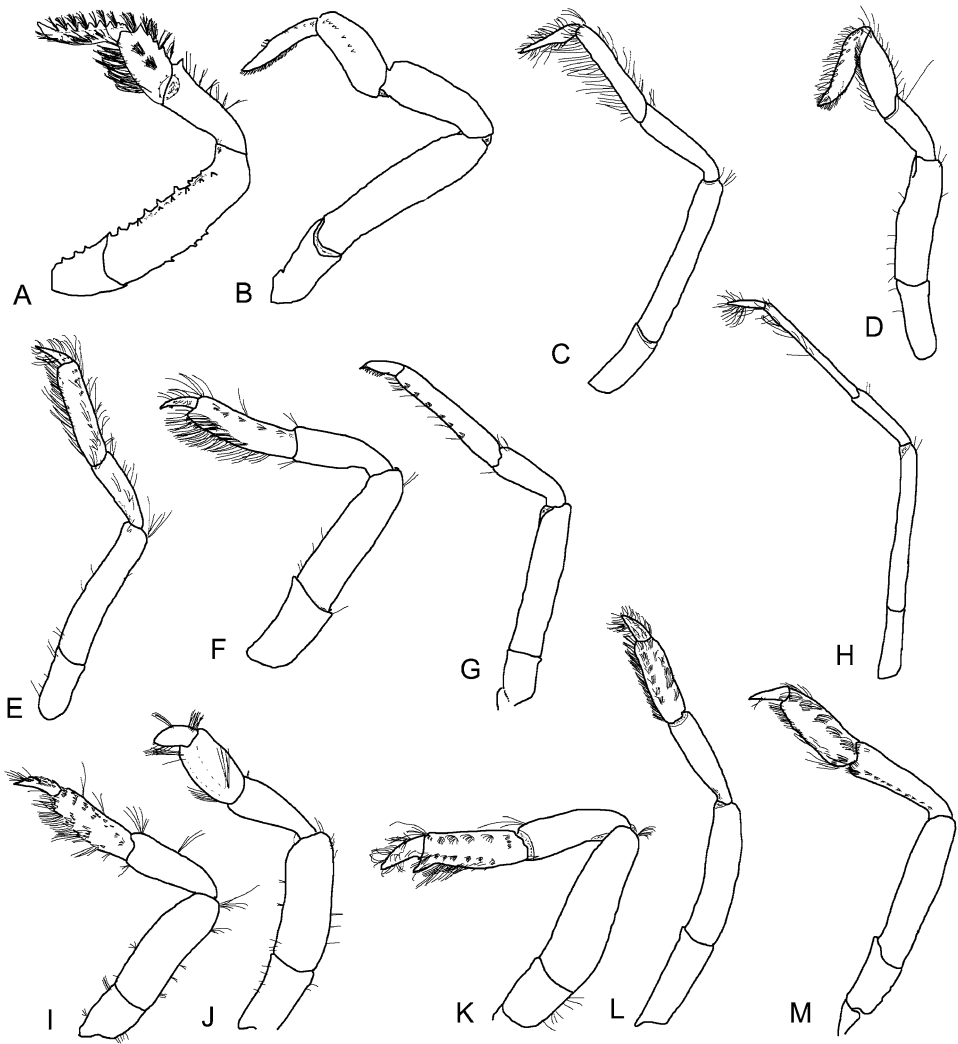


Fig. 69.17. Fourth pereiopod: A, *Thalassinoma anomala* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 5F]; B, *Upogebia deltaura* [modified from LeLoeuff & Intès, 1974, fig. 19f]; C, *Jaxea nocturna* [modified from Ngoc-Ho, 2003, fig. 23G]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 3F]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2J]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7C]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5K]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6K]; I, *Michelea leura* [modified from Poore, 1997, fig. 18F]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 36K]; K, *Callianidea typa* [modified from Sakai, 1992b, fig. 5C]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9K]; M, *Ctenocheles balssi* [modified from Sakai, 1999a, fig. 2h].

Thalassinoma, the male first pleopod is uniramous, unsegmented with a vestigial **appendix interna** mesiodistally (fig. 69.19A). The right and left pleopods are placed with appendices

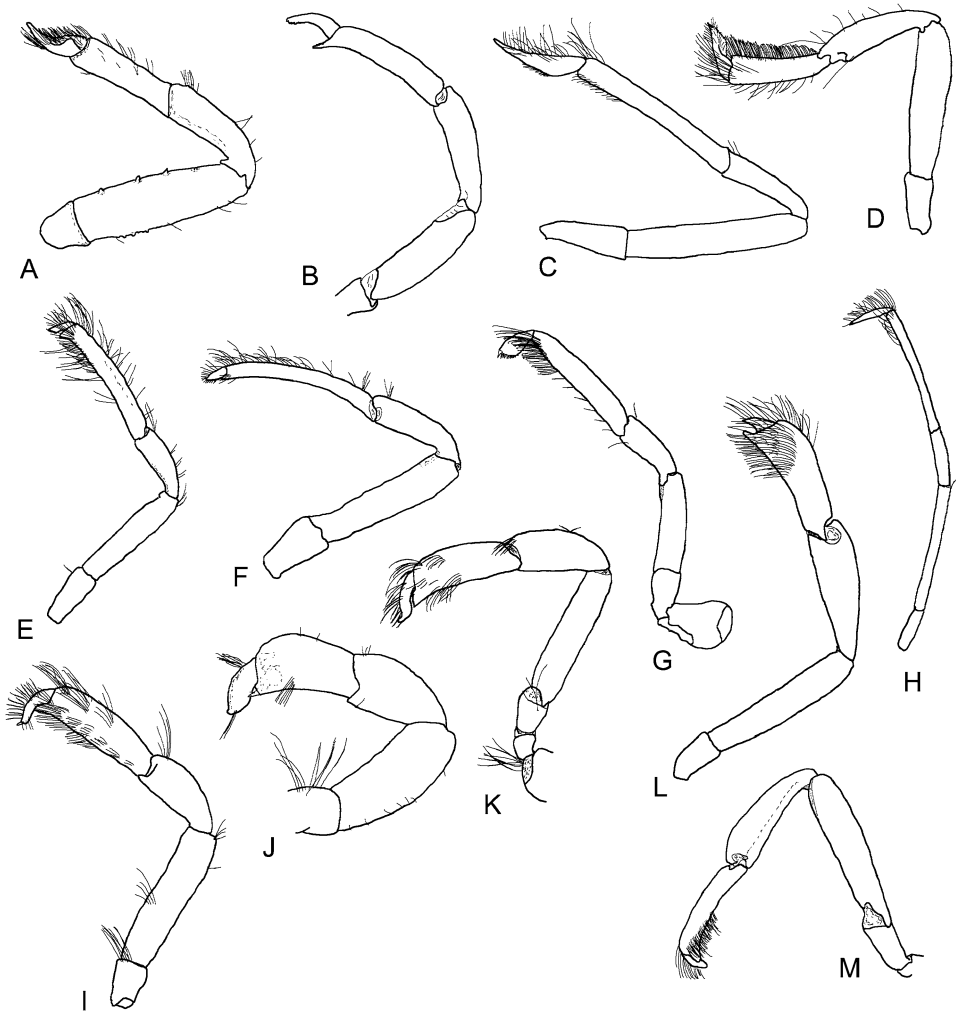


Fig. 69.18. Fifth pereopod: A, *Thalassinia kremphi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 9G]; B, *Upogebia deltaura* [modified from LeLoeuff & Intès, 1974, fig. 19g]; C, *Jaxea nocturna* [modified from Ngoc-Ho, 2003, fig. 23H]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 3G]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2I]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 7D]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5L]; H, *Calocaris macandreae* [modified from Ngoc-Ho, 2003, fig. 6L]; I, *Michelea leura* [modified from Poore, 1997, fig. 18G]; J, *Thomassinia gebioides* [modified from Poore, 1997, fig. 36L]; K, *Callianidea typa* [modified from Sakai, 1992b, fig. 5D]; L, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9L]; M, *Ctenocheles balssi* [modified from Sakai, 1999a, fig. 2g].

internae adpressed and facing the **gonopores** on the coxae of the fifth pereopods. Male Micheleidae have a similar first pleopod (fig. 69.19E), while it is simple (fig. 69.19B) or lacking in Axiidae and Callianideidae. In Calocarididae, it consists of two articles, is di-

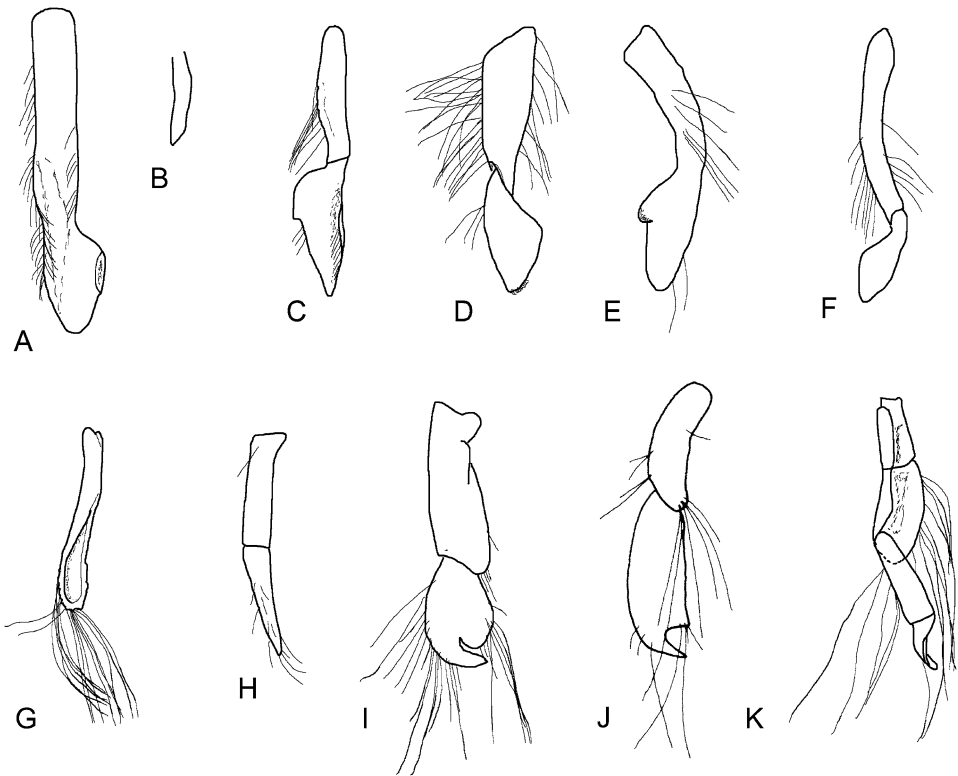


Fig. 69.19. First pleopod (male): A, *Thalassina krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3I]; B, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2E]; C, *Spongiaxius brucei* [modified from Sakai, 1986, fig. 6C]; D, *Calocaris macandreae* (hermaphrodite) [modified from Ngoc-Ho, 2003, fig. 7C]; E, *Michelea paraleura* [modified from Poore, 1997, fig. 24E]; F, *Crosniera minima* (Rathbun, 1901) [modified from Kensley & Heard, 1991, fig. 5H]; G, *Callianidea typa* [modified from Sakai, 1992b, fig. 5E]; H, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9G]; I, *Neocallichirus lemaitrei* Manning, 1993 [modified from Felder & Manning, 1995, fig. 6b]; J, *Gourretia coolibah* [modified from Dworschak, 2009, fig. 18]; K, *Ctenocheles balssi* [modified from Sakai, 1999a, fig. 3a].

rected anteromesially along the posterior thoracic sternites, and the distal article is broadened with cincinnuli mesiodistally (fig. 69.19D). In Thomassiniidae and Callianideidae, the male first pleopod has two articles, the distal one expanded with a vestigial appendix interna (fig. 69.19G). When present, the male first pleopod is a simple bud and consists of one or two articles in the callianassid subfamily Callianassinae (fig. 69.19H). In the other callianassid subfamilies, the distal article is bilobed and hooked, with one rounded and one acute tip (fig. 69.19I). In Ctenochelidae, the distal article is similar to the latter ones in *Dawsonius*, is hooked with two acute tips in *Gourretia* (fig. 69.19J) and uniramous, and is composed of four articles with the two proximal articles flattened in *Ctenocheles* (fig. 69.19K).

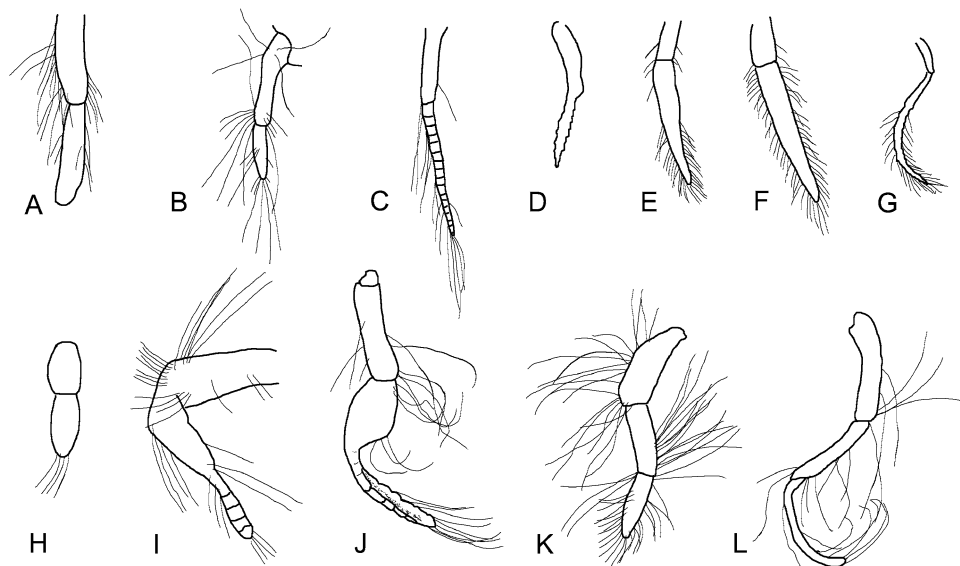


Fig. 69.20. First pleopod (female): A, *Thalassinia krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3H]; B, *Upogebia aristata* [modified from LeLoeuff & Intès, 1974, fig. 16r]; C, *Jaxea nocturna* [modified from Ngoc-Ho, 2003, fig. 22H]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 3B]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1L]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 6G]; G, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5G]; H, *Michelea leura* [modified from Poore, 1997, fig. 18I]; I, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37I]; J, *Callianidea typa* [modified from Sakai, 1992b, fig. 5G]; K, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9O]; L, *Ctenocheles balssi* [modified from Sakai, 1999a, fig. 3e].

The first pleopod is present in all **females** (fig. 69.20). It is uniramous, consisting of one (Axianassidae), two (most families), or three (some Callianassidae and some Ctenocheilidae) articles, with the distal part sometimes appearing as a **flagellum** (Laomediidae, Thomassiniidae, Callianideidae). The first pleopod is used for **attaching the eggs**.

Second pleopod. – The endopod and exopod are slender in Thalassinidae, Laomediidae, Axianassidae, Eiconaxiidae, Calocarididae, and Callianassidae (figs. 69.21 and 69.22); all taxa also show second pleopods in males. In Callianassidae, the second pleopod is more slender than the third to fifth. The other families have broad rami. An **appendix masculina** is present in the male second pleopods of most families except Upogebiidae, Laomediidae, Axianassidae, Strahlaxiidae, Eiconaxiidae, and many callianassids (Callianassinae). An appendix interna is present in most families on the endopod, or on the appendix masculina (in males only), except in Upogebiidae, Laomediidae, Axianassidae, several axiid genera (*Eutrichocheles* and *Paraxiopsis*), and many callianassids (Callianassinae). In Calocarididae, the appendix masculina is enlarged (*Ambiaxius*, fig. 69.21G) and in most callianassids with male second pleopods the appendix masculina is often indistinctly demarcated from the endopod, and the appendix interna is present only as a field of cincinnuli.

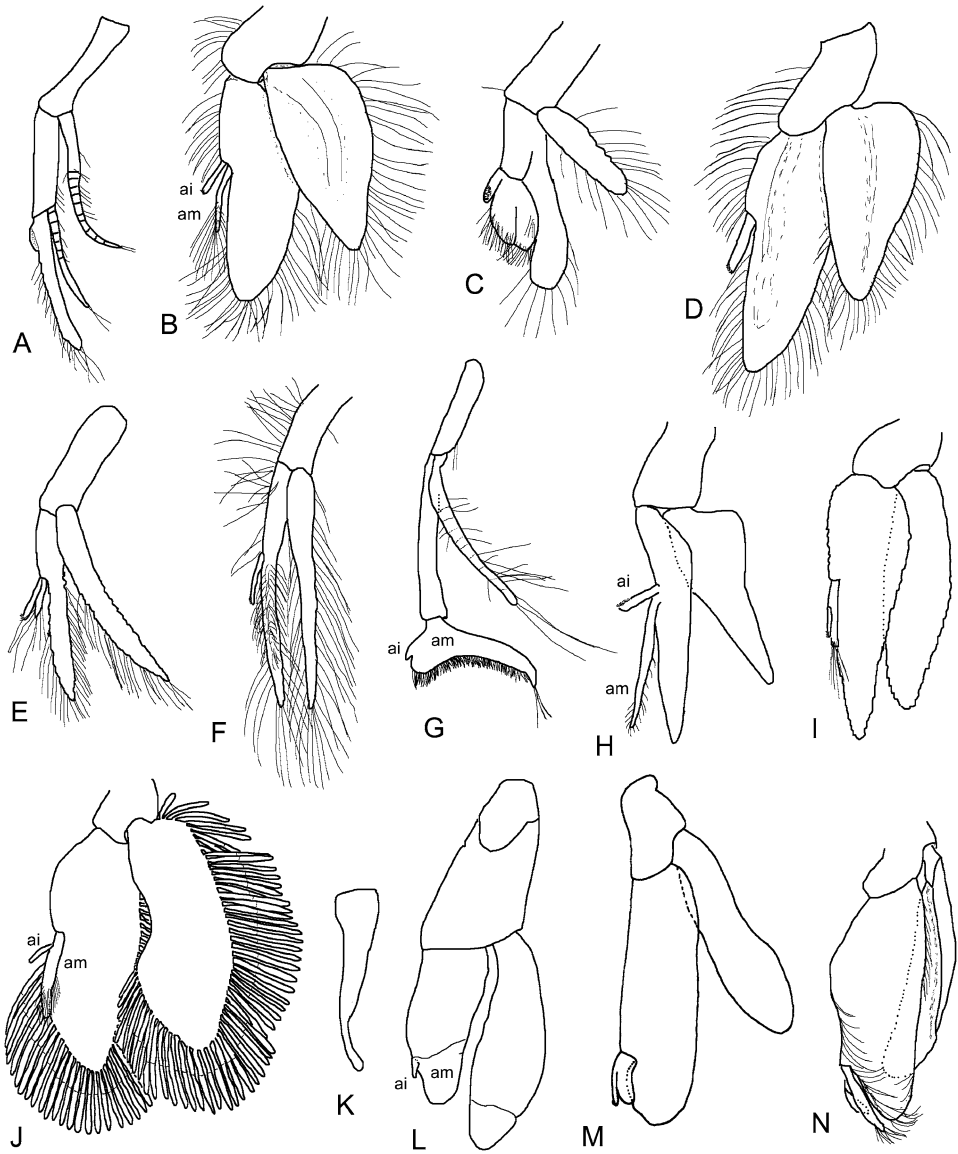


Fig. 69.21. Second pleopod (male): A, *Thalassina krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3J]; B, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 2F]; C, *Coralaxius abelei* [modified from Kensley & Gore, 1981, fig. 6h]; D, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 6I]; E, *Eiconaxius albatrossae* [modified from Kensley, 1996b, fig. 5H]; F, *Calocaris macandreae* (hermaphrodite) [modified from Ngoc-Ho, 2003, fig. 7D]; G, *Ambiaxius surugaensis* (hermaphrodite) [modified from Sakai & Ohta, 2005, fig. 10F]; H, *Michelea vandoverae* [modified from Kensley & Heard, 1991, fig. 21J]; I, *Crosniera minima* [modified from Kensley & Heard, 1991, fig. 5I]; J, *Callianidea laevicauda* [modified from Kensley & Heard, 1991, fig. 4I]; K, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9H]; L, *Lepidophthalmus tridentatus* [modified

Third to fifth pleopod. – The third to fifth pleopods (fig. 69.23) are of similar shape to the second in all families except Callianassidae and Ctenochelidae (see above and fig. 69.22), including the presence or absence of an appendix interna. In Callianassidae, the endopod and exopod are very broad and the appendices internae are of different shapes (finger-like to stubby and embedded in the endopod), which allow interlocking between the two sides. In Callianideidae, the second to fifth pleopod rami are variously fringed with **filaments** (fig. 69.22I) or **lamellae** (presumed to have a supplemental **respiratory function**). Such foliaceous rami also occur in Micheleidae (fig. 69.22G), but they are considered quite different from those in callianideids and are not homologous (Poore, 1994, 1997). The third to fifth pleopods are used, via intermittent beating, for irrigation of the burrow or support of a forward movement within the burrow, and (in females) for the attachment of the eggs.

Uropod. – The uropodal endopod and exopod (fig. 69.4) are similar, slender, and unarmed in *Thalassinina*. Both uropods are much broader and of various shapes in all other families. There are various spines along the borders and on the dorsal surfaces, especially in Axiidae. A **suture**, both on endopod and exopod, occurs in Laomediidae (except *Saintlaurentiella* where the suture is only on the exopod) and all Axiidae only have a suture on the exopod. In Callianassidae and some Ctenochelidae, the anterior part of the exopod is more or less elevated and forms a “**dorsal plate**” fringed distally by setae.

INTERNAL MORPHOLOGY

General reviews of the internal systems of all decapods are provided by both McLaughlin (1980, 1983) and Felgenhauer (1992b). The following synthesis is thus limited to subsequent or more detailed works specific to thalassinidean internal systems.

Nervous, neuromuscular, and neurosensory organization

The general design of the **central nervous system** has been illustrated for several genera, in limited ways representing both of the infraorders and reaching back to the early work of Bouvier (1889) and Pike (1947). As in the design of other systems, what initially appears as very similar organization in Gebiidea and Axiidea, differs in fundamental ways, with Gebiidea sharing some features of gross anatomy with anomuran groups.

The dissertation of Rodrigues (1966) provides the best overview of gross anatomy in a thalassinidean nervous system (fig. 69.24A, B), being based on the axiidean species *Sergio mirim* (Rodrigues, 1971) of Callianassidae, which has been previously treated under *Callichirus* or *Callianassa* (the genus *Sergio* is polyphyletic, pending revision, Felder & Robles, 2009). In general design, a massive **supraesophageal ganglion** (SEG) or **brain**

from Sakai, 1999b, fig. 14e]; M, *Gourettia coolibah* [modified from Dworschak, 2009, fig. 19]; N, *Ctenocheles balssi* [modified from Sakai, 1999a, fig. 3b]. Abbreviations: ai, appendix interna; am, appendix masculina.

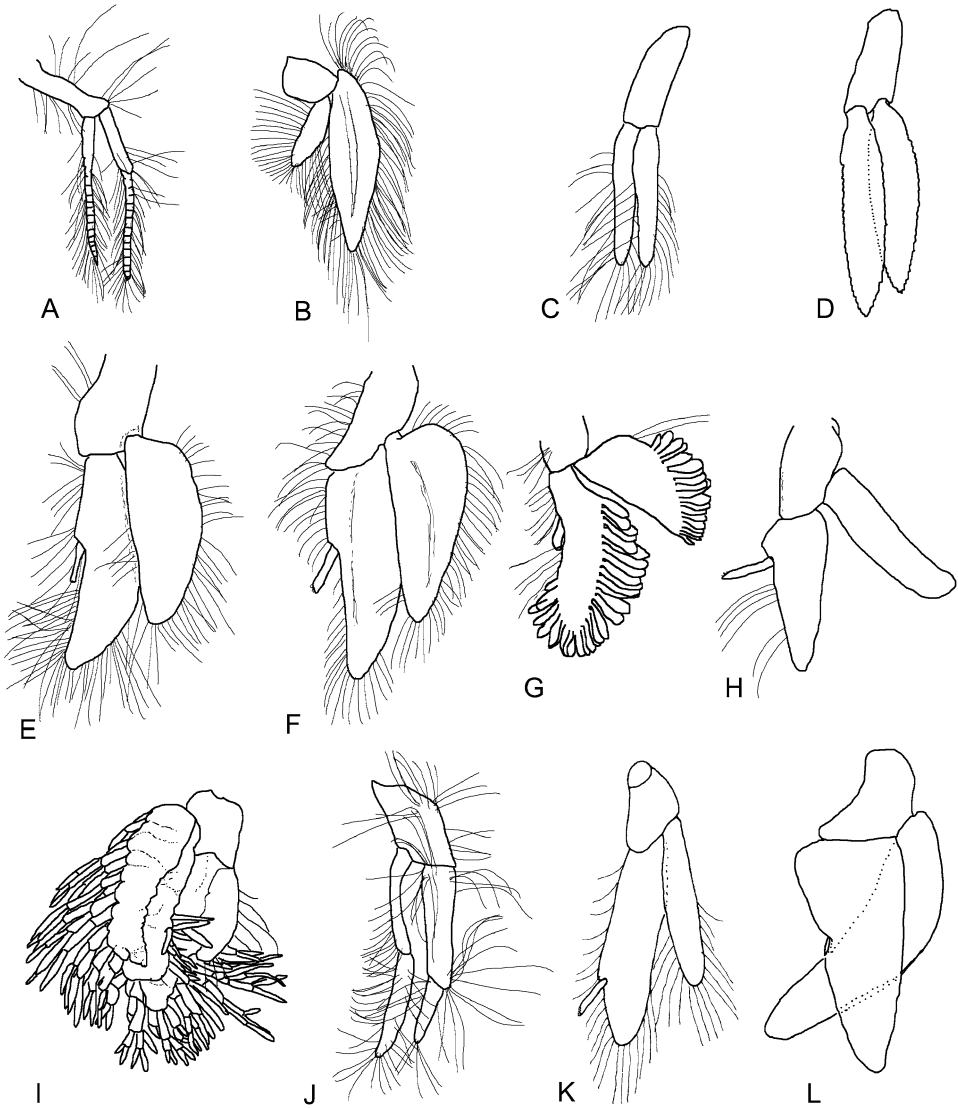


Fig. 69.22. Second pleopod (female): A, *Thalassinia krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3G]; B, *Upogebia lincolni* [modified from Ngoc-Ho, 1977a, fig. 3E]; C, *Laomedea paucispinosa* [modified from Ngoc-Ho, 1997, fig. 2F]; D, *Axianassa intermedia* [modified from Kensley & Heard, 1990, fig. 3C]; E, *Axius stirhynchus* [modified from Ngoc-Ho, 2003, fig. 1M]; F, *Neaxius trondlei* [modified from Ngoc-Ho, 2005, fig. 6H]; G, *Michelea leura* [modified from Poore, 1997, fig. 18J]; H, *Thomassinia gebioides* [modified from Poore, 1997, fig. 37J]; I, *Callianidea typa* [modified from Sakai, 1992b, fig. 5H]; J, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9P]; K, *Gourretia coolibah* [modified from Dworschak, 2009, fig. 11]; L, *Ctenocheles balsasi* [modified from Sakai, 1999a, fig. 3h].

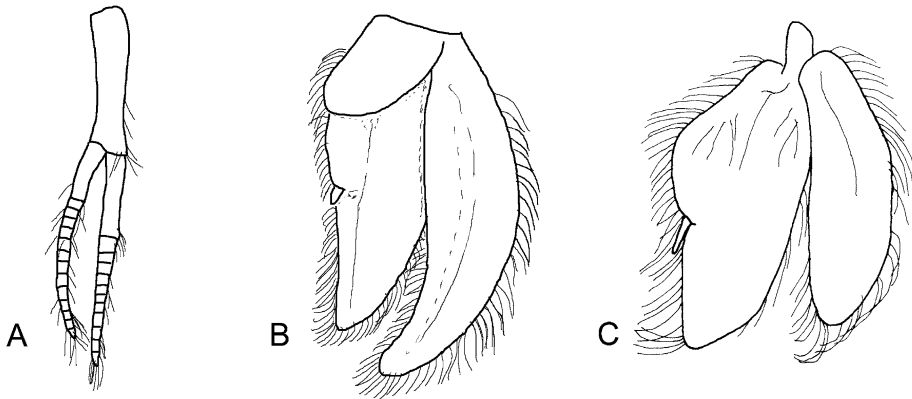


Fig. 69.23. Third pleopod: A, *Thalassina krempfi* [modified from Ngoc-Ho & de Saint Laurent, 2009, fig. 3K]; B, *Callianassa subterranea* [modified from Ngoc-Ho, 2003, fig. 9N]; C, *Gourretia coolibah* [modified from Dworschak, 2009, fig. 27].

is evident immediately behind the **ocular peduncles**, with major **nerve tracts** extending to the eyes, antennae, and surrounding tissues. Extending ventrolaterally to either side are tracts of the **tritocerebrum** or **periesophageal connectives** that extend to the **ventral ganglion chain**, and these give rise to **para-esophageal ganglia** (PEG) to either side of the esophagus, each of which gives rise to four major **nerves**. Two of these innervate walls of the esophagus, while the other two from each side join in the anterior wall of the esophagus to form the **stomatogastric nerve** (SGN), which innervates walls of the very complex stomach and gastric mill apparatus in the foregut. Ventral to the paraesophageal ganglia and immediately posterior to the esophagus, there is a transverse **postesophageal commissure** (PEC) bridging between the periesophageal connectives, which themselves join to the fused **anterior ganglion mass** (AGM) of the ventral nerve tract.

The supraesophageal ganglion or brain in Axiidea and Gebiidea has been studied histologically, but extensively in only the calocaridid *Calocaris macandreae* Bell, 1853 and the callianassid *Trypaea australiensis* Dana, 1852, both of which are axiideans (Scheuring, 1923; Hanström, 1924, 1947; Bullock & Horridge, 1965; Sandeman et al., 1993; Sullivan & Beltz, 2004; Harzsch & Hansson, 2008). However, some comparisons are also made of brain ganglia in *Callianassa* and *Upogebia* (senior synonym of *Gebia*) to those in other decapods, not always with authors reaching full agreement (see Helm, 1928; Hanström, 1947). Assuming that present knowledge will generally apply across a broad selection of genera once studied, the thalassinidean brain is distinct in its overall shape, with the **optic ganglia** largely integrated into a **cerebral mass** and thus giving it a robust trapezoidal shape (fig. 69.24C-E). Instead of a pedunculate optical lobe tract extending to the brain, there is typically a smaller short length of optical nerve that leads to the lamina (L) and thereafter the external and internal medullae (EM, IM) of the **protocerebrum**. These, as well as large lateral protocerebral **neuropils** are in *Trypaea* and *Calocaris* positioned relatively close to the medial protocerebrum. **Olfactory lobes** (ON) dominate the **deutocerebrum** and link to a large **hemiellipsoid body** (HN) by way

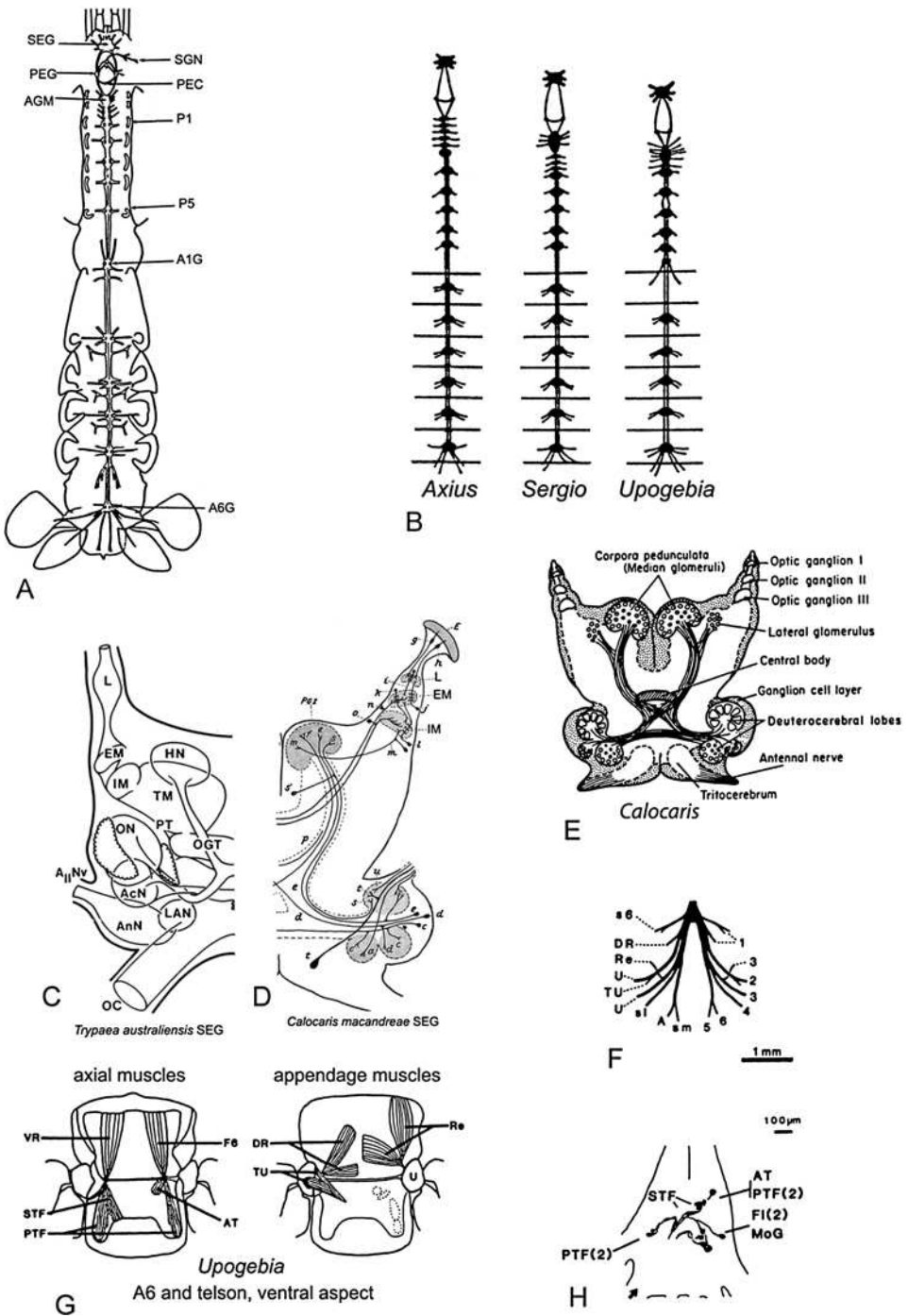


Fig. 69.24. A, central nervous system, ventral perspective, *Sergio mirim* [modified from Rodrigues, 1966, fig. 171]; B, comparative distribution of major central nervous system ganglia for the

of an **olfactory globular tract** (OGT). Overall, the resultant shape of the brain is about as long as broad, but as noted by Sandeman et al. (1993), this is the result of the anteriorly positioned lateral optical protocerebral neuropils becoming fused into the brain proper, and it would otherwise be of the ‘broader than long’ type. The aforementioned authors observe similarities to the crayfish brain, but note divergence from that basic architecture and conclude that all of the then-grouped thalassinideans share this derived character.

Characteristic **accessory lobes** (AcN) are somewhat smaller than the large olfactory lobes and positioned just posterior to them in the deutocerebrum. These accessory lobes are proposed to have originated *de novo* in “eureptantian” decapods, and are joined by a commissure from one side to the other. These may afford a unifying character of lobsters, crayfish, axiideans, and gebiideans, being in all cases among the most prominent of their brain neuropils. Attention has been called to the distinct barrel or spheroid shapes of the **glomeruli** formed by these neuropils in several thalassinidean genera, suggesting that this characteristic histology might also reflect phylogenetic relationships (Sullivan & Beltz, 2004; Harzsch & Hansson, 2008). Additionally, glomerular density in brain olfactory lobes and convergence of receptor neurons onto these olfactory glomeruli, has been examined in *Trypaea*, as compared to selected other decapods (Beltz et al., 2003). *Trypaea* exhibited comparatively low glomerulus counts and low convergence of neurons per olfactory glomerulus, placing it to some surprise among a group of mud- and mangrove-dwelling intertidal crabs that spend part of their time in air. While *Trypaea* was seen as the exception, that may not be the case as facultative respiration occurs in both axiideans and gebiideans under oxygen stress at low tide (Felder, 1979; Hill, 1981).

Posterior to the cephalic ganglia, the chain of ganglia associated with the **paired ventral nerve cord** reflects an expected pattern of **somite tagmosis**, but with variations in how tightly fused thoracic ganglia have become, and a very striking difference in the location of the anteriormost pleonal ganglion (fig. 69.24A, B). In *Sergio mirim*, the ganglia corresponding to metameres of the second maxilliped, third maxilliped, and first pereopod are positioned in close serial proximity, but clearly distinguishable, while those to the anterior are fused into a single ganglionic mass (Rodrigues, 1966). In this regard, it is more similar to *Upogebia* than to *Axius*, so far as can be deduced from available illustrations (Bouvier, 1889; Pike, 1947). However, in *Upogebia*, the only member of the infraorder

thalassinidean genera *Axius*, *Sergio*, and *Upogebia* [modified from parts of Rodrigues, 1966, fig. 173]; C, left half of supraesophageal ganglion (brain), *Trypaea australiensis* [modified from Sandeman et al., 1993, fig. 8]; D, right half of supraesophageal ganglion (brain), *Calocaris macandreae* [modified from Hanström, 1947, fig. 34]; E, complete supraesophageal ganglion (brain) of *Calocaris macandreae*, as labeled by Prosser (1973, fig. 15-20), based upon originals by Hanström (1925, 1928); F, terminal pleonal ganglion (G6) and roots in *Upogebia pugettensis*, labeled on left by the target they innervate, numbered on right to correspond to reported homologous roots in crayfish [modified from Paul et al., 1985, fig. 4B]; G, axial and appendage muscles from ventral perspective in sixth pleomere and telson of *Upogebia pugettensis* [modified from Paul et al., 1985, fig. 1B1, B2]; H, motoneurons in terminal pleonal ganglion (G6) of *Upogebia pugettensis* that have axons in root six (R6) that innervate axial muscles [modified from Paul et al., 1985, fig. 5B].

Gebiidea among these three genera, the ganglion corresponding to the first pleomere (A1G) is both diminutive and displaced anteriorly into the posterior of the thoracic region, with nerves of the first pleopods extended posteriorly. Previously noted by Schram (1986), this suggests at least a slight tendency toward pleonal ganglion arrangement in *Meiura* (*Anomala* and *Brachyura*), the proposed sister group of the previously lumped thalassinideans, though its importance has been discounted as there is no fusion with the last thoracic ganglion (Scholtz & Richter, 1995). It may nonetheless reflect a fundamental difference between what are now accepted as separate thalassinidean infraorders, with one bearing closer resemblance to anomurans and the other to macrurans.

Comparative study of sixth pleonal and telsonal **neuromusculature** has included *Upogebia pugettensis* (Dana, 1852), providing the account for thalassinidean decapods (Paul et al., 1985), except for brief reporting of A6G synaptic delays by Bullock & Horridge (1965). Neuromusculature of the telson was inferred to be ontophyletically derived from the seventh pleomere characteristic of decapod ancestors. Musculature of the sixth pleomere and telson was very similar to that of crayfish, but with absence of the ventral telsonal flexor muscles, also lacking in several anomurans to which it was compared (fig. 69.24G). However, *Upogebia* lacked three regional motoneurons present in crayfish, two of which are fast flexor motoneurons and one a motor giant (fig. 69.24F, H). Like crayfish, *Upogebia* retains the anterior telsonal muscle (AT) and associated motoneurons, which are lacking in the examined anomurans. There is also one motogiant (MoG), a fast flexor motoneuron, evident in the sixth pleonal ganglion of *Upogebia*, innervating the posterior telsonal flexor muscle (PTF), though it is not present in the examined anomurans. The somewhat intermediate arrangement of sixth pleonal and telson neuromusculature in the gebiidean *Upogebia* was believed to reflect secondary adaptation to the typical thalassinidean burrowing habitat, thus modification of the apparatus that macrurans like crayfish use in **rapid escape flexions** of the pleon and tail fan. The same may be true of giant interneurons, which occur as one or two pairs in macrurans (the medial and lateral giants, or MG and LG). The single pair of giant interneurons in *Trypaea* and *Upogebia* is homologous to the medial giants of crayfish, and the loss of the lateral giants likely reflects adaptation as an obligate burrow dweller (Turner, 1950). Their loss in thalassinidean and anomuran lineages is believed to have occurred independently (Paul, 2003).

The variety of form and function among **sensory organs** is for the most part known from only superficial descriptions, some noted only in the course of external comparative morphological studies and not thereafter further examined. For example, **eyes** in many of these burrow-adapted species are known to be diminutive and either non-pigmented or with very small areas of **pigment** beneath (sometimes extended beyond) a faceted or non-faceted **cornea** on a flattened and very short **eyestalk** (for examples, see Poore, 1994; Felder & Manning, 1997; Sakai, 1999b, 2005a). By contrast, axiids and upogebiids, along with selected genera of other groups, can have small but well protruded eyestalks bearing terminally or subterminally rounded and faceted corneas, even in some deep dwelling species that appear to lack dark eye pigments (for examples, see Sakai & de Saint Laurent, 1989; Poore, 1994, 1997). The dispersal of eye pigment in the eyestalk can also vary

greatly by sex and maturity or under other apparent influences. Also, in at least one genus, a small spot of possibly light-sensory pigment has been repeatedly observed on a joint membrane of antennules, and may represent an **accessory sensor** (Felder & Manning, 1997).

The **eyes** are usually small or degenerate in both infraorders, with their ganglia so intimately fused to the protocerebrum (see above) that they are not commonly drawn upon as study models. However, detailed early anatomical descriptions of eye structure in both axiideans and gebiideans have been made, along with comparisons to eyes in other decapods and some observations on eye **ontogeny** in *Upogebia*, albeit without the advantage of modern microscopy techniques (see Scheuring, 1923, and earlier works cited therein). Working with upogebiid specimens he labeled as “*Gebia lacustris*” [his population today most likely assignable to *Upogebia deltaura* (Leach, 1815)] and materials of callianassids including *Callianassa subterranea* and what he termed “*Callianassa stebbingi*” [the latter being today most likely assignable to *Pestarella tyrrhena* (Petagna, 1792)], Scheuring (1923) gave detailed descriptive accounts of corneal surfaces, retinula cells, rhabdomeres, ommatidia, crystalline cones, pigments, basal membranes, eyestalk muscles, and innervation, drawing comparisons between species where possible. Most notably, he found all typical elements of a **complex arthropod compound eye** and well developed **eyestalk musculature** in *Upogebia*, but highly degenerate eyes with limited eyestalk motion in *Callianassa* and *Pestarella*, wherein their very continued function as light sensory organs was questioned. In terms of anatomical components, *Callianassa* was noted to have even more degenerate eyes than *Pestarella*, which at least retained recognizable rhabdomal structure of a retinula. In *Callianassa*, nothing more than remnants of crystalline cones, diffusely organized pigments and a thin strand of optic nerve were found as evidence that the structure was once an eye. While too little is known at this level of structure for other representative taxa to broadly classify levels of **eye degeneration** among major clades of axiideans and gebiideans, relative development of corneas has been used to support some generic separations. It clearly varies strikingly within families, as evident in comparison of eye development in *Callianassa* with that, for example, in *Calliapagurops* (see Ngoc-Ho, 2003, fig. 16A).

Diverse **sensory functions** are also suggested by the extreme variety of **setae**, **setal pits**, and **aesthetascs** documented in descriptive works. In at least one case, such setal pit patterns on pleonal pleura have provided the basis for family-wide phylogenetic interpretations (Kensley & Heard, 1991), though functions remain unknown. Where similar very small rows of such pits have been found in immediate proximity to **appendage joints** in decapods (though apparently lacking in brachyurans), many appear to be **CAP sensilla**, with apparent connectives to internal **proprioceptive chordotonal organs**. These potentially serve as sensors of joint mechanics, and they are documented to occur in several thoracic appendages of *Upogebia* (cf. Alexandrowicz, 1972; Laverack, 1978). Also occurring in serially repeated pairs along the metameric bundles of longitudinal extensor muscles in the thalassinidean pleon, are internal **muscle receptor organs** (MROs), which can be found as well in other macruran and anomuran infraorders (Pilgrim, 1960; Bullock & Horridge, 1965; Paul, 2003). Finally, a long-sought sensory organ, inferred by varied

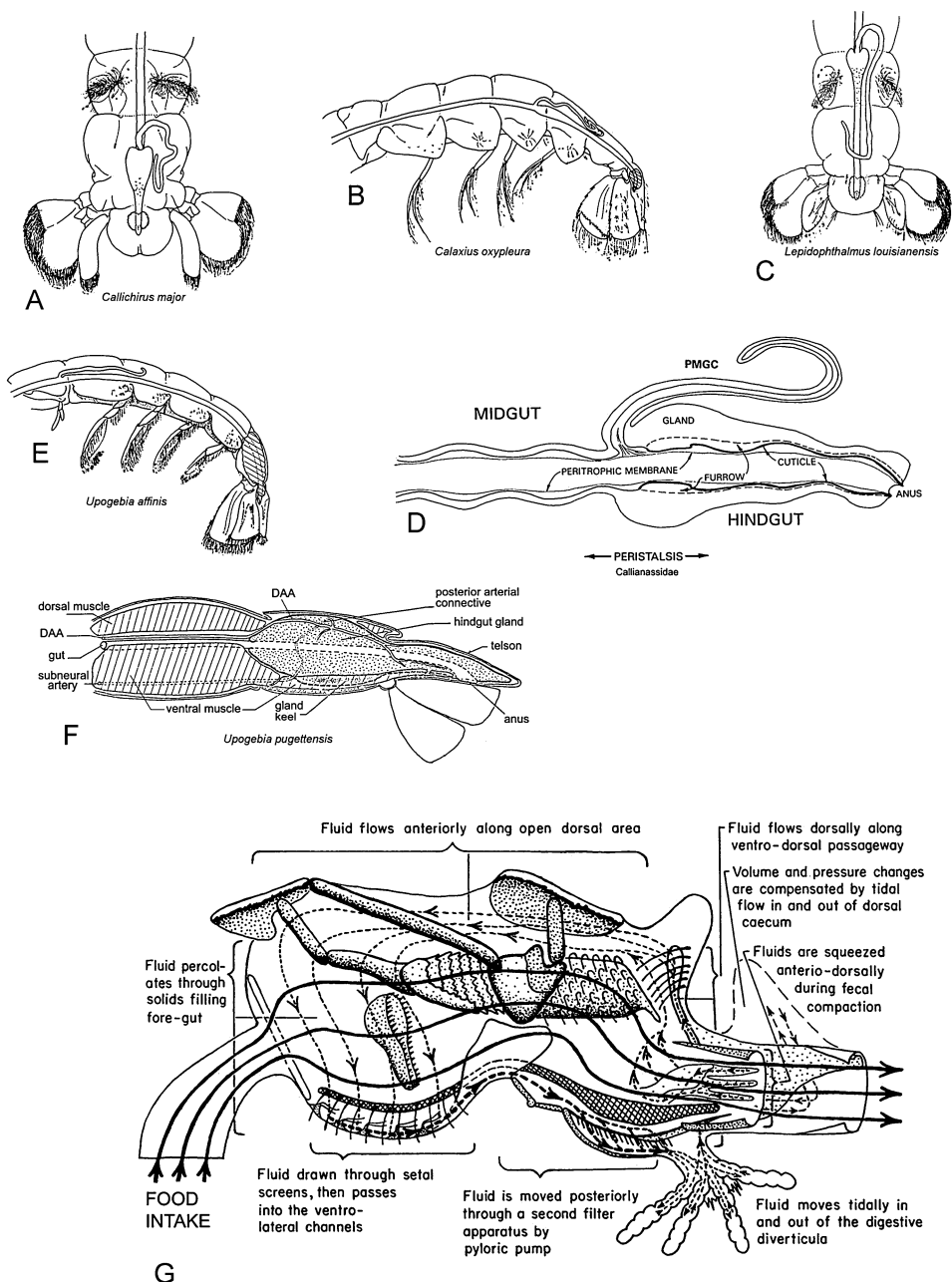
physiological and behavioral studies, is an **oxygen sensor** (Farley & Case, 1968; Felder, 1979; Hill, 1981). Of potentially critical importance to burrowers in hypoxic substrates, the nature of this receptor remains a mystery, as does the location and histology of most other hypothesized chemoreceptors inferred from physioecological studies.

Digestive system

Much has been written of general structure and function in this system of both infraorders, in part because so little can otherwise be directly observed of feeding adaptations, but also because **variations in structure** appear to bear on **phylogenetic placements**. Overall design at first inspection appears very similar between the gebiideans and axiideans, perhaps owing to convergent adaptation to a **fossorial habitat** and a similar suite of food substrates, but it varies between representatives of these groups in striking ways. Recently, Sakai (2005b) and Sakai & Sawada (2006) have reported fundamental differences in **pyloric ossicle structure**, supporting division of the thalassinidean taxa into the separate infraorders, as called for by Tsang et al. (2008a, b), Robles et al. (2009), and Bracken et al. (2009, 2010) on genetic bases. However, though not previously reported, we find that digestive tract differences may go much further.

Structures of **midgut** and **hindgut** regions in axiideans such as *Callichirus* and *Calaxius* generally conform to those previously reported in the axiidean genus *Lepidophthalmus* by Felder & Felgenhauer (1993a), with a **posterior midgut caecum** (PMGC) branching anywhere between the fourth and sixth pleomere regions and the chitinous cuticular lining of the hindgut extending from there to the **anus** (fig. 69.25A-D). By contrast, the arrangement in gebiideans such as *Upogebia* (fig. 69.25E) differs fundamentally from the aforementioned, with the posteriormost caecum in examples studied to date originating in the first pleomere, and the chitin-lined hindgut extending fully to the anus from there. Not here figured, there is also no evidence of a caecum anywhere posterior to the first pleomere in the gebiidean genus *Axianassa*, this entire region being chitin-lined and therefore apparently hindgut. Thus, for Gebiidea, there is extreme reduction in any reach of intestine that can be called a **midgut trunk** (*sensu* Felder & Felgenhauer, 1993a). It is noteworthy that the segmental position of the **midgut to hindgut transition** with the pleon has been long noted to vary between major subgroups of decapods, but that it appears to be conserved within given infraorders (Smith, 1978). This supports the infraordinal level of

Fig. 69.25. A, *Callichirus major*, dorsal perspective, midgut trunk giving rise to posterior midgut caecum immediately anterior to junction with hindgut in sixth pleomere; B, *Calaxius oxypleura* (Williams, 1974), lateral perspective, midgut trunk giving rise to posterior midgut caecum immediately anterior to junction with hindgut in fourth pleomere; C, *Lepidophthalmus louisianensis*, dorsal perspective, midgut trunk giving rise to posterior midgut caecum immediately anterior to junction with hindgut in fifth pleomere; D, generalized callianassid, lateral perspective of longitudinal section, diagram of midgut trunk to hindgut transition; E, *Upogebia affinis*, lateral perspective, midgut trunk giving rise to posterior midgut caecum immediately anterior to junction with hindgut in first pleomere, large (cross-hatched) hindgut gland in sixth pleomere and telson; F,



Upogebia pugettensis, lateral perspective of longitudinal section, diagram of fourth pleomere to telson, large (stippled) hindgut gland in sixth pleomere and telson [modified from Thompson, 1972, fig. 45]; G, *Neotrypaea californiensis*, mid-sagittal diagram in lateral perspective depicting movements of solids (arrows on solid lines) and liquids (arrows on varied broken lines) in the foregut and anterior midgut (including hepatopancreas digestive diverticula) [modified from Powell, 1974, fig. 1].

separation in modern treatment of thalassinideans, and calls to attention a unique similarity between gebiideans and at least some galatheid anomurans (see Calman, 1909; Pike, 1947). The function of the caeca themselves is unknown in both infraorders.

Given their difference in morphology, it may be ill-advised to generalize functions of midguts and hindguts across both infraorders, especially with limited documentation across representative genera of each group. Functioning of **two-way peristalsis** is at least evident in a representative genus of each (Powell, 1974; Felder & Felgenhauer, 1993a), and the hepatopancreas or digestive gland, as well as its arterial blood supply, extend somewhat uniquely into the anterior pleon (Rodrigues, 1966). Many functions of the hindgut, as documented in callianassids (fig. 69.25D), are likely accomplished in similar ways by both groups, but the associated configurations of **hindgut valve** structures and **acinar glands** are not strictly comparable (Thompson, 1972; Powell, 1974; Felder & Felgenhauer, 1993a). Massive accumulations of tegumental gland tissues fill most of the hemo-coel of both the sixth pleomere and telson in *Upogebia* (fig. 69.25E, F), while comparable tissue appears limited to a relatively light covering over the anterior hindgut and a separate preanal glandular mass in the telsons of *Callichirus*, *Lepidophthalmus*, and *Calaxius* (fig. 69.25A-C). An extensive study of the glandular structures in *Upogebia* by Thompson (1972) provides evidence that they therein constitute ‘**Schleim**’ [= **mucus**] **glands** for cementing of burrow walls, releasing their products via dense fields of transcuticular pores in posterior reaches of the hindgut. However, while the axiidean callianassid *Lepidophthalmus* also cements burrow walls, it has no comparable pore densities or integumental gland mass in the posterior hindgut, most glandular pores instead being restricted to the anterior hindgut. It and other species of callianassids instead appear to have concentrations of tegumental glands for **cementing of burrow walls** elsewhere on their bodies, including on anterior thoracic appendages (see also Dworschak, 1998).

Clearly the most complex and difficult to depict digestive system structures of axiideans and gebiideans are to be found in the **foregut** and the **foregut to midgut transition**, the **hepatopancreas** being of midgut origins. Building in part upon an early study and modeling of foregut function in *Upogebia* by Schaefer (1970), the detailed work of Powell (1974) focused on two species, *Upogebia pugettensis* and *Neotrypaea californiensis* (Dana, 1854) (formerly treated in *Callianassa*) that offer at least selected examples for the two infraorders, along with a diagram of foregut function and interface with the hepatopancreas in a callianassid (figs. 69.25G, 69.26). What was therein reported for the callianassid *Neotrypaea californiensis*, is augmented by the earlier unpublished dissertation of Rodrigues (1966), who made detailed illustrations of foregut structure in what is now *Sergio mirim* (cf. Rodrigues, 1971), thus representing yet another subfamily of callianassid. For the gebiidean *Upogebia*, illustrations are augmented by the SEM micrographs of Felgenhauer & Abele (1983) and the more recent comparative studies by Ngoc-Ho (1984).

Even with the welcomed accrual of recent studies on **dietary habits** and food-capture setation in a number of genera (Nickell & Atkinson, 1995; Nickell et al., 1998; Stamhuis et al., 1998a, b; Coehlo et al., 2000b; Coehlo & Rodrigues, 2001a, b) complementary insights on variations in particle sorting, masticatory, and filtering functions in the foregut have

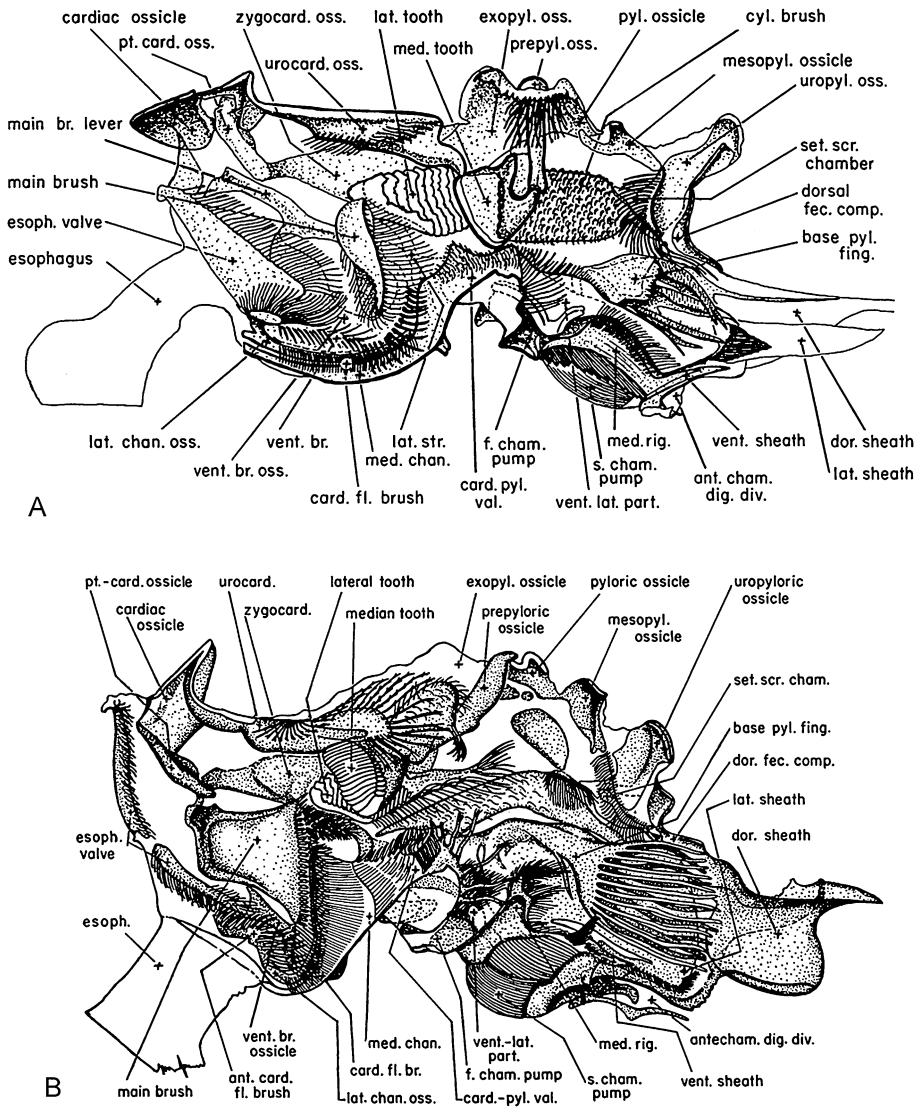


Fig. 69.26. A, *Neotrypaea californiensis*, illustrated mid-sagittal section with labeled internal structures of foregut [after Powell, 1974, fig. 2]; B, *Upogebia pugettensis*, illustrated mid-sagittal section with labeled internal structures of foregut [after Powell, 1974, fig. 36].

not come to fore. Yet, there are cases in which a gebiidean like *Upogebia* demonstrates **suspension/filter feeding** behaviors that appear to be in contrast with **deposit feeding** or **resuspension** as reported in an axiidean like *Neotrypaea* (see, for example, Dworschak, 1987b; Dumbauld et al., 2004), and this might suggest interpretations to be made of foregut structure. However, direct knowledge of the food substrates and how these are processed is usually too limited for highly specific explanations of function in foregut elements. Our

observations lead us to agree with Atkinson & Taylor (2005), who after recent review of an extensive literature suggest that most species resort to varied strategies, even if they appear to have a dominant mode as deduced from mouthpart setation, mesocosm observations, and instantaneous study of gut contents.

Dietary organisms and micro-organisms can be obtained from deposit processing and resuspension, burrow wall surfaces, burrow water, or even macroscopic materials that are intentionally brought into and accumulated within the burrow, in a form of microbial gardening (Ott et al., 1976; Dworschak, 1987b; Dworschak & Ott, 1993; Nickell & Atkinson, 1995; Boon et al., 1997; Bird et al., 2000; Stapleton et al., 2002). What the thalassinidean foreguts do to process these materials are but variations on a common decapod model for moving and turbating ingested solids, while maintaining a specific pattern of fluid circulation and squeezing out of liquids for entry to the hepatopancreas (and midgut trunk, if present) for absorption. From the work of Powell (1974), both thalassinidean infraorders appear to have structural adaptations for handling of such unconsolidated materials, including large setal brushes to push materials through the **gastric mill** of three teeth and abundant setae-covered posteriorly directed prominences to hold loose particles in place while the **liquid** is squeezed out in the process of **fecal compaction**. Powell (1974) could only speculate that a unique secondary **cardiac floor of setae**, developed in *Neotrypaea* but not *Upogebia*, was there because of the former's high intake of sand, which this bank of setae could prevent from entry into the ventral fluid passageway. Similarly, the "**gizzard-like action**" of flexible lateral teeth in *Neotrypaea* was interpreted as an adaptation to a high intake of abrasive sand, while more typical rigid lateral teeth were reported in *Upogebia*. With the recent separation of these genera at the infraordinal level, further study of such structural adaptations would be of value for both its ecological and potential phylogenetic interpretations.

Circulatory and respiratory systems

Circulatory and respiratory functions in axiideans and gebiideans are so integrated that they are rarely treated independently in physiological studies. **Branchial blood supply** and **respiratory pigments** reflect function of one system as much as the other, and even **ventilatory functions** of the scaphognathite and **burrow irrigation** by pleopods may be linked in compensatory ways to **heart rates** and the distribution of oxygenated blood. Most strikingly, structures and functions of these systems in the thalassinidean infraorders uniquely reflect adaptation to respiratory challenges of burrow environments, this being evident in shape of the organisms and their limbs, specialized ventilatory appendages, ability to endure hypoxic ambient waters, and unique blood and tissue chemistries.

In general design, there is close resemblance between the circulatory systems as reported for thalassinidean taxa and those of either astacoid macrurans or those of galatheoid anomurans (Bouvier, 1891; Pike, 1947; Rodrigues, 1966, 1984). However, both the Axiidea and Gebiidea differ from known representatives of the other infraorders in conspicuous ways, and appear to differ from each other in minor features (fig. 69.27A, B). By far the best general anatomical accounts of the circulatory system for any thalassinidean, the

work of Rodrigues (1966, 1984), centers almost exclusively on the axiidean callianassid *Sergio mirim* as a model (fig. 69.27C-E), while also offering a few original observations on systems in *Callichirus major* (Say, 1818) and *Upogebia* spp. As in all axiideans and gebiideans, the circulatory system reflects positioning of the primary respiratory exchange surfaces (likely always the **thoracic gills**, even if there are accessory surfaces) in immediate vicinity of the pericardium or pericardial cavity (PCC). The muscular **heart** is positioned within the **pericardium** centered in the posterior half of the thorax immediately beneath the “cardiac region” of the carapace, itself delimited anteriorly by the transverse cervical groove across the carapace, laterally by the linea thalassinica (when evident, or upper edge of branchiostegite if not), and posteriorly by the posterodorsal margin of the carapace. This positions it directly above an area where the foregut narrows to join the midgut, in a pericardial cavity where the flow of oxygenated blood collected from efferent branchial canals (EC) into branchiocardial channels (BCC) gains access to internal heart cavities via three pairs of **valved ostioles** (fig. 69.27C, D).

From the heart, blood is routed anteriorly by way of an **anterior median artery** (AMA), anterolaterally by a pair of **lateral arteries** (LA), posterolaterally and somewhat ventrally to pleonal reaches of the digestive gland by a pair of **hepatic arteries** (HA), posterodorsally to the pleon by the large median **dorsal pleonal artery** (DAA), and ventrally for distribution (to immediate left of the median dorsal artery) by the large **descending sternal artery** (SA), which in turn supplies the **ventral thoracic artery** (VTA) to the anterior, and the **ventral pleonal artery** (VAA) to the posterior. From the dorsal pleonal artery, segmental rami or branching arteries (SBA) distribute blood dorsally and ventrally, including by smaller segmental rami (SR) to the ventral nerve cord (VNC). Anteriorly, rami of the ventral thoracic artery include segmental branches and distal rami serving the branchiostegites (BR). Return flow to the heart is by way of **lacunae** as in other decapods, but these interconnected spaces appear to be of comparatively large volume relative to body size. The largest volumes are dorsal, positioned above and in front of the stomach, and ventral, which includes the pleonal and the sternal or thoracic. The latter forms afferent canals (AC) supplying blood to the gills, from which efferent canals collect blood into branchiocardial channels (BCC) and carry it to the pericardial cavity, and from there back to the heart.

The extension of the **hepatic arteries** into the pleon reveals a perhaps unique system feature shared between the two thalassinidean infraorders. While this obviously relates to both these groups having **digestive glands** that somewhat uniquely **extend into the pleon**, it is reported that hepatic arteries do not by comparison penetrate into the pleonal cavity of paguroids (Jackson, 1913; Rodrigues, 1984a), which also have **pleonal digestive glands** (served instead by the dorsal pleonal artery). To slight degree, distance of hepatic artery penetration into the pleon differs between the axiidean *Sergio* and the two species of *Upogebia* that have been examined (one having been originally reported under the junior synonym *Gebia*). Also, relative development of the ventral pleonal artery and bifurcation in the posteriormost reaches of the dorsal pleonal artery appear to vary between thalassinidean taxa, with possible **phylogenetic significance** (Pike, 1947; Rodrigues, 1984a). While examination of additional genera might confirm such significance, it has

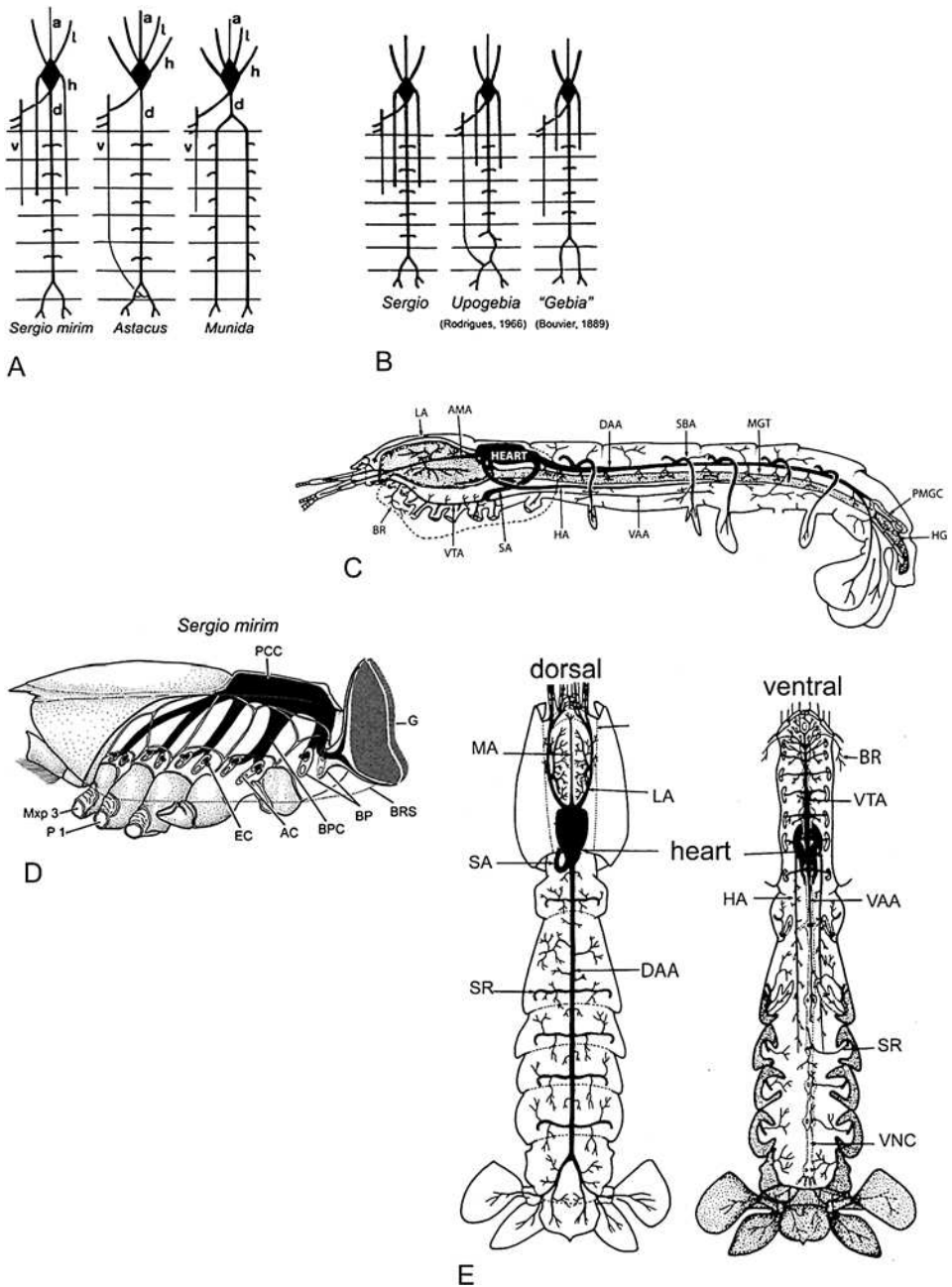


Fig. 69.27. A, major arteries extending from heart in the axiidean callianassid *Sergio mirim* as compared to a crayfish (*Astacus*) and galatheid squat lobster (*Munida*) [modified from Rodrigues, 1984, fig. 5] in which: a, anterior median artery; l, lateral artery; h, hepatic artery; d, dorsal pleonal artery; and v, ventral pleonal artery; B, major arteries extending from the heart in the axiidean genus *Sergio* as compared to diagrams for two species of the gebiidean genus *Upogebia* (formerly

also been shown that major displacements of blood vessels in the posterior pleon of *Upogebia* could relate to an **apomorphic feature** like the massively developed tegumental glands there, used for cementing of burrow wall sediments (Thompson, 1972).

By way of afferent canals (AC) blood from the thoracic or sternal lacuna is shunted to **gills** (= **branchiae**; G), which may be arthrobranchs as shown for *Sergio mirim* (fig. 69.27D). Depending upon the infraorder and often varying within certain ranges by family or genus (sometimes within a genus), gills can be **podobranchs**, **arthrobranchs**, or **pleurobranchs**, often with more than one of these on the same thoracic somite. Such gill combinations are commonly reported as **taxonomic characters** (for examples see, among others, de Saint Laurent & Le Loeuff, 1979; Sakai & de Saint Laurent, 1989; Kensley & Heard, 1991; Poore, 1994, 1997). As noted by Poore (1994), the loss of a plesiomorphic arthrobranch on the first thoracopod (first maxilliped) and the loss or reduction of a pleurobranch on the eighth thoracopod (fifth pereopod) are the only gill apomorphies common to all of the formerly grouped thalassinidean taxa. Thus, gills of some form can be associated with the second through eighth thoracopods, though losses and reductions in branchial complements are very common, these likely reflecting apomorphic variations in physioecology. For example, Astall et al. (1997) have documented greater weight-specific branchial surface areas and reduced branchial filament cuticular thickness in **hypoxia tolerant** species of *Callianassa* and *Jaxea*, than in *Upogebia*. **Accessory respiratory surfaces** are suspected to also sometimes play a role in **gas exchange**, as much of the body surface is thinly cuticularized. Within Callianideidae and Micheleidae, two genera, *Callianidea* and *Michelea*, have developed conspicuous arrays of what at least appear to be cylindrical or lamellate pleonal “respiratory filaments” (fig. 69.22G, I) along margins of the second to fifth pleopods (Kensley & Heard, 1991). However, their function remains somewhat in question.

Respiratory exchange across branchial surfaces of the thoracic gills is facilitated by the maintenance of **exchange gradients** within **branchial cavities** that enclose the gills on either side of the thorax immediately above the thoracic appendage coxae, and **flow** through these chambers is facilitated as in most other decapods by **beating of the scaphognathites**. A branchiostegite, derived as a fold of the thorax, forms this cavity into which water can enter ventrally, posteriorly, and to some extent anteriorly. In most genera (not all) the branchiostegite flexes from the thoracic wall along a longitudinal hinge-like seam commonly termed the **linea thalassinica**, sometimes argued to be a homolog of the **linea anomurica** in anomalans (figs. 69.2, 69.3; and fig. 70.6a-c, Anomura chapter, this volume). When well developed, this flexure line allows lateral

treated under *Gebia* by Bouvier, 1889) [modified from Rodrigues, 1966, fig. 172]; C, diagram of arterial blood supply in the callianassid *Sergio mirim*, lateral perspective in relation to digestive tract, hepatopancreas not shown [modified from Rodrigues, 1984, fig. 3]; D, diagram of afferent and efferent (dark) branchial blood channels, lateral perspective of partially exposed thoracic region in the callianassid *Sergio mirim* [modified from Rodrigues, 1984, fig. 4]; E, diagram of horizontal exposures of arterial system from dorsal and ventral perspectives in *Sergio mirim* [modified from Rodrigues, 1984, figs. 1, 2].

extension of the branchiostegites and thus marked enlargement of the branchial chamber volume and increased exposure of branchiae; in species lacking rigid calcification of the branchiostegites, these structures can inflate or balloon under positive pressure exerted by the scaphognathites. However, in at least some species, the branchiostegites can also be retracted to more tightly enclose gills or achieve **flushing** of the branchial chamber. Literature documents wide variations in ventilatory behaviors, respiratory adaptations, and related burrow irrigation patterns (Farley & Case, 1968; Thompson & Pritchard, 1969b; Torres et al., 1977; Felder, 1979; Dworschak, 1981; Hill, 1981; Mukai & Koike, 1984a, b; Anderson et al., 1991; Nickell, 1992; Paterson & Thorne, 1995; Stamhuis et al., 1996; Astall et al., 1997; Stanzel & Finelli, 2004). **Metachronal beating** of the **pleopods** can facilitate laminar movement of oxygenated waters to irrigate the burrow (Stamhuis & Videler, 1998). Endopods and exopods of the third, fourth, and fifth pleopods are commonly very broad and marginally setose, with endopods of each side interlocked by appendices internae. When laterally flared during the power stroke, their marginal setae can reach to or near the burrow walls, and thus propel water with high efficiency.

Both scaphognathite ventilatory rates and pleopodal burrow irrigation rates alter in response to ambient oxygen concentrations, and ranges in these behaviors are coupled to varied abilities of thalassinideans to function as metabolic regulators or in some cases, unlike most decapods, to tolerate extended exposure to **anoxia** (Thompson & Pritchard, 1969b; Felder, 1979; Zebe, 1982). Some intertidal species appear to move above the water-air interface within the burrow when burrow waters become strongly hypoxic, as they survive for long periods in water-saturated air (Felder, 1979; Hill, 1981). However, many species also undergo protracted periods of adapted metabolism under **hypoxia** or **anaerobic metabolism** with accumulation of **lactate** (Pritchard & Eddy, 1979; Zebe, 1982; Hanekom & Baird, 1987; Felder & Felgenhauer, 1993b; Anderson et al., 1994; Paterson & Thorne, 1995; Powilleit & Graf, 1996; Astall et al., 1997; Felder, 2001). Among adaptations to these ends may be unique hemocyanin subunit associations and oxygen affinity profiles (Miller et al., 1976, 1977; Miller & Van Holde, 1981; Taylor et al., 2000), along with abilities to tolerate normally toxic concentrations of reduced substrates like sulfide (Johns et al., 1997; Nates & Felder, 1998, 1999; Bourgeois & Felder, 2001; Felder & Kensley, 2004). Recently, unique adaptations have also been found in *Lepidophthalmus* that potentially reduce cell **apoptosis** during ionic disturbances, and thus avert impairment of **mitochondria** when lactate accumulates (Holman & Hand, 2009).

Excretory and osmoregulatory systems

As in other groups of aquatic decapods, the **thoracic gills** and the **digestive tract** almost certainly play as large a role in **excretory** and **osmoregulatory system** function as do the **antennal or “green glands”** of the **nephridial system**. For **clearing** of highly soluble waste products like **ammonia**, or in active **uptake of ions**, large gill surfaces provide ready diffusion and transport pathways, given high rates of branchial water exchange and burrow water exchange gradients enhanced by pleopod-modulated burrow irrigation. At the same time, both **peristalsis** (downstream) and **antiperistalsis** (upstream, including

anal drinking) in the midgut trunk (where present) and hindgut could also facilitate such waste clearance and other release to, or uptake from, the ambient environment. Furthermore, there is a yet to be explained finding of unique **lamellar bodies** formed in walls of the posterior midgut caecum of at least one species, these being extruded by **exocytosis** into the hemocoel (Felder & Felgenhauer, 1993a). It remains uncertain whether these could serve some function in ion or water regulation, as previously proposed.

While direct measurements of excretory wastes from axiideans and gebiideans cannot be found, there is at least evidence of negative impacts from waste accumulation (likely protons and ammonia) in the course of contained tolerance experiments with both callianassids and upogebiids (Felder, 1979; Hill, 1981; Holman & Hand, 2009). Clearly, large loads of reduced nutrients are also removed from callianassid burrows in the course of pleopodal irrigation (Nates & Felder, 1998), but it cannot be assumed that these in any major way represent wastes from the animals themselves, given high nutrient loads of interstitial waters in the studied habitats.

While a general model of axiidean and gebiidean excretory processes can be taken from literature on other decapods, insights specific to the group must be drawn by inference. Some features of the **antennal nephridial gland** in *Upogebia* were explored in early work by Picken (1936), who placed it among decapods that had a common design of **coelomic sac**, **labyrinth**, **nephrostome**, and **blood supply**. Sampling of excretory products (**urine**) from the **nephridiopore** of this gland has been undertaken on the callianassids *Neotrypaea californiensis* and *Callichirus kraussi* (Stebbing, 1900), and the upogebiid *Upogebia pugettensis*, but only in the course of osmoregulatory studies, which in turn warranted analysis limited to ion concentrations and osmolality (Thompson & Pritchard, 1969a; Forbes, 1974). For all three species, which represented **osmoregulators** and **osmoconformers**, urinary products remained isotonic to the blood even when animals were under low salinity stress, indicating that the antennal gland does not overall recapture salts from urine. However, if compensatory uptake of sodium is achieved elsewhere, it may nonetheless play a role in what is clearly volume regulation, or in selective regulation yet to be measured ions like magnesium (Forbes, 1974; Felder, 1978). Thoracic gills are well known as a primary site of **active sodium uptake** (which chloride follows) in decapods, and the process has been demonstrated to center in that region for at least one osmoregulating callianassid, even in larval stages prior to gill formation (Felder et al., 1986).

Genital apparatus and reproduction

Information on the external and internal **reproductive morphology** of the infraorders Axiidea and Gebiidea is virtually non-existent. There are just a few papers, short descriptions in papers, or an occasional image in book chapters describing this aspect of the biology for this interesting group. The **external genital apparatus** consists of small spherical or oval **gonopores** on the ventral **coxal segment** of the **third pereopod** in **females** and **fifth pereopod** in **males** (LeBlanc, 2002), as has been described universally for the reptant decapods (Felgenhauer, 1992a). LeBlanc (2002, her chapter 2, fig. 4) showed that both

the male and female gonopores for *Lepidophthalmus* and *Axianassa* are **operculate**, or at least covered by a thin, cuticular membrane. Variations on the pattern of gonopores on the third pereopod in females and fifth pereopod in males have been described by several authors for **hermaphrodite** (Runnström, 1925; Kang et al., 2008) or **intersex** individuals (Pinn et al., 2001; Dworschak, 2003) where usually both sets of gonopores are visible externally. The development of the internal reproductive system in these cases is generally not described.

In some species (especially in *Callianidea*, *Marcusiarius*, and *Trypaea*) the males possess very small and simple gonopods on the first pleonal somite, but their size, distance from the gonopores on the coxae of the fifth pereopod, and their unornamented morphology leave questions as to their function.

The **internal morphology** of the male and female reproductive system has been briefly described and illustrated by Felgenhauer (1992b), as a general overview of the Decapoda, and by LeBlanc (2002) for particular callianassids and axianassids. The **male system** involves paired **testes**, usually in the first or second pleonal somite, linked to the gonopores by a pair of **vasa deferentia**. The **female system** is very similar except that the **ovaries** extend well into the pleonal somites (at least the first three) and **oviducts** link ovary to gonopore. The extension of ovaries and testes **posteriorly** into the **pleon**, rather than anteriorly into the cephalothorax, appears to uniquely separate the thalassinidean infraorders and other reptant decapods, such as anomurans and brachyurans.

The microstructure and ultrastructure of male **spermatophores** and **spermatozoa** is, unusually, the best described aspect of their reproductive biology (fig. 69.28). Oval, thin-walled spermatophores have been recorded in the callianassid *Trypaea australiensis* by Tudge (1995a), and more triangular-shaped spermatophores containing a few (~20) spermatozoa are illustrated by LeBlanc (2002) for *Lepidophthalmus louisianensis* (Schmitt, 1935), another member of the same family. Tudge (1995a, b, 1997) showed the ultrastructure of thalassinidean spermatozoa of four species, and these taxa, along with some earlier light microscope work, were later reviewed by Jamieson & Tudge (2000). LeBlanc (2002) added descriptions of three more thalassinidean sperm types in her unpublished masters thesis. As of 2002, there are nine thalassinidean species for which some information is known about sperm structure. For three of these [*Calocaris macandreae*, *Biffarius arenosus* (Poore, 1975), and *Upogebia pusilla* (Petagna, 1792)] only light microscope observations are available (see Jamieson & Tudge, 2000). Scanning electron microscopy (SEM) observations are available for the three species LeBlanc (2002) investigated (*Axianassa australis* Rodrigues & Shimizu, 1992, *Callichirus major*, and *Lepidophthalmus louisianensis*) and transmission electron microscope (TEM) observations have been published for *Neaxius glyptocercus* (Von Martens, 1868), *Thalassina squamifera* De Man, 1915, and *Trypaea australiensis* by Jamieson & Tudge (2000). These nine species represent six currently recognized families and are evenly split between the Gebiidea (Axianassidae, Thalassinidae, Upogebiidae) and Axiidea (Callianassidae, Calocarididae, Strahlaxiidae). In general, the **sperm cells** are spherical to subcylindrical (*Thalassina*), with between four and six long microtubular arms, and either a small circular (*Trypaea*), or larger plate-like (*Axianassa*), or sub-cylindrical (*Thalassina*) acrosome vesicle at one pole. Very little can

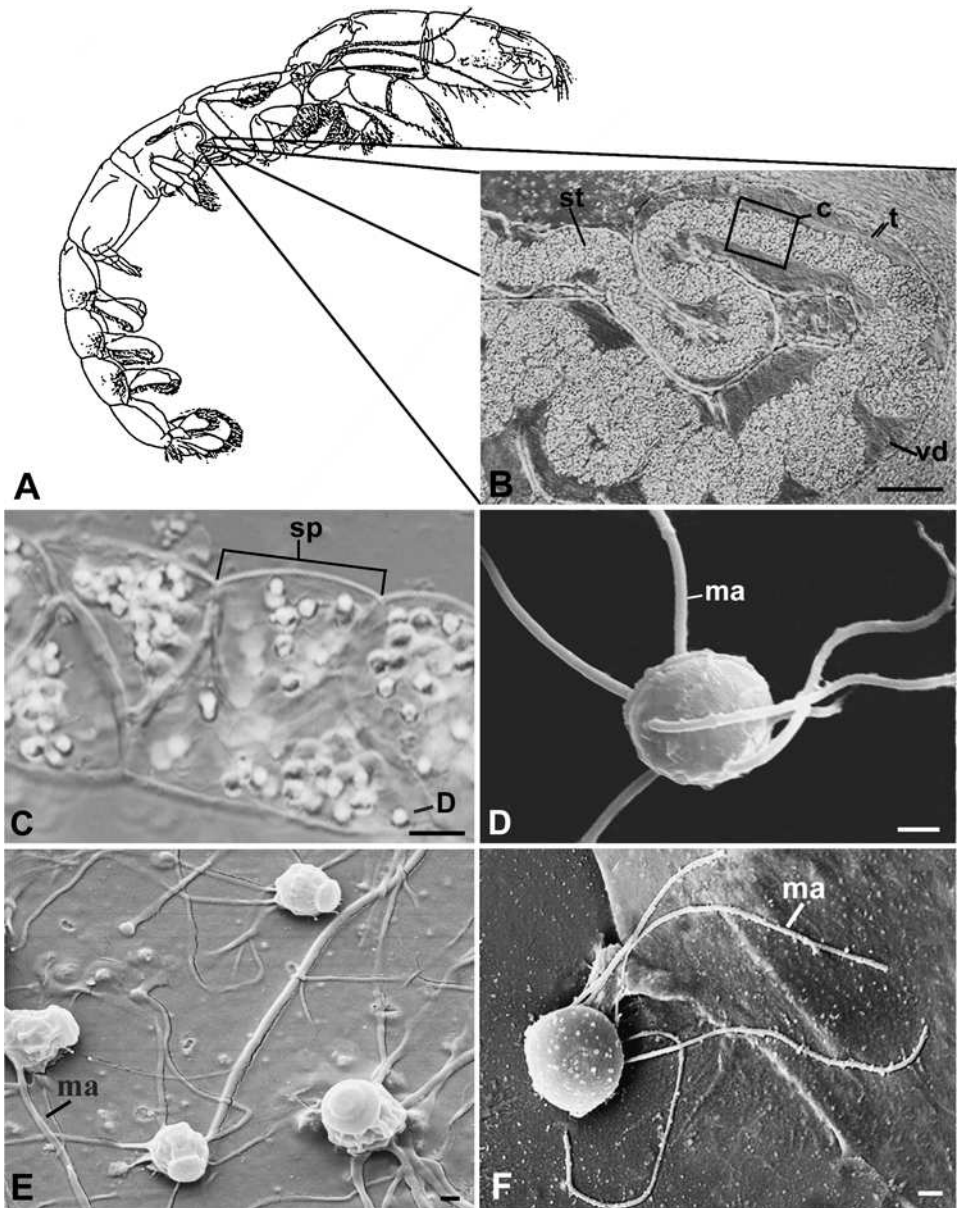


Fig. 69.28. A-D, diagram of reproductive structures in males of *Lepidophthalmus louisianensis*, and E-F, spermatozoa in *Axianassa australis* and *Callichirus major*, respectively. A, sagittal view of male to show location of vas deferens and testis; B, vas deferens and testis containing spermatophoric tubule (scale bar = 0.4 mm); C, spermatophoric tubule containing spermatozoa (scale bar = 0.2 mm); D, spermatozoon with six microtubular arms (SEM) (scale bar = 0.1 mm); E, spermatozoa of *Axianassa australis* (SEM) (scale bar = 1 μ m); F, spermatozoon of *Callichirus major* (SEM) (scale bar = 1 μ m). Abbreviations: ma, microtubular arm; sp, spermatophore; st, spermatophoric tubule; sz, spermatozoa; t, testis; vd, vas deferens. [Figure courtesy of Leigh Ann Nieminen, from LeBlanc, 2002.]

be said about comparing the sperm morphologies recorded so far, as only the three investigated at the TEM level provide detailed comparative data. As previously stated, the variety of sperm morphologies seen in axiideans and gebiideans so far are as diverse as those recorded for Anomura, and with the study of more taxa they could provide a rich **phylogenetic signal**.

From the perspective of female reproductive biology, descriptions of ovaries and/or eggs are available only in Ishikawa (1891), Butschinsky (1894), and Oka (1941). To this can be added some more recent data on callianassid **fecundity** (Thessalou-Legaki & Kiortsis, 1997; Hernández et al., 2008) and egg and clutch size in an upogebiid (Kubo et al., 2006). The scarcity of good descriptive biology on the female reproductive system is indicative of the general lack of information on the biology of most axiidean and gebiidean species.

DEVELOPMENT AND LARVAE

Brooding and larval development

While a large body of literature refers to many aspects of **larval life histories** in thalassinideans, the focal subjects, scope, and quality vary widely, and taxonomic coverage of the group is not comprehensive. Accounts of complete larval histories are very much biased to common and accessible members of Callianassidae and Upogebiidae, which at very least represent the two now-separated infraorders. A limited literature herein cited is referenced primarily as a starting point for those who might wish to pursue it, but it otherwise is not integrated into character comparisons and analyses to avoid exceeding present objectives. That noted, such an independent effort is warranted and encouraged, especially now that molecular phylogenetic insights have fostered efforts to not only reclassify these animals into two infraorders, but also reconsider family memberships within each and re-examine both morphology and ecology in search of characters that might support diagnoses of constituent natural groups. Assuming such efforts are to follow, it should be noted that early **phylogenetic interpretations of larval characters** for purposes of partitioning the thalassinideans, may not be directly adoptable in support of current phylogenetic insights. For example, dividing thalassinidean larvae into “**homarine**” versus “**anomuran**” series as suggested by Gurney (1938) would appear to support modern separation of thalassinideans into two infraorders, but the characters (at least as originally used to diagnose these groups) may not broadly apply as larval histories of more genera and families become known (Konishi, 1989; Poore, 1994).

Relatively little is known of **pre-hatch histological development** in eggs of thalassinidean decapods, though some observations on **egg maturation** have been reported for a callianassid, *Callinectes major* (cf. Rodrigues, 1976; fig. 69.29A). Otherwise, many papers that describe larval histories also offer brief comments regarding changes in egg shapes and colors that immediately precede hatching. On the physiological side, pre-hatch activation of ion regulatory processes has been documented (Felder et al., 1986) and assay of egg fatty acid composition undertaken (Nates & McKenny, 2000) in a member of the

estuarine genus *Lepidophthalmus*. As in the aforementioned lipid study, it is often noted that **egg sizes and numbers vary markedly** among thalassinidean taxa. Large, lipid-rich, yolky eggs usually suggest highly abbreviated larval development with settlement of post-larvae near the parental populations, whereas large numbers of relatively small eggs infer a protracted larval history with multiple, perhaps widely dispersing, larval stages. In most soft bodied species, the egg masses borne by females extensively cover the highly exposed pleopods, with little or no enclosure being afforded by the pleonal tergites, themselves often poorly calcified and of limited ventrolateral extension. Protection of the egg brood is instead afforded by the confines of the burrow, and the ovigerous female may optimally position itself to take advantage of proximity to overlying waters or to burrow shapes that favor efficient pleopod-modulated irrigation of eggs with oxygenated water. In at least one case, unique burrow sculptures also have been postulated to perhaps protect ovigerous females from egg predators such as pink wormfish, *Microdesmus longipinnis* (Weymouth, 1910) (cf. Felder, 2001). Movement toward the burrow opening by females immediately prior to hatch is likely, as inferred by an elevated frequency of ovigerous females when sampling is restricted to the upper sediments (Felder & Mouton, 1995).

When larval series are cultured from egg-bearing females held in the laboratory, the thalassinidean egg almost always **hatches** as either a **prezoal or zoal stage**, lacking functional free uropods (figs. 69.29B-C, I, J; 69.30A, B, G, H, N). Exceptional cases of direct development without planktonic larvae are known, however, as exemplified by the exceptionally large-egged *Strahlaxius plectrorhynchus* (Strahl, 1862), in which eggs hatch as **postlarvae** that subsequently cling for a period to the pleopods of the parental female (Hale, 1927). Another exception appears to occur in an undescribed tropical species of the callianassid genus *Lepidophthalmus*, for which only a postlarval stage could be found within a few hours of hatching (DLF, unpubl.). Prezoal stages (fig. 69.29B, C) of varied forms have been reported to occur in Axiidae, Callianassidae, and Strahlaxiidae among the axiideans (Hale, 1927; Gurney, 1938; Aste & Retamal, 1983, 1984; Nates et al., 1997; Strasser & Felder, 1999, 2000; Abrunhosa et al., 2005) and at least Thalassinidae and Axianassidae among the gebiideans (Sankolli, 1967; Strasser & Felder, 2005). It remains debatable what role this stage might serve in nature, and some workers are inclined to regard it as primarily an artifact of unsuccessful laboratory rearing. Generally, if it is not passed through within a few hours, as it is for example in the callianassid genus *Lepidophthalmus* (where it commonly occurs), few if any such hatchlings molt successfully to the first zoal stage.

The course of complete post-hatch development through at least the **decapodid stage** (= **megalopa**, herein regarded as the first postlarval stage as per Felder et al., 1985) has now been reported for a number of thalassinideans of both infraorders, even though it falls far short of representing generic level diversity of both groups. Initially, many observations of such early life histories were based upon net collections of wild larval populations, and in some cases putatively complete series of successive stages were pieced together from these collections. In other cases, live captured larvae were cultured until they molted to subsequent stages, and molted exuvia were used to compare morphological changes. These methods have produced many reports of partial larval histories, sometimes treating

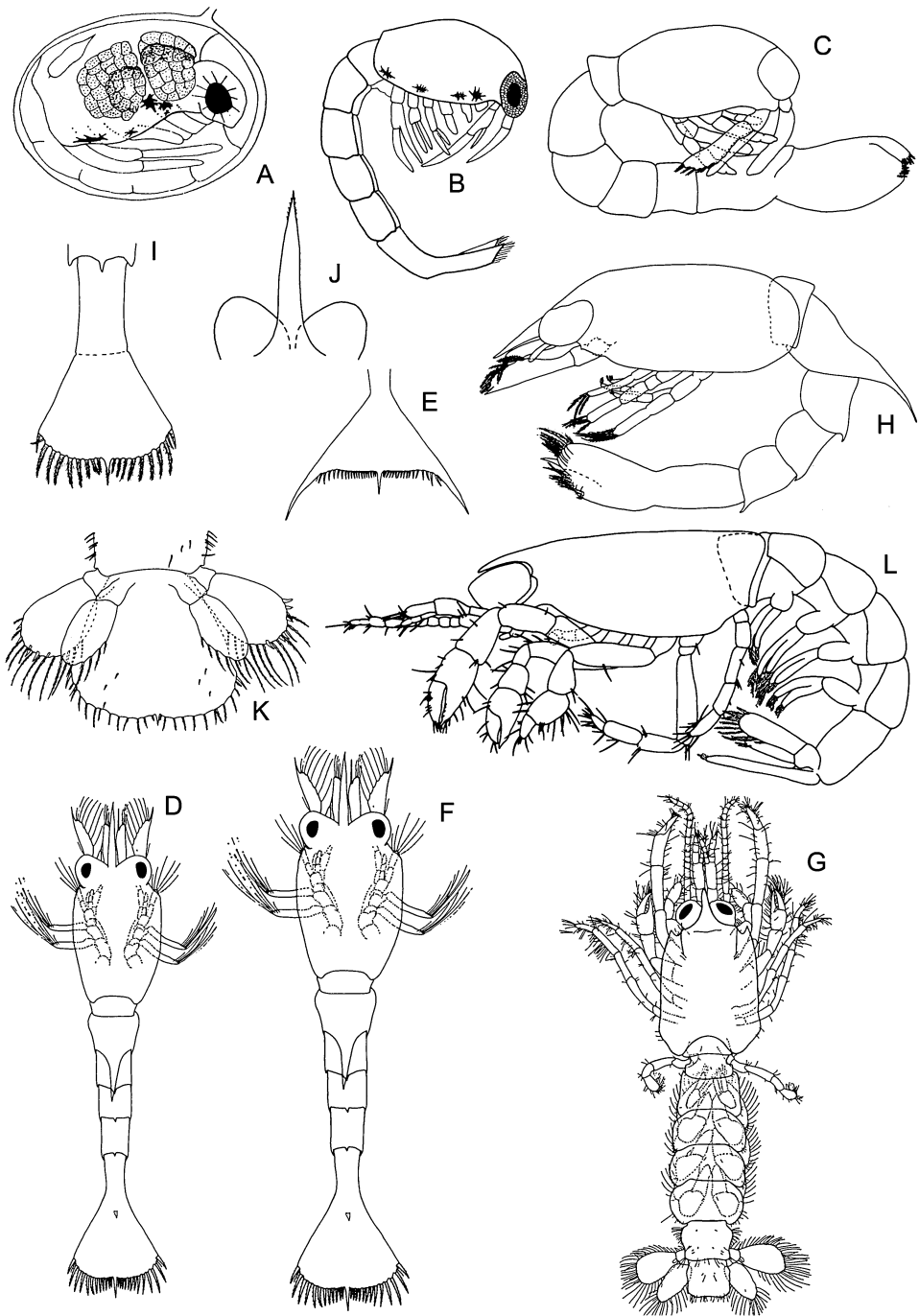


Fig. 69.29. Representative egg (pre-hatch embryo) and larval stages of infraorder Axiidea, family Callianassidae. A-B, *Callichirus major*, Brazilian population: A, late stage egg; and, B, prezoea

no more than a stage or two of questionable parentage (most not included in this review), or in other cases have produced possibly valid series for which the parental species remains in question or possibly a mix of species. When coupled with recent taxonomic revisions that have subdivided assumed parental stocks of a region, species level identifications for some planktonic larval series are assumptions, at best. Notwithstanding these limitations, myriad insights on thalassinidean larvae can be found in early compilations (Gurney, 1924, 1937, 1938, 1942; Gurney & Lebour, 1939). Obviously, when ovigerous females can be obtained and hatchlings reared through complete development, identities of parental females can much more certainly be determined, especially when those females are properly cataloged and archived for confirmation by subsequent investigators. The primary shortcoming of laboratory larval rearing is pervasive concern that rearing conditions and foods may not duplicate those in nature. Such concerns aside, as they most often impact stage durations or subtle meristics of thalassinideans studied to date, these methods have begun to produce detailed insights into thalassinidean **metamorphosis**.

For members of the infraorder Axiidea (fig. 69.29B-L), complete larval histories are known for genera of Axiidae and Callianassidae, in addition to that for the aforementioned member of the Strahlaxiidae, which has **direct development**. For Strahlaxiidae, direct development is not likely the rule, as observations of *Neaxius* suggest it to hatch as a zoeal stage (Berrill, 1975). Within Axiidae, complete developmental histories for a species of *Axius* and another of *Calocaris*, the latter formerly treated a member of Calocarididae, have been assembled from plankton (Bourdillon-Casanova, 1960).

Within Callianassidae, knowledge of complete histories is based upon a growing number of species, though coverage is biased to accessible shallow and intertidal representatives of this very diverse family. Several **planktonic studies** ultimately produced the apparently complete history for *Callianassa subterranea*, representing the type genus for the family (Webb, 1921; Gurney, 1942), as did early plankton studies for *Trypaea* in Australia (Dakin & Colefax, 1940). Sharing subfamily assignment to the Callianassinae with these genera, two species of *Nihonotrypaea* and another of *Pestarella* also now have their larval histories fully documented, but by laboratory rearing (Konishi et al., 1990; Thessalou-Legaki, 1990; Miyabe et al., 1998). An almost complete account has been reported for a species of the related genus, *Neotrypaea* (cf. Aste & Retamal, 1984). Laboratory rearing has also produced thorough accounts of larval histories for a number of callianassid genera representing the subfamily Callichirinae, five of which represent subtidal species of *Callichirus* (fig. 69.29D-G), those for *Callichirus kraussi* and *Callichirus masoomi* (Tirmizi, 1970) being originally reported under previous generic assignments (Forbes, 1973; Aste & Retamal, 1983; Strasser & Felder, 1999, 2000). Within this same subfamily, laboratory

[modified from Rodrigues, 1976]. C, *Lepidophthalmus louisianensis*, prezoaea; D, F, G, *Callichirus islagrande*: D, zoea I dorsal habitus; F, zoea IV dorsal habitus; G, decapodid dorsal habitus [modified from Strasser & Felder, 2000]. E, *Callichirus major*, Gulf of Mexico population: zoea I telson [modified from Strasser & Felder, 1999]. H-L, ditto: H, zoea I lateral habitus; I, telson; and, J, rostrum; K, decapodid tail fan; and, L, lateral habitus [modified from Nates et al., 1997].

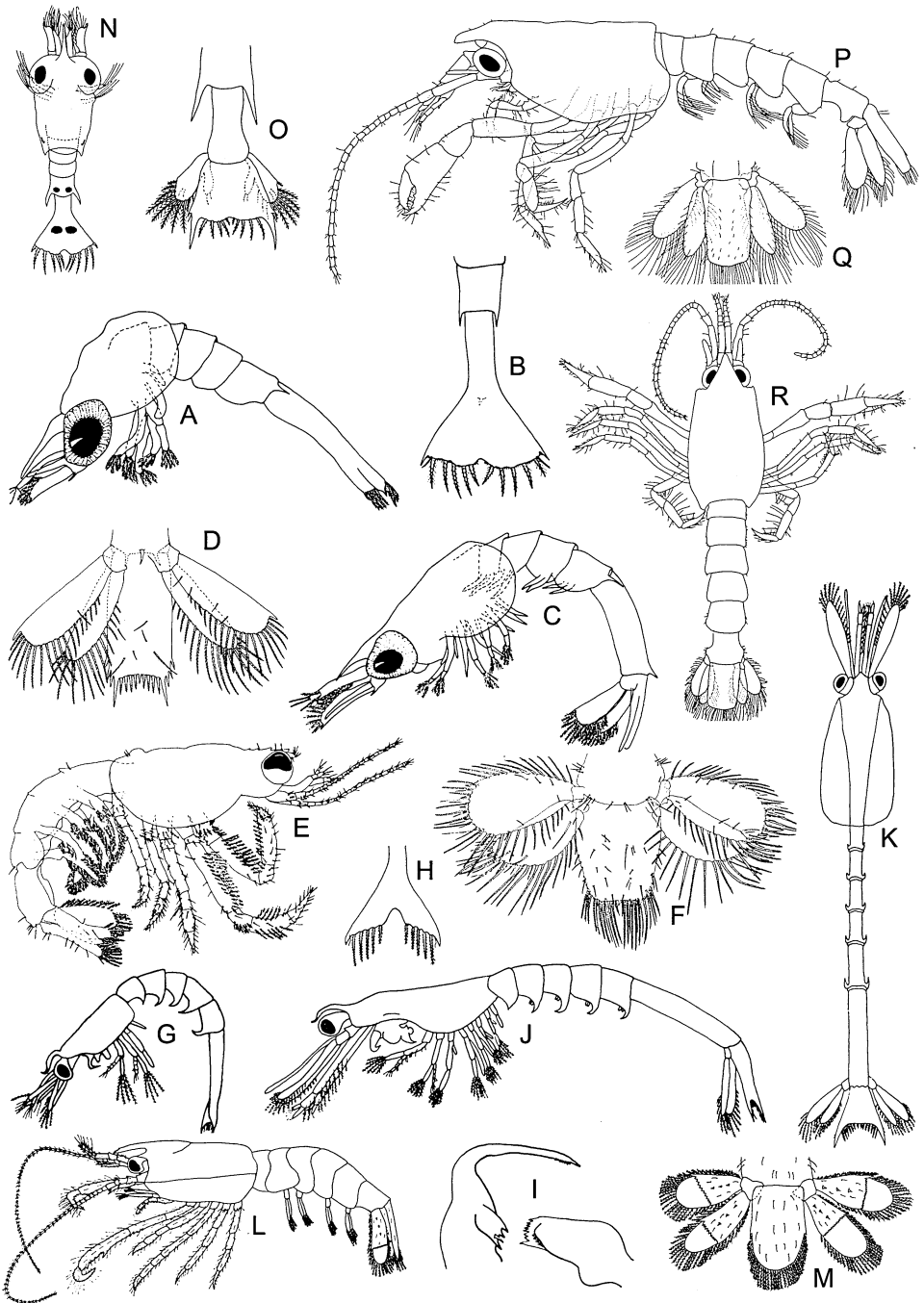


Fig. 69.30. Representative larval stages of infraorder Gebiidae, families Upogebiidae, Laomediididae, and Axianassidae. A-F, *Upogebia* sp., Venezuelan population: A, zoea I lateral habitus; and, B, telson; C, zoea IV lateral habitus; and, D, tail fan; E, decapodid lateral habitus; and, F, tail fan

rearing has produced full accounts through metamorphosis for a species of *Sergio* (cf. Rodrigues, 1984b) as well as for three species of *Lepidophthalmus* (fig. 69.29H-L), the latter of which exhibit highly abbreviated larval development (Nates et al., 1997; Abrunhosa et al., 2005, 2008).

Among members of Gebiidea (fig. 69.30A-R), complete larval histories are known for primarily species of Upogebiidae assignable to *Upogebia*. Of these, the results for four species are based upon planktonic larvae (Webb, 1919; Gurney, 1924, 1937; Heegaard, 1963; Sandifer, 1973; Ngoc-Ho, 1981; Andryszak, 1986), and for another six upon laboratory rearing (Shenoy, 1967; Ngoc-Ho, 1977b; Konishi, 1989; Siddiqui & Tirmizi, 1995; Shy & Chan, 1996; dos Santos & Paula, 2003). Complete description for yet another laboratory-reared species is pending, and selected figures are herewith reproduced to represent typical larval habitus (fig. 69.30A-F). The full **planktonic history** is also known for a species of *Acutigebia*, originally treated as a congener of the aforementioned group (Gurney, 1924).

Complete larval histories for Laomediidae are limited to those based upon plankton for two species of *Jaxea* (cf. Gurney, 1942; Bourdillon-Casanova, 1960; Wear, 1965) and those based upon very unique laboratory reared stages (fig. 69.30G-M) for a species of *Naushonia* (cf. Goy & Provenzano, 1978). A full detailed account of development through metamorphosis in Axianassidae is available for one species of *Axianassa* (cf. Strasser & Felder, 2005), and comparative studies of the larvae (fig. 69.30N-R) were in this case used to support separation of Axianassidae from the laomediids. Even so, larvae of these families appear to share notably asymmetrical mandibles (fig. 69.30I). Remarkably, the larval history for Thalassinidae remains incompletely known (Sankolli, 1967; Pillai, 1982) despite accessibility and some commercial harvest of *Thalassina*.

ECOLOGY AND ETHOLOGY

Habitats

The axiideans and gebiideans share apparent **convergent adaptations** to a **cryptic lifestyle**. Most species **burrow in various types of sediments** from **coarse coral rubble to sand and mud**, or even in rather **firm substrates**. An under-sampled habitat exists in **cavities**, sediment filled **interstices**, and eroded substrates of **coral reefs** where many axiid shrimp live cryptically. A few species of Upogebiidae and members of Eiconaxiidae are **sponge commensals** (Williams, 1987; Kensley, 1996b), while members of the upogebiid genus *Pomatogebia* **bore into coral skeletons** (Williams, 1986; Williams & Scott, 1986).

[modified from unpublished illustrations by E. Viso and S. Nates]. G-M, *Naushonia crangonoides*: G, zoea I lateral habitus; H, telson; and, I, asymmetrical mandibles; J, zoea IV lateral; and, K, dorsal habitus; L, decapodid lateral habitus; and, M, tail fan [modified from Goy & Provenzano, 1978]. N-R, *Axianassa australis*: N, zoea I dorsal habitus; O, zoea III tail fan; P, decapodid lateral habitus; Q, tail fan; and, R, dorsal habitus [modified from Strasser & Felder, 2005].

All axiideans and gebiideans live in **marine habitats** or in habitats under seawater influence. Many Upogebiidae and Callianassidae are found in **estuaries** with reduced salinity. Members of the genus *Lepidophthalmus* Holmes, 1904 are especially known for **low-salinity habitats** (Manning & Felder, 1991) and **mass migrations into rivers** have been reported in Cameroon for *Lepidophthalmus turneranus* (White, 1861) (see Vanhöffen, 1911). Among specialized environments from which axiideans and gebiideans have been recorded are **hypoxic** and **sulphidic sediments** (Atkinson & Taylor, 2005), **hydrocarbon seeps** (Felder & Kensley, 2004), and **volcanic hot springs** (Türkyay & Sakai, 1995).

Depth distribution

Thalassinideans can occur from the upper intertidal to water depths of more than 2000 m, the deepest dwelling being a member of Axiidae. While both infraorders occur widely across this range, most species (95%) live in shallow water (<200 m) (Dworschak, 2000).

Role in food chains

In intertidal settings, **birds** are the most important **predators** on thalassinidean shrimp. Stenzel et al. (1976) described three different methods how long-billed curlews (*Numenius americanus* Bechstein, 1812) obtain their prey: the “burrow-probe”, which is used in emerged areas, the “pause-probe” method, which is used in areas submerged with 5-10 cm of water, and by pecking. These authors found that in a central Californian estuary, *Neotrypaea californiensis* accounted for 20-24% and *Upogebia pugettensis* for 7-15% of the curlew’s food. For the willet (*Catoptrophorus semipalmatus* (Gmelin, 1789)) the burrowing shrimp constitute 3-12% and 3-19% of the prey, respectively. In a north Californian estuary, Leeman et al. (2001) reported that the curlew feed only on *Neotrypaea californiensis* that account for 1-16% of its diet. Turpie & Hockey (1996) found that mud prawns (*Upogebia africana* (Ortmann, 1894)) in a South African estuary accounted for 89% and 88.5% of the net energy consumption of grey plovers (*Pluvialis squatarola* (Linnaeus, 1758)) and whimbrels (*Numenius phaeopus* (Linnaeus, 1758)), respectively. The birds were able to catch even large-sized shrimp up to 70 mm total length.

During high tide in the intertidal and on sublittoral bottoms, **fish** are the main predators of thalassinidean shrimp. Two major groups of fish appear to be the most important predators: sharks and rays. Russo (1975) reported that the leopard shark (*Triakis semifasciata* Girard, 1855) shows a shoveling or burrowing habit in capturing its prey *Upogebia pugettensis* and *Neotrypaea californiensis* in California. In the Mediterranean, *Upogebia pusilla* and *Upogebia tipica* (Nardo, 1869) are regularly found in the stomachs of sharks (*Squalus fernandinus* Molina, 1792, *Scyliorhinus canicula* (Linnaeus, 1758), and *Mustelus mustelus* (Linnaeus, 1758)) and rays (*Raja miraletus* Linnaeus, 1758 and *Raja clavata* Linnaeus, 1758) (Jardas, 1972a, b; Ajayi, 1982; Morte et al., 1997; Saglam & Bascinar, 2008).

On intertidal sand flats in Kyushu, Japan, feeding of the stingray *Dasyatis akajei* (Müller & Henle, 1841) during high tide leaves numerous large pits on the flat (Harada

& Tamaki, 2004). The authors found that feeding of the rays and its sediment disturbance reduced densities of *Nihonotrypaea harmandi* (Bouvier, 1901) by up to 78%.

Day (1967) reported that the white steenbras *Lithognathus lithognathus* (Cuvier, 1829) developed the capacity of blowing holes in the sand to feed on *Upogebia africana*. This shrimp forms also the dominant food item in the diet of the sea-catfish *Galeichthys* (as *Tachysurus*) *feliceps* Valenciennes, 1840, *Pomadasys commersoni* (Snyder, 1909), and *Monodactylus falciformis* Lacépède, 1801, and is also consumed by *Argyrosomus hololepidotus* (Lacépède, 1801), *Elops machnata* (Forsskål, 1775), and *Platycephalus indicus* (Linnaeus, 1758) in South African estuaries (Marais, 1984). The catfish *Galeichthys feliceps* has been reported to feed on *Upogebia africana* and *Callinectes kraussi* (cf. Tilney & Hecht, 1990). In the Mediterranean, the seabream *Diplodus annularis* (Linnaeus, 1758) and the common sole *Solea solea* (Linnaeus, 1758) feed on *Upogebia* (cf. Molinero & Flos, 1992; Molinero et al., 1994; Matic-Skoko et al., 2004). In a Californian estuary, *Neotrypaea californiensis* constitutes up to 39% of the diet of the staghorn sculpin *Leptocottus armatus* Girard, 1854 (cf. Posey, 1986a, b) that feeds also on *Upogebia pugettensis* (cf. Armstrong et al., 1995). Tamaki et al. (1992) studied the predation impact of the snake eel *Pisodonophis cancrivorus* (Richardson, 1848) on *Nihonotrypaea harmandi* and estimated that 4.6% of the ghost shrimp population was consumed by the snake eel per year. Yamahira et al. (1996) reported that the puffer *Takifugu niphobles* (Jorsan & Snyder, 1901) feeds mainly on *Nihonotrypaea japonica* on tidal flats in Kyushu, Japan and *Trypaea australiensis* is temporally the main food source for juvenile King George whiting (*Sillaginodes punctatus* (Cuvier, 1829)) in Western Port, Victoria (Robertson, 1977).

The yellow-bellied mangrove **snake** *Fordonia leucobalia* (Schlegel, 1837), whose prey are mainly crabs, occasionally feeds also on *Thalassina anomala* (Herbst, 1804) (cf. Shine, 1991; Voris & Murphy, 2002; Nobbs & Blamires, 2004).

Weitkamp et al. (1992) and Darling et al. (1998) reported that *Neotrypaea californiensis* at Vancouver Island and in Puget Sound is the prey of juvenile **grey whales** (*Eschrichtius robustus* Lilljeborg, 1861), which feed by suction sieving involving the whale rolling on its side above the bottom, sucking benthic material into the mouth, and then straining the material through the baleen plates to expel fine particles. By this activity, feeding pits are formed. An estimated 75 tons of thalassinidean shrimp, which represents an energetically valuable prey, has been removed by the whales in one particular year at the study site.

Burrows

The most reliable method for studying the **shape of the burrows** is *in situ* casting. In the early 1930s, burrows were cast with plaster of Paris, but better replicas were later produced with the application of resin (polyester or epoxy) using a method developed by Shinn (1968) (see also Atkinson & Chapman, 1984). The burrows of more than 60 species have been documented in literature to date.

Disadvantages of the casting method are the limitation in connection with the depth limitations of SCUBA-diving, and the incomplete documentation of filled burrow parts.

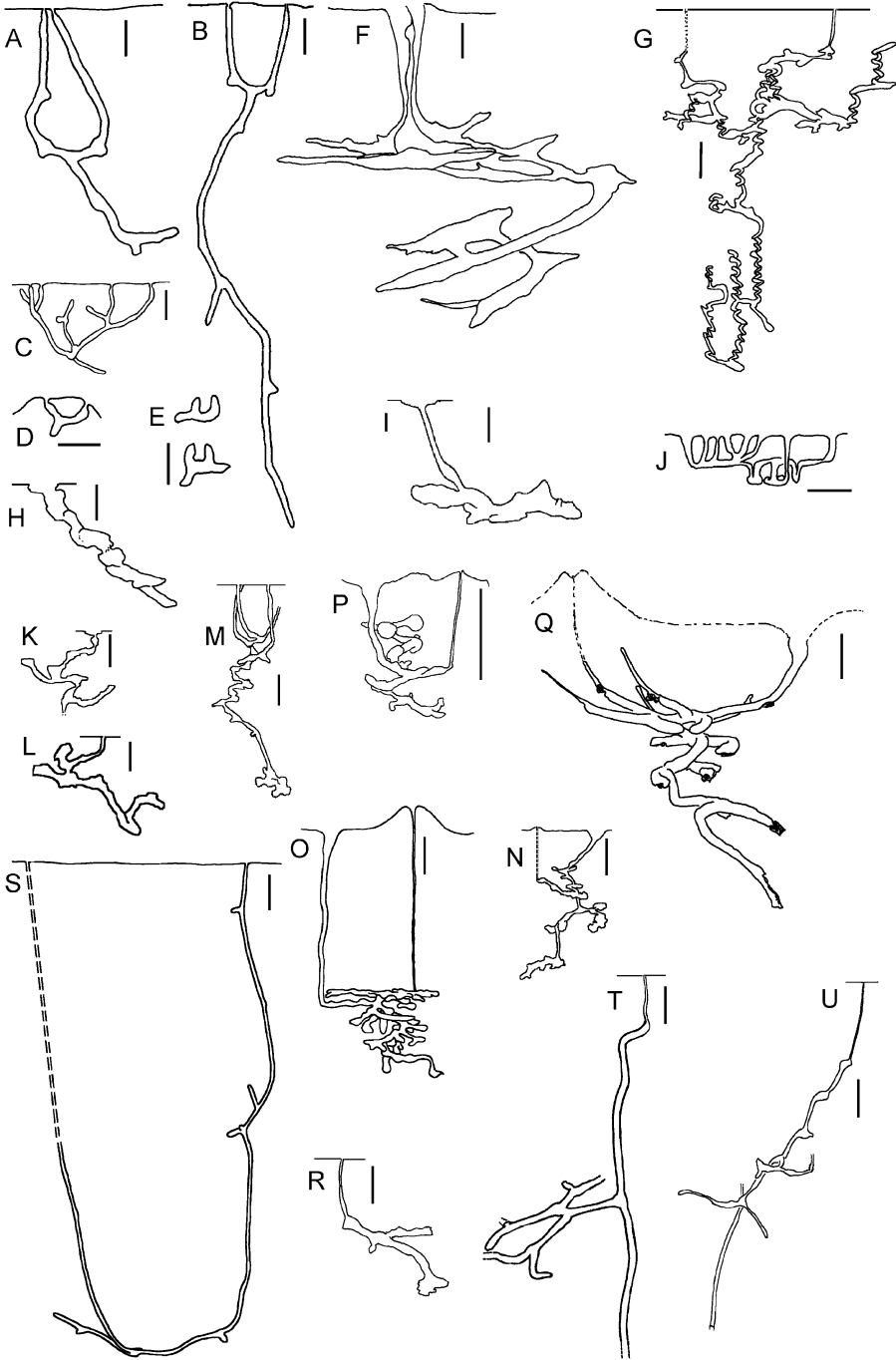
These structures are better investigated by removing layer for layer, either in box-cores, *in situ* with an air-lift sampler (“archeological method”), or in the intertidal by digging.

In most cases the inhabitant is entombed within the cast and the producer of the burrow can be identified. If this is not the case, animals have to be captured around the casting site. Placing of live animals in narrow aquaria filled with ambient sediment (limoria) has also been used to observe their burrowing and feeding behavior, the assumption being that animals removed from field sites will re-burrow and produce some semblance of a natural burrow. At very least, such laboratory observations may yield additional information on **burrow shape** and **dynamics**.

The burrows of the **mud-lobster**, *Thalassina anomala*, are characterized by large (up to 1 m in height) **mounds** and are described as being mainly **vertical with horizontal side branches** (Sankolli 1963).

Upogebiidae have a rather **simple** burrow shape consisting of one or more **upper U-shaped sections** and a **central vertical shaft** (fig. 69.31A-C). Along the sides of the “U” and also along the shaft are extensions, the **turning chambers** (Dworschak, 1983). This basic pattern is also visible in the coral boring species *Pomatogebia operculata* (Schmitt, 1924) (see Kleemann, 1984; fig. 69.31D), the firm substrate borer *Upogebia mediterranea* Noël, 1992 (see Asgaard et al., 1998), and the sponge-inhabiting species *Upogebia acanthura* Coelho, 1973 (as *Upogebia synagelas* Williams, 1987) (Scott et al., 1988; fig. 69.31E). The burrows may reach to depths of up to 2 m as in *Upogebia major* (De Haan, 1841) from Japan (Kinoshita, 2002). A characteristic interspecific difference in the burrow shapes of the two sympatrically occurring species *Austinogebia narutensis* (Sakai, 1986) and *Upogebia issaeffi* (Balss, 1913) was found by Kinoshita & Itani (2005) on a Japanese tidal flat. Variations due to environmental conditions have also been found. The burrows of *Upogebia pusilla* for instance, are less deep in the sublittoral than in the intertidal (Dworschak, 1987a) and Li et al. (2008) noted that the burrows of *Austinogebia edulis* (Ngoc-Ho & Chan, 1992) were deeper in mud than in sand, but did not vary in size

Fig. 69.31. Burrows: A, *Upogebia pusilla* [modified from Dworschak, 1983, fig. 12.1]; B, *Upogebia major* [modified from Kinoshita, 2002, fig. 1A]; C, *Upogebia stellata* [modified from Nickell et al., 1995, fig. 1C]; D, *Pomatogebia operculata* [modified from Kleemann, 1984, fig. 4]; E, *Upogebia acanthura* [modified from Scott et al., 1988, fig. 1c, as *U. synagelas*]; F, *Jaxea nocturna* [modified from Pervesler & Dworschak, 1985, pl. 2, fig. 5]; G, *Axianassa australis* [modified from Dworschak & Rodrigues, 1997, fig. 5D]; H, *Axiopsis serratifrons* [modified from Dworschak & Ott, 1993, fig. 4B]; I, *Neaxius acanthus* [modified from Kneer, 2006, fig. 18]; J, *Calocaris macandreae* [modified from Nash et al., 1984, pl. 1, fig. e]; K, *Pestarella whitei* [modified from Dworschak, 2002, fig. 2c]; L, *Nihonotrypaea petalura* [modified from Shimoda & Tamaki, 2004, fig. 3A]; M, *Biffarius arenosus* [modified from Bird & Poore, 1999, fig. 2A]; N, *Pestarella tyrrhena* [modified from Dworschak et al., 2006a, fig. 1d]; O, *Callianassa subtterranea* [modified from Nickell et al., 1995, fig. 1A]; P, *Paratrypaea bouvieri* [modified from Dworschak & Pervesler, 1988, pl. 2, fig. 5]; Q, *Glypturus acanthochirus* [modified from Dworschak & Ott, 1993, fig. 7B, different view]; R, *Neocallichirus grandimana* [modified from Dworschak & Ott, 1993, fig. 6B]; S, *Corallianassa longiventris* [modified from Dworschak et al., 2006a, fig. 2b]; T, *Callichirus major* [modified from Rodrigues, 1983, fig. 91A]; U, *Lepidophthalmus louisianensis* [modified from Dworschak, 2000b, fig. 3C]. Scales: 10 cm in A-C, F-K, M-O, Q-U; 5 cm in D, E, L, P.



between tidal levels. Some upogebiids though, have more complex burrows. For example, those of *Upogebia deltaura* can be extensive with several branches, but still have U-shaped components (Hall-Spencer & Atkinson, 1999). The burrows of *Upogebia stellata* also contain several U-shaped parts (Nickell & Atkinson, 1995).

Burrows of **Laomediidae** are generally a **spiral**, like that of *Laomedea astacina* De Haan, 1841 from Japan (Ohshima, 1967; Sakai, 1968; Utashiro, 1973) or *Jaxea nocturna* from the Mediterranean. The latter consist of **two inclined or crossing “J’s”**, which after joining, lead downwards in the form of a spiral with several **wide chambers** (Pervesler & Dworschak, 1985; fig. 69.31F). Casts made of the burrows of *Jaxea nocturna* off Scotland show a similar shape, but had up to 7 openings (Nickell & Atkinson, 1995) and the burrows cast in the middle of the Gulf of Trieste had a large horizontal extension (Pervesler & Hohenegger, 2006).

The **most complex burrows** reported to date for a thalassinidean are those of *Axianassa australis*, which show numerous regular **corkscrew spirals**, for which varied functions have been postulated (Dworschak & Rodrigues, 1997; Felder, 2001; fig. 69.31G).

The **axiid** *Axius serratus* Stimpson, 1852 from the Atlantic coast of North America (muddy bottoms in 10 m) has a simple, **slightly spiral shaft with side branches** and reaches a depth of over 2 m (Pemberton et al., 1976). Kensley & Simmons (1988) described the burrow of *Axiorygma nethertoni* Kensley & Simmons, 1988 as simple, unlined, reaching to a depth of only 15 cm. Another simple inclined burrow without lining is that of *Axiopsis serratifrons* (A. Milne-Edwards, 1873) from coral rubble in the Caribbean (Dworschak & Ott, 1993; fig. 69.31H).

The burrows of the **strahlaxiid** *Neaxius acanthus* (A. Milne-Edwards, 1878) from Sulawesi are similar, and their burrows have a **lined burrow wall** (Kneer, 2006; Kneer et al., 2008b; fig. 69.31I). No information is available about the “burrow” shape of **Eiconaxiidae** that live in sponges. The burrows of the **calocaridid** *Calocaris macandreae* from 20-30 m deep muddy bottoms in the North Sea have several (2-7) **funnel-shaped openings** and consist of a series of “U’s” in two sediment depths with **loops and rings** (Nash et al., 1984; fig. 69.31J). No information is available on the burrows of **Micheleidae**, but the burrow of the **callianideid** *Callianidea laevicauda* Gill, 1859 is simple, similar to that of *Axiopsis*, but with lined burrow roofs as observed in the laboratory by Rodrigues (1983). The **thomassiniid** *Thomassinia gebioides* de Saint Laurent, 1979b constructed a simple burrow in narrow aquaria.

The greatest **diversity** with respect to burrow shape occurs among **Callianassidae**. Simple burrows with one or two openings are found in species like *Pestarella whitei* (Sakai, 1999) (as *Callianassa*, see Dworschak, 2002) and *Nihonotrypaea petalura* (Stimpson, 1860) (see Shimoda & Tamaki, 2004), living in boulder fields where they wind among boulders and cobbles (fig. 69.31K, L). *Nihonotrypaea japonica* (Ortmann, 1891) (as *Callianassa* sp.) has burrows with alternating shafts and chambers, with a single burrow opening, while that of *Nihonotrypaea harmandi* (as *Callianassa japonica*) is basically Y-shaped with two surface openings (Tamaki & Ueno, 1998). A similar shape with symmetrical U-shaped components and simple openings on the surface (fig. 69.31M) has been observed in the burrows of *Neotrypaea* (as *Callianassa*) *californiensis* and *Neotrypaea* (as *Callianassa*) *gigas* (Dana, 1852), *Trypaea australiensis*, and *Biffarius*

arenosus (cf. Kenway, 1981; Swinbanks & Murray, 1981; Griffis & Chavez, 1988; Bird & Poore, 1999; Stapleton et al., 2002; Butler & Bird, 2008). Slightly asymmetrical and shallow is the upper U-shaped section in the burrows of *Callianassa filholi* (cf. Berkenbusch, 1999; Berkenbusch & Rowden, 2000) and *Pestarella tyrrhena* (fig. 69.31N), the latter showing several debris-filled chambers along the spiral shaft (Dworschak, 2001; Dworschak et al., 2006a). Burrows with different openings, one as a funnel and the other as a small mound with a dense lattice, were observed in *Callianassa subterranea* (cf. Atkinson & Nash, 1990; Nickell & Atkinson, 1995; fig. 69.31O). A similar asymmetrical “U” with a vertical shaft leading to a funnel and a thin shaft leading to a mound is found in the burrow of *Paratrypaea* (as *Callianassa*) *bouvieri* (Nobili, 1904) (see Dworschak & Pervesler, 1988; fig. 69.31P). Also seen here are spiral shafts with bulbous chambers that lead further down or up towards the surface. Ziebis et al. (1996a) describe the burrows of *Callianassa truncata* (Giard & Bonnier, 1890) to consist of an upper compartment comprising three connected chambers with two shafts leading to funnels, and a thin shaft ending in a mound at the sediment surface; the burrow then continuing downward with chambers at regular intervals.

The burrows of *Glypturus acanthochirus* Stimpson, 1866 (fig. 69.31Q) are characterized on the sediment surface by **large mounds** and **nearby funnels**, and often avalanches of sediment fall from the mounds into the funnels. The burrows consist of a spiral with several radiating tunnels branching from the upper level, one of them leading to a funnel, the other to a mound. The others are blocked and are either filled funnels or “irrigation tunnels”. Deeper side branches are filled with coarse shell material (Dworschak & Ott, 1993). Similar burrows have been described for the other three species of this genus, *Glypturus* (as *Callichirus*) *armatus* (A. Milne-Edwards, 1870) (see de Vaugelas, 1990), *Glypturus* (as *Callichirus*) *laurae* (de Saint Laurent, 1984) (see de Vaugelas, 1984, 1990), and *Glypturus motupore* Poore & Suchanek, 1988 (see T. Suchanek, pers. comm., 1987, in de Vaugelas, 1990).

The burrow shape within the genus *Neocallichirus* is **variable**. That of *Neocallichirus maryae* Karasawa, 2004 (as *Callianassa rathbunae* Schmitt, 1935) is similar to those of *Glypturus*, showing large mounds and funnels at the surface and radiating branches and a shaft, however, with shorter side branches (Suchanek, 1983). The burrow shape of *Neocallichirus grandimana* (Gibbes, 1850), on the other hand, is simple, leading to a sediment depth of 36 cm (fig. 69.31R). The burrow is only partially lined with dark brown sediment as opposed to the whitish surrounding sediment (Dworschak & Ott, 1993). A very complex burrow with several shafts leading to small mounds and small funnels and a reticulated network of tunnels between dead coral blocks has been described for *Neocallichirus vaugelasi* Dworschak, 2011 (as *Callichirus jousseaumei* (Nobili, 1904)) (see de Vaugelas, 1984, 1990).

Of a completely different construction are the burrows of *Corallianassa longiventris* (A. Milne-Edwards, 1870). They consist of a **deep “U”** (down to 1.5 m) with upper and lower **chambers** (fig. 69.31S), some of them filled with macrophyte debris. The burrows are closed most of the time, but when open, the shrimp can be observed near the opening (Suchanek, 1985; Dworschak & Ott, 1993; Dworschak et al., 2006a). The same burrow

shape has been reported for the Indo-Pacific congener *Corallianassa coutierei* (Nobili, 1904) (see Kneer, 2006; Kneer et al., 2008b).

The burrows of *Callichirus major* mainly consist of a **vertical shaft with three distinct regions** and several side branches (fig. 69.31T). The upper section is narrow and in greater sediment depth the shafts are interconnected by horizontal tunnels, thus forming a large **network** reaching to a sediment depth of 3-5 m (Frey et al., 1978; Rodrigues, 1983). Burrows of *Lepidophthalmus louisianensis* (fig. 69.31U) are similar as they also have an upper narrow passage, vertical shafts, horizontal tunnels, can reach a depth of up to 2.5 m, and may be interconnected (Felder & Staton, 1990; Felder & Griffis, 1994; Nates & Felder, 1998; Dworschak, 2000b). The burrows of *Lepidophthalmus sinuensis* Lemaitre & Rodrigues, 1991 on the other hand, are Y-shaped with two burrow openings (Lemaitre & Rodrigues, 1991) while Felder & Griffis (1994) described burrows of this species as having three openings, more branches (than *Lepidophthalmus louisianensis*) and to reach a depth of only 30-50 cm. Burrows of the Pacific *Lepidophthalmus bocourti* (A. Milne-Edwards, 1870) are described as being similar to those of the other species (Nates & Felder, 1998a, b).

No information is yet available on the burrow shape of **Ctenochelidae**. Burrows of Laomeidiidae, Axiidae, Strahlaxiidae, Calocarididae, and Callianideidae have a much **wider diameter** than the shrimp's cross-section, while Upogebiidae, Thomassiniidae, and Callianassidae show a **tight fit** between their body and the burrow diameter.

A **survey of burrow shapes** for all thalassinidean shrimp known at that time was presented by Dworschak (1983). A **classification of burrow shape** according to feeding mode was later introduced by Suchanek (1985). He identified three **ecological types**: filter/suspension feeders, deposit/detritus feeders, and seagrass/algae harvesters. Griffis & Suchanek (1991) published an extensive review on burrow shapes and dimensions and expanded the 1985 model with three feeding types to **6 general types**: (1) those of deposit feeders with tiered galleries, or, (2) simple branches; (3) of drift catchers with simple chambers; and those of filter/suspension feeders, which are, (4) deep reticulate, show (5) a simple "U", or (6) multiple "U"s. Dworschak & Ott (1993) criticized Griffis & Suchanek's (1991) model as they had difficulties assigning certain species to a burrow type considering the variety of feeding modes and the environmental differences. They concluded that burrow shape must be regarded as due to both **phylogenetic affinities** and the **ecological adaptation** of the animal constructing them.

Another **classification** of thalassinidean burrows, along with burrows of some other decapods, was given by de Vaugelas (1990). He distinguished **four burrow types**, mainly based on feeding types and the appearance of the openings. He showed an increasing isolation of the shrimps from the surface from the simple type I (omnivorous shrimp, which eventually leave the burrow, e.g., *Axiopsis serratifrons* and *Corallianassa longiventris*), to type II (detritivorous, large mounds, e.g., burrows of the genus *Glypturus*), and type III (mixed suspension and deposit feeders with narrow upper sections and small mounds, e.g., temperate species of *Callianassa* s.l.), to type IV (suspension feeders, e.g., *Upogebia*).

Nickell & Atkinson (1995) presented an alternative approach to thalassinidean **trophic classification** based on the burrows. Rather than classifying complete burrow morphologies, they recognized 12 individual components of the burrows that indicate a possible

feeding mode. By considering the overall burrow morphology, conclusions can be drawn about the relative importance of each trophic mode to the species under study.

Behavior

Burrowing behavior. – Most members of Axiidea and Gebiidea are **obligate burrowers** and are rarely or never seen outside their burrows once they have settled from early developmental stages. Exceptions include *Thalassina anomala*, which has been observed to push sediment out of its burrow (Ng & Kang, 1988) and those species that periodically position themselves at the burrow opening to catch floating seagrass, like *Axiopsis serratifrons* (cf. Kensley, 1981; Dworschak & Ott, 1993), *Neaxius acanthus* (cf. Kneer, 2006; Kneer et al., 2008b) or *Corallianassa longiventris* and *Corallianassa coutierei*. The **behavior** of the latter three species has been studied in detail (Dworschak et al., 2006a; Kneer, 2006; Kneer et al., 2008b). Other exceptions are seen in what remain as poorly understood periodic upper estuarine and coastline **river swarms**, and **migrations in the water column**, especially by some members of the genus *Lepidophthalmus* (cf. Monod, 1927; Felder & Lovett, 1989).

When removed from their burrows, intact shrimp are usually able to **re-burrow**. It takes only seconds for small callianassids to disappear in the sediment, but larger specimens need more time. In the initial phase, a pit is formed by lifting sediment with the basket formed by the first two pereopods, and the material is dumped at the surface. When the excavation has reached body length, material from deeper layers is transferred to upper parts of the burrow so that burrows are mainly constructed by compaction of the surrounding sediment rather than excavation. The stereotypical procedure of constructing a new burrow was studied in detail for *Callianassa subterranea* by Stamhuis et al. (1997). They found that the final burrow length is reached in about 100 hours. In some species, however, adult individuals are not able to re-burrow, and this has been observed in *Upogebia affinis* (Say, 1818) (C. Jenner, pers. comm., 1989) and *Glypturus acanthochirus* (see Dworschak & Ott, 1993).

Feeding behavior. – Due to the cryptic lifestyle of all species, observations on behavior have been limited to the laboratory. These observations range from early natural history accounts (MacGinitie, 1930, 1934; Pearse, 1945) to more detailed studies (Dworschak, 1987b) that mainly concentrate on the **feeding behavior**, especially comparing this behavior between different species of upogebiids and callianassids. Upogebiids show a stereotypic behavior of **suspension feeding**, which takes place in the turning chambers (Dworschak, 1987b; Coelho et al., 2000b). In this behavior, the animal arches its dorsal side to fit tight against the inner burrow wall of the “U”, with the anterior region positioned just above the turning chamber and the pleon in the narrow flat part of the “U”, just behind the turning chamber. The chelate first pereopods and the simple second pereopods (fringed with long setae) are held upwards and pressed against the sides of the burrow wall. The setae of both pereopods overlap, thus forming a basket. The third, fourth, and fifth pereopods are pressed onto the side walls and stabilize the animal. A posteriorly-directed water current is created by intermittent beating of the pleopods. Suspended matter entering the burrow is intercepted by the setae of this basket and from time to time the

third maxillipeds, which are fringed with short stiff, saw-toothed setae, are swept over the basket to clear the setae and transfer the material to the second maxillipeds. Between four and nine movements of the maxillipeds could be observed in one minute. The animals spend about 50% of their time feeding in this position (Dworschak, 1987b). Although suspension feeding is the main trophic mode in upogebiids, some flexibility has been observed. Dworschak (1987b) noted **ingestion of deposited material** from around the burrow opening, or the burrow wall, either directly or after re-suspension in the basket in *Upogebia pusilla*. A similar **re-suspension feeding behavior** has also been observed in *Upogebia omissa* Gomes Corrêa, 1968 and *Pomatogebia operculata* by Coelho et al. (2000b). Nickell & Atkinson (1995) noted that *Upogebia stellata* is primarily a suspension feeder, but can make use of deposited material by direct transfer to the mouthparts or by re-suspending it within the burrow.

The laomediid *Jaxea nocturna* was found to be a **re-suspension feeder** (Nickell & Atkinson, 1995) and the axianassid genus *Axianassa* is considered to be a deposit feeder (Coelho & Rodrigues, 2001a). Few observations exist on feeding in axiids. Many seem to be **omnivorous**, like *Axiopsis serratifrons* (see Kensley, 1981), although a study using stable isotopes identified seagrass and brown algae as the main food source of this species (Abed-Navandi & Dworschak, 2005). Other species, such as *Axius stirhynchus* Leach, 1815, are thought to deposit feed (Ellis & Baker, 1973). Among the strahlaxiids, *Neaxius vivesi* (Bouvier, 1895) seems to be omnivorous (Berrill, 1975), while the main food of *Neaxius acanthus* is plant material (Kneer, 2006; Kneer et al., 2008b). The calocaridid *Calocaris macandreae* is generally considered to be a deposit-feeder (Buchanan, 1963; Calderon-Perez, 1981; Pinn et al., 1998a, b) and recent observations of Pinn & Atkinson (2009) provided evidence of **carnivory** and **caching behavior** in this species.

Contrary to the mainly suspension feeding upogebiids, callianassids have been considered primarily **deposit feeders**. They are almost constantly engaged in taking up sediment from one part of the burrow, manipulating it between the mouthparts, and then transporting it to another location (Dworschak, 1987b). During which of these activities the ingestion actually takes place is often difficult to identify. Stamhuis et al. (1998a, b) performed a detailed analysis of the mechanisms involved in the selective feeding of *Callianassa subterranea*. In a previous study on time allocation in the same species, Stamhuis et al. (1996) identified in an ethogram 12 behavioral states which, after a sequence analysis, resulted in six behavioral classes: “wander”, “rest”, “burrow”, “survey”, “groom”, and “ventilate”. No behavioral class “feeding” was identified, which is interpreted that the shrimp feed while they burrow. In a similar analysis of the feeding behavior of *Pestarella tyrrhena* and *Corallianassa longiventris*, Dworschak et al. (2006a) could also identify no “feeding” behavioral class. Besides manipulating seagrass debris that is introduced into the burrow, the shrimp mainly manipulate sediment and the authors conclude that ingestion may take place while the shrimp are **“sorting sediment”**, a behavior that has also been observed in *Callianassa subterranea* by Nickell & Atkinson (1995). This involves alternate movements of the right and left third maxilliped that draw sediment into a channel created by the expanded meri of these limbs. The second maxillipeds also imitate the movements of

the third and help to draw particles towards the mouth. While only small amounts of sediment are handled during this behavior by *Pestarella tyrrhena* with gentle movements of the appendages, *Corallianassa longiventris* more vigorously shake a full load of sediment between their second pereopods, thus creating a cloud of suspended matter. This somewhat resembles the “re-suspension” feeding described for the mainly filter-feeding upogebiids (see above), and also the callianassid *Trypaea australiensis* (see Stapleton et al., 2002). In this method of feeding the animals fluidize the sediment in the setal basket with the second and third pereopods, throw it upwards in front of the mouthparts, and the third maxillipeds then transfer the particles to the mouth. Other callianassids, *Sergio mirim* for example, are regarded mainly as deposit feeders, but occasionally they bury organic matter in some parts of the burrow and feed on this enriched substrate later (Rodrigues, 1966; Coelho & Rodrigues, 2001b). On the other hand, *Callichirus major* is considered a **generalist** feeder, being able to suspension and deposit feed (Coelho & Rodrigues, 2001b). The suspension feeding behavior involves the antennae, as well as the second pereopods and third maxillipeds (Rodrigues, 1966).

Grooming behavior. – In a sedimentary environment, **grooming** of the body surfaces is important to prevent fouling and infestation by parasites. The special setal arrangements on the appendages involved (see above) have been dealt with in several SEM studies (Nickell et al., 1998; Batang & Suzuki, 1999, 2003; Batang et al., 2001). The time allocated for grooming, which can take place also during other activities, was 15% in *Callianassa subterranea* (cf. Stamhuis et al., 1996) and 10-18% in *Corallianassa longiventris* and *Pestarella tyrrhena* (cf. Dworschak et al., 2006a), while Kneer et al. (2008b) found that *Neaxius acanthus* spent only 5% of its time grooming.

Individuality and burrow maintenance. – Most axiideans and gebiideans live **individually**, each inhabiting a burrow of its own, except for some axiids (*Axiopsis serratifrons*), strahlaxiids (*Neaxius*), and coral boring or sponge inhabiting upogebiids and axiids that live in **male-female pairs** (some only occasionally). In several cases, resin casting has shown that individual burrows are interconnected (Coelho et al., 2000a; Candisani et al., 2001). These connections are probably the passages through which males and females get together for **mating**, as Candisani et al. (2001) described such an encounter in the laboratory. The male dug a straight and almost horizontal 10 cm long connection to the female’s burrow, and “As soon as the connection was completed, the male and female immediately paired their ventral parts within the U-part of the burrow, both lying with carapaces turned to opposite sides. The animals remained almost immobile for nearly 30 min., only gently moving the pleopods. After separation, the male moved back to its burrow and promptly started to close the connection”.

Suspension feeding upogebiids spend much of their time in **irrigating** their burrows (see above), while deposit feeding callianassids allocate very little time for irrigation: 9% in *Callianassa subterranea*, and 5-8% in *Pestarella tyrrhena* and *Corallianassa longiventris* (cf. Stamhuis et al., 1996; Dworschak et al., 2006a).

Antagonistic behavior. – During laboratory observations, **antagonistic behavior** has been noted several times in aquaria when the same or opposite sex was encountered (MacGinitie, 1934; Berrill, 1975; Griffis, 1988; Felder & Lovett, 1989; Witbaard &

Duineveld, 1989; Rodrigues & Hödl, 1990; Rowden & Jones, 1994; Tamaki et al., 1997; Candisani et al., 2001). A detailed study on the intraspecific behaviors of three callianassid species, the tidal flat burrowers, *Nihonotrypaea japonica* and *Nihonotrypaea harmandi*, and one species living in boulder fields, *Nihonotrypaea petalura*, was performed by Shimoda et al. (2005). They described in detail the antagonistic behavior after a forced encounter. The attacks take place by protruding the major cheliped towards an opponent and grappling major chelipeds. The fights end either by a tie, where a mutual burrow blocking takes place, or a win and loss where the loser retreats quickly, often breaking its own burrow, or is driven out of the burrow by the winner. Males interacted aggressively with each other, the intensity being higher in *Nihonotrypaea petalura* than in *Nihonotrypaea harmandi*, and that of *Nihonotrypaea japonica* similar to the latter. Females of the two tidal flat species were non-aggressive, whereas those of *Nihonotrypaea petalura* were as aggressive as the males. Intersexually, males of all three species and females of *Nihonotrypaea petalura* were much less aggressive than intrasexually.

Bioturbation

The **burrowing** and **burrow irrigation activity** of axiidean and gebiidean shrimp can markedly influence **chemical and geophysical properties of sediments**, as well as **exchange of nutrients** between reduced **interstitial waters** of sediments and the overlying **water column** (Ziebis et al., 1996a, b; Felder, 2001). By way of burrows, these animals **penetrate** deep into the sediment, in some cases exceeding two meters, often reaching pore waters that are strongly hypoxic or anoxic. By irrigating the burrows, the shrimp bring oxygen-rich water into these deeper layers and the burrow walls become oxidized, often with a steeper gradient of change in oxygen concentrations than on the overlying sediment surface (Dworschak, 1983, 2001). This, in turn, influences the micro-environment and surface availability of nutrients that determines the distribution of **burrow associated microflora, bacteria, and meiofauna** (Branch & Pringle, 1987; Dobbs & Guckert, 1988; Dittmann, 1996; Bird et al., 2000; Kinoshita et al., 2003a, 2008; Papaspyrou et al., 2005; Koller et al., 2006). In addition, solubilized reduced nutrients of decomposing organic sediments diffuse into burrow waters that are periodically discharged by the animal's irrigation activity, providing an important pathway for **return cycling of nutrients** to the water column (Nates & Felder, 1998; Felder, 2001; Felder et al., 2003). In the case of the suspension feeding upogebiids with their permanent burrows, the increase in the oxidized burrow wall, and thus the sediment-water interface over which the exchange of nutrients takes place, may be up to 8-15 fold (Ott et al., 1976; Kinoshita et al., 2003b). With their suspension feeding activity, upogebiids remove phytoplankton from the water column (Griffen et al., 2004), influence nutrient recycling (DeWitt et al., 2004), and their burrows serve as traps for **organic matter** (Kinoshita et al., 2003a). Individual pumping rates of the shrimp have been shown to range from 5 to 900 ml per hour (Dworschak, 1981; Mukai & Kioke, 1984a; Allanson et al., 1992). Based on these values it was estimated that the **water exchange** through the burrows of the total *Upogebia pusilla* population in the

lagoon of Grado is in the same order of magnitude as the exchange of water with the open sea due to tides (Dworschak, 1981).

Those thalassinidean shrimp that capture seagrass debris introduce large quantities of **organic matter** into the sediment. Vonk et al. (2008) found that *Neaxius acanthus* and an alpheid shrimp collected 50% of a seagrass meadows' leaf production in their burrows and thus were an important sink for litter in this ecosystem.

A different effect is the bioturbation resulting from the predominantly deposit feeding activity of callianassid shrimp. By constantly burrowing they **rework the sediment** and have a great influence on the **macrofauna communities** (Posey, 1986a; Tamaki, 1988, 1994; Berkenbusch et al., 2000; Pillay et al., 2007a, b, c) and interact also with seagrasses (Suchanek, 1983; Bird, 2004; Siebert & Branch, 2005a, b, 2006a, b; Berkenbusch et al., 2007). Sorting sediment may lead to accumulation of larger (shell) particles in deeper sediment layers (Tudhope & Scoffin, 1984) and expelled finer sediment in large mounds may be re-suspended (Roberts et al., 1981; Rowden et al., 1998) influencing nearby coral reef communities (Aller & Dodge, 1974). Figures given for the reworking rates are difficult to compare due to different units but they range from 96 kg (dry weight) per square meter per year for the small-sized *Callianassa filholi* (cf. Berkenbusch & Rowden, 1999, 2006) to over 9000 kg per square meter per year in large-sized tropical species of *Glypturus* and *Neocallichirus* (cf. Suchanek, 1983; de Vaugelas, 1985). These reworking rates, however, represent only snapshots and do not consider temporal variations in burrowing activity and population densities (Rowden & Jones, 1993; Berkenbusch & Rowden, 1999). Callianassid shrimps have therefore been scaled as important **ecosystem engineers** (Berkenbusch & Rowden, 2003, 2006).

Symbionts

Many organisms are **associated** with both axiidean and gebiidean shrimp. In many cases, the exact nature of the relation is not known, especially for those animals that live in the burrows. Other organisms are clearly **ecto- or endoparasites**.

Bacteria. – In a study on the **gut microflora** of *Upogebia africana* and *Callichirus* (as *Callianassa*) *kraussi* using SEM, Harris et al. (1991) reported the midgut walls and gut contents to be extensively coated by filamentous bacteria and only the hindgut epithelium of *Upogebia africana* to be coated by unique rod-shaped bacteria. The digestive glands of both species contained bacteria in the lumen. The dominant genera isolated from the guts were *Vibrio* and *Pseudomonas*, and the genus *Pseudomonas* occurred in the digestive gland. Harris (1993) found mats of closely-packed epimural rods and scattered epimural rods to be the most common types of bacteria observed in the hindguts of *Upogebia africana*, *Trypaea australiensis*, *Neotrypaea californiensis*, and *Callichirus kraussi*, followed by unattached rods. Scattered epimural cocci only occurred in *Upogebia pugettensis*. They conclude that the abundance of hindgut microflora was unrelated to the host's taxon, habitat or geographical locality, but appeared to be affected by the feeding habits of the animal. Mats of epimural rods were associated exclusively with detritivores.

Pinn et al. (1997) found in the midgut of *Upogebia stellata* both filamentous and rod-shaped bacteria whereas the hindgut microbial populations were dominated by dense mats of epimural rod-shaped bacteria. The bacterial populations were dominated by X-ferm bacteria and the genera *Vibrio* and *Aeromonas*. The enzyme capabilities of the gut bacteria suggested that the microflora plays an important role in the **digestion** of the gut content. In a comparative SEM study on the gut morphology and gut microflora of seven species (*Upogebia stellata*, *Upogebia deltaura*, *Upogebia pusilla*, *Jaxea nocturna*, *Axius stirhynchus*, and *Calocaris macandreae*) Pinn et al. (1999) noted that a gut flora was observed for six of the seven species, the exception being *Calocaris macandreae*, which is considered an opportunistic scavenger.

In a study on the genetic diversity of the attached hindgut bacteria of *Neotrypaea californiensis* using 16S rDNA analyses, Lau et al. (2002) found three main groups of bacteria: Cytophaga-Flavobacteria-Bacteroides, proteobacteria, and gram-positives, and all had novel sequences suggesting new species. The bacteria in the shrimp's hindguts were species that have not yet been found in other environments and were closely related to known symbiotic and sedimentary bacteria.

Using 16S rRNA analyses of bacteria on the setal tufts and the midgut of *Pestarella tyrrhena*, Demiri et al. (2009) found no specific bacteria on the setal tufts, while the midgut shows a specific bacterial community dominated by putative **symbiotic bacteria** in this shrimp species.

“Fungi”. – **Mesomycetozoean thalli** (class Mesomycetozoa, order Eccrinales; formerly treated as fungi, see Cafaro, 2005), mainly the species *Enteromyces callianassae* Lichtwardt, 1966 have been found in the guts of several species of Upogebiidae and Callianassidae (cf. Lichtwardt, 1986; Dworschak, 1987b; Felder & Felgenhauer, 1993b; Kimura et al., 2002). Though many are **commensal**, at certain stages of development and under particular environmental conditions, they may be **parasitic** or **mutualistic** (Lichtwardt, 2008).

Metazoa. – The **turbellarian** *Stylocus ellipticus* (Loosanoff, 1956) lives in burrows of *Upogebia affinis* (see Ruppert & Fox, 1988). Rodrigues (1971) found the **nemertean** *Coenemertes caravalas* Corrêa, 1966 and a **polyclad turbellarian** of the genus *Stylochoplana* to be associated with *Sergio guassutunga* (Rodrigues, 1971). Manning & Felder (1995) reported that *Sergio mericeae* Manning & Felder, 1995 is almost always taken along with scarlet red **commensal worms**, up to 12 in number from a single burrow.

Upogebia pusilla is known to be an intermediate host for **trematode metacercaria** and acanthor- or acanthella-stages of **Acanthocephala** (cf. Dworschak, 1988). The **cestode** *Prochristianella hispida* (Linton, 1890) was reported with a prevalence of 32% in the hepatopancreas of *Callinectes seilacheri* (Bott, 1955) (see Iannacone et al., 2008). Juvenile stages of the **nematode** *Ascarophis* sp. were found with high prevalence in *Calocaris macandreae* (cf. Calderon-Perez, 1986).

Among the **polychaetes**, species of the polynoid genus *Hesperonoe* have been found in burrows of various thalassinideans (Sato et al., 2001).

Among **copepods**, members of Clausidiidae are commonly found on the body or on the burrow wall of some genera. Of the 68 species of clausidiids (Boxshall & Halsey,

2004) members of the genera *Clausidium* and *Hemicyclops* especially have been reported in association with thalassinideans (Humes, 1984). About 20 named clausidiid species have such confirmed associations, along with a few members of Catiniidae (cf. Kihara et al., 2005).

The **cephalocarid** *Lightiella incisa* Gooding, 1963 was collected from burrows of *Glypturus acanthochirus* (cf. Gooding, 1963).

Gammarid amphipods have been found regularly in the burrow of *Upogebia pusilla* (see Dworschak, 1983) and Fox (1978) reported the genus *Idunella* from pleopods of *Gilvossius setimanus* (DeKay, 1844), *Biffarius bififormis* (Biffar, 1971), and *Upogebia affinis* (see Overstreet, 1983: 227). Compared to anomurans and caridean shrimp, thalassinidean shrimps are the third-most common hosts for **bopyrid isopods**. Fifty-six species of Bopyridae from 4 subfamilies (37 Pseudioninae, 17 Ioninae, 1 Phylloporinae, 1 Entophilinae) have been reported to infest axiidean and gebiidean taxa (Boyko, 2009). Most bopyrids are external parasites, the female and dwarf-male being lodged in one of the gill chambers and creating its obvious swelling, but others occur between the pleopods (*Phylloporus*), and one species of the genus *Entophilus* has been described recently as internal parasite from a callianassid (Markham & Dworschak, 2005).

Other crustacean parasites include a few **rhizocephalan barnacles**. Internal parasitization by the root system is rarely seen in the host specimen, and the infestation is obvious only from the single or multiple sac-like structures on the ventral side of the pleomeres (*Parthenopea*), or several smaller stalked ellipsoid **externae** distributed over the ventral side of the pleomeres (*Polysaccus*) (see Høeg & Lützen, 1993; Lützen & Takahashi, 1996; Öksnebjerg, 2000).

Recently, a large (2 cm) **entoniscid isopod** has been found to internally parasitize a species of callianassid. Similarly, some small, Indo-Pacific callianassid shrimp have been found to be parasitized by undescribed **cryptoniscid isopods**. These infestations are manifested by a sac-like structure on the ventral side of the pleomeres that looks very similar to an externa of a rhizocephalan, but lacks the mantle opening. The cryptoniscids are supposedly **hyperparasites** of rhizocephalans (Trilles, 1999).

Small **alpheid shrimps** of the genera *Salmonaeus*, *Athanas*, *Leptalpheus*, *Richalpheus*, *Jengalpheops* (cf. Williams, 1965; Dworschak et al., 2000; Anker et al., 2001; Anker & Dworschak, 2007; Anker & Marin, 2009) have been regularly retrieved from burrows of thalassinidean shrimps, usually in association with the callianassid genera *Glypturus* and *Neocallichirus*. The exact nature of the symbiotic relation is not known.

Many species of **Pinnotheridae** live in the burrows of callianassid and upogebiid shrimps (Manning & Felder, 1989; Alves & Pezzuto, 1998; Coelho, 2005; Campos, 2006; McDermott, 2006). Host specificity appears to be low as most have been found also in tubes or burrows of other invertebrates.

The **grapsid crabs** *Sestrostoma balssi* (Shen, 1932) and *Sestrostoma toriumii* (Takeda, 1974) were found in the burrows of *Upogebia quddusiae* Tirmizi & Ghani, 1978 and *Upogebia major*, respectively (as *Acmaeopleura*, see Ghani & Tirmizi, 1991; Itani, 2002). Itani (2002) observed that the grapsid crab *Sestrostoma toriumii* lives free in the burrow of

Upogebia major, while the other species, *Sestrostoma* sp. always clings to the pleon of the host on whose tissue the crab obviously feeds.

The free-living **bivalve** *Bornia sebetia* (O. G. Costa, 1829) is found in the burrows of *Pestarella tyrrhena* and *Pestarella candida* (Olivi, 1792) (see LeGall, 1969), and three species of *Ephippodonta* occur in burrows of axiids and strahlaxiids (Matthews, 1893; Buick & Bowden, 1951; Boss, 1965). The myid bivalve *Cryptomya* is found in great numbers associated with several species of upogebiids and callianassids (Swinbanks, 1981; Lawry, 1987; Itani & Kato, 2002; Nara et al., 2008). These bivalves extend their short siphons into the burrow lumen, and can remove up to 39% of suspended particles (Griffen et al., 2004). The lucinid bivalve *Phacoides pectinatus* (Gmelin, 1791), known to harbor sulfur-metabolizing chemoautotrophic bacteria in its gills, has alternatively been found to congregate along burrow walls of *Axianassa australis* in organic muds of mangrove-lined shores, presumably there accessing sulfide-rich waters pumped by these axianassids from deep within reduced substrates (Felder, 2001).

By contrast, the bivalve *Pseudopythina rugifera* (Carpenter, 1864) lives attached with byssus threads to the ventral side of *Upogebia pugettensis* (Dall, 1899). The bivalves *Peregrinamor ohshimai* Shoji, 1938 and *Peregrinamor gastrochaenans* Kato & Itani, 2000 have been found to parasitize *Upogebia major* and *U. carinicauda* (Stimpson, 1860), respectively (Kato & Itani, 1995; Itani et al., 2002), living attached to the ventral surface of the shrimp's pleon.

Adults of the **phoronid** *Phoronis pallida* (Schneider, 1862), are found embedded in the burrow wall of *Upogebia major* and *Upogebia pugettensis* (cf. Kinoshita, 2002; Santagata, 2004).

MacGinitie (1939) and MacGinitie & MacGinitie (1949) reported on the biology of the blind **gobiid fish** *Typhlogobius californiensis* Steindachner, 1879 that lives in the burrows of the callianassid *Neotrypaea biffari* (Holthuis, 1991). Kinoshita (2002) reported the gobiid fish *Chaenogobius macrognathus* (Bleeker, 1860) from the burrow of *Upogebia major* in Japan. Two newly described gobiid fish of the genus *Didogobius* are associated with *Axiopsis serratifrons* at São Tomé, Príncipe, and the Cape Verde Islands (Wirtz, 2005, 2008; P. Wirtz, pers. comm.; Schliewen & Kovacic, 2008). The gobiid fish *Austrolethops wardi* Whitley, 1935 lives in burrows of the strahlaxiid *Neaxius acanthus* in tropical seagrass beds in Sulawesi, Indonesia (Kneer et al., 2008a; Liu et al., 2008).

ECONOMIC IMPORTANCE

Impacts as “pests”

In many areas of the tropics, *Thalassina anomala* is considered a “**pest**” (Holthuis, 1991; Pillay & Kutty, 2005; Ngoc-Ho & de Saint Laurent, 2009). It is known to cause **damage to bunds of prawn ponds** by its burrowing activity and also to **embankments** or the **dykes of ponds**, making them leak water and eventually collapse (Macintosh, 1988). Paddy fields and backyards of houses in the proximity of mangrove creeks in India

are also subject to this kind of damage (Sankolli, 1963). A detailed account of damage caused to coastal bunds by crabs and especially by *Thalassina anomala* was presented by Ferguson (1951). Dammerman (1929) reported that the mud lobster is destructive to nipa seedlings (*Nypha fruticans* Wurmb, 1781). Scharff & Tweedle (1942) stated that the burrowing of the mud lobster makes ordinary **anti-malaria measures** ineffective, because of the unsuspected **breeding places for mosquitoes** that the mud-holes provide. Andriesse et al. (1973) indicated in field studies on mangrove swamps in Sarawak (east Malaysia) that mud-lobsters build large mounds out of subsoil material that acidifies strongly upon aeration and oxidation. Such **acid soil** is unsuitable for agricultural development. Control measures were presented by Scharff & Tweedle (1942) and Ferguson (1951).

Along the Pacific coast of North America, the callianassid *Neotrypaea californiensis* and upogebiid *Upogebia pugettensis* are common inhabitants of estuaries (MacGinitie, 1930, 1934). These estuaries are also used for **aquaculture** of the **Pacific oyster** (*Crassostrea gigas* (Thunberg, 1793)). The burrowing shrimp adversely affect oyster aquaculture by increasing turbidity and sediment overturn rates, thus reducing compaction of sediment and causing oyster mortality as they sink and are rapidly covered with sediment (Dumbauld et al., 1997, 2004). A solution to this problem was found by the oyster culture industry in applying the pesticide carbaryl to the surface of the sediment at low tide that effectively killed the shrimp. Detailed studies on the shrimp's population biology by Dumbauld et al. (1996) allowed a better timing of pesticide application and identified *Neotrypaea californiensis* as the species to be targeted, because it causes much more significant damage than *Upogebia pugettensis* (cf. Feldman et al., 2000; Dumbauld et al., 2004).

The callianassid shrimp *Lepidophthalmus sinuensis*, *Lepidophthalmus bocourti*, *Lepidophthalmus louisianensis*, and at least one undescribed congener have been reported to **invade penaeid shrimp ponds** along coastlines from Mexico to Central and northern South America (Nates & Felder, 1999; Felder, 2001; Felder et al., 2003). With their abbreviated larval cycle, recruits accumulate at the site of the parental population and densities of the burrowing shrimp often exceed several hundreds of individuals per square meter. The burrowing shrimp are adapted to tolerance of strong hypoxia and reduced nutrients in pond substrates that are rich in decomposing organic material. As a result of their bioturbation and burrow irrigation, reduced nutrients and hypoxic effluent waters from the sediment are moved into the water column with a **negative effect on penaeid shrimp survival and growth**, evident in shrimp yields that are negatively correlated with callianassid burrow density. Farm operators treat the ponds periodically with carbaryl or trichlorfon (organophosphorus) pesticides to control callianassid infestations, as they otherwise survive deep in pond muds even over long periods of drying, before restocking with penaeid larvae. Fukuda (2004) reported populations of *Nihonotrypaea japonica* that had invaded Kuruma prawn ponds in Japan were important **carriers of the white spot syndrome** that infected the cultured prawns and reduced the farm's yield. In this case, it was found that sterilizing the ponds by drying as long as possible before stocking was a good method to limit accumulations of these pests in the ponds.

Importance as “fisheries”

In the FAO Catalogue of species of interest to fisheries, Holthuis (1991) listed altogether 14 species of thalassinideans. Only a few of them are used for **human consumption**. The mud lobster *Thalassinia anomala* is considered edible but is not very popular in Singapore (Tan & Ng, 1988), and only in Fiji does it appear to constitute an important food source (Pillai, 1985). Several Upogebiidae are harvested for local consumption, e.g., *Upogebia major* in Japan and Korea, *Austinogebia wuhsienweni* (Yu, 1931) in China (Liu, 1955) and *Austinogebia edulis* in Taiwan (Ngoc-Ho & Chan, 1992). The only callianassid used as food is *Lepidophthalmus turneranus*. This shrimp swarms periodically into rivers in the Gulf of Guinea (Vanhöffen, 1911) where local fishermen collect them with baskets. The female shrimps are eaten whole, but the males are said to contain a substance that irritates the throat. The male pleons are instead pressed to produce a kind of oil (Monod, 1927, 1928).

All other harvested thalassinidean species are collected mainly for use as **bait for commercial and recreational fishing**: *Upogebia pusilla* and *Pestarella tyrrhena* in the Mediterranean and the eastern Atlantic (Chaud, 1984; Erzini et al., 1998), *Upogebia africana* and *Callichirus kraussi* in Southern Africa (Wynberg & Branch, 1991, 1994; Hodgson et al., 2001), *Nihonotrypaea japonica* and *Nihonotrypaea harmandi* in Japan, Korea, and China (Liu, 1955), *Trypaea australiensis* in Australia (Hailstone, 1962; McPhee & Skilleter, 2002; Contessa & Bird, 2004; Rotherham, 2004), *Callianassa filholi* in New Zealand (Devine, 1966), *Upogebia pugettensis*, *Neotrypaea californiensis*, *Neotrypaea gigas*, and *Neotrypaea biffari* along the Pacific coast of North America (Dumbauld et al., 1988; Pernet et al., 2008), *Callichirus seilacheri* (Bott, 1955) and *Neotrypaea uncinata* (H. Milne Edwards, 1837) along the Pacific coast of South America (Garcia et al., 2003; Hernaez & Wehrmann, 2007), *Callichirus major* and *Sergio mirim* along the Atlantic coast of North and South America, respectively (Borzzone & Souza, 1996; Pezzuto, 1998; Souza & Borzzone, 2003; Botter-Carvalho et al., 2007), and *Callichirus islagrande* (Schmitt, 1935) and *Callichirus major* in the western Gulf of Mexico (DLF, unpubl.).

The burrowing shrimp are dug up with forks and spades, forced out of their burrows with a “prawn pusher” (Hodgson et al., 2001), by liquifying the sediment by trampling (Garcia et al., 2003), or using a water jet (Bybee, 1969), or extracted by suction with a “yabby pump” designed specifically for bait collection (Hailstone, 1962).

As thalassinidean shrimp are often used extensively as bait, some species, e.g., *Upogebia africana* and *Callichirus kraussi* in South Africa, are protected and each person is allowed to collect not more than a certain number of specimens per day (Day, 1969; Tietz & Robinson, 1974). Wynberg & Branch (1991) estimated that recreational harvesters removed 1.2 million specimens of *Callichirus kraussi* from a single South African lagoon per year. Hodgson et al. (2001) monitored the exploitation of *Upogebia africana* for bait in a South African estuary. They found that the harvest per trip was an average of 59 mud prawns for leisure anglers and 101 for non-leisure anglers. They estimated that about 740 kg dry mass shrimp was removed by bait collectors annually which represents about 8.5% of the shrimp stocks at these sites and 0.9% of the entire estuary stock. They conclude

that the shrimp populations are not over-exploited. Rotherham (2004) estimated that about 2% of the stock sizes of *Trypaea australiensis* are harvested by recreational anglers and concludes that restrictive management is not advocated for this species in New South Wales, Australia. On the other hand, Souza & Borzone (2003), in a study evaluating the impact of the recreational bait fishery along a southern Brazilian sandy beach, estimated that the annual fishing harvest removed nearly 10% of the total stock of *Callichirus major*. Similarly, Botter-Carvalho et al. (2007) concluded from studies of population parameters, that the same species is over-exploited at a beach in north-eastern Brazil.

Besides the effects on the populations of the targeted species, bait-collecting also **disturbs sedimentary environments** and potentially impacts associated macrofauna (Wynberg & Branch, 1991, 1997; Contessa & Bird, 2004; Skilleter et al., 2005).

PHYLOGENY AND BIOGEOGRAPHY

Phylogeny

Published works dealing with the phylogeny of thalassinideans span a more than 100 year period from Borradaile's intuitive tree of relationships in his classic 1903 classification of the group (Borradaile, 1903), to the predominantly molecular analyses of the present day.

Morphological analyses of thalassinidean phylogeny fall into two categories: those in which **solely thalassinideans** (sometimes even single families) are investigated, and those in which thalassinidean representatives are part of **broader analyses of decapod constituent groups**. Borradaile (1903) presented a **monophyletic intuitive tree** of relationships for 12 genera (from seven families) and showed basal calocaridids, laomediids, and axiids, intermediate thalassinids, and more terminal genera like upogebiids, callianideids, and callianassids. Gurney (1938) using only **larval characters** constructed a similar intuitive tree, but this time it was **dichotomous** with axiids and callianassids on one major branch and upogebiids and laomediids (grouping with anomurans) on the other. There was then a hiatus of 56 years before any other morphological phylogenies were attempted and these were constructed using computer **cladistic methodologies**. Poore (1994) assembled a large dataset of 97 **morphological characters** for 22 thalassinidean genera (representing 11 families) and his resultant tree divided thalassinideans into two major clades. One clade grouped Calocarididae, Axiidae, Strahlaxiidae, and Micheleidae, and the other Thalassinidae, Laomediidae, Upogebiidae, Callianideidae, Thomassiniidae, Ctenochelidae, and Callianassidae. He subsequently split the infraorder into three superfamilies, Axioidea for the one clade, Thalassinioidea just for the Thalassinidae, and Callianassoidea for the remainder of the second clade.

Thalassinidean representatives have been part of larger phylogenetic analyses of decapod relationships since 1986, but more commonly in the last five years. Martin & Abele (1986), while investigating the placement of the enigmatic freshwater aeglid anomurans

from South America, used five thalassinidean families in their phylogenetic analysis using 54 morphological characters. They found the thalassinidean families formed a monophyletic clade at the base of the anomuran tree between the monophyletic Anomura and the outgroup taxon, *Penaeus*. With this very limited taxon sample of the thalassinideans (not being the focus of the analysis) they recovered two subclades within the thalassinidean monophylum, with laomeidiids and axiids in one, and thalassinids, upogebiids, and callianassids in the other. It was a further 10 years before Tudge (1997) used **spermatophore and spermatozoal characters** to produce a novel cladogram of anomuran relationships. The resultant “sperm tree” included only three thalassinidean representatives (*Axius*, *Trypaea*, and *Thalassina*) with species from nine anomuran families, and some Astacidea and Brachyura. The diverse spermatozoal morphologies found in the thalassinidean species, the small sample size (three), and incomplete data for *Thalassina*, meant that they were inconsistently placed around the base of the cladograms and *Thalassina* was even placed within Anomura in some. Dixon et al. (2003) performed a morphological cladistic analysis of 60 decapod taxa using **external morphology** only, in which nine thalassinidean representatives (from 7 families in all three superfamilies) were included. Thalassinidean taxa were therein concluded to be a monophyletic group of three subclades. The laomeidiid, *Jaxea*, was alone basal to the other two subclades, which were composed of thalassinids, calocaridids, and axiids on one branch, and callianideids, callianassids, and upogebiids on the other. This was not inconsistent with Poore’s (1994) scheme except for the placement of the laomeidiid and thalassinid. Ahyong & O’Meally (2004) then **combined** essentially the same **morphological dataset** with **molecular sequences** from three genes for all Decapoda. The six representative thalassinidean genera (from five families) were analyzed using 105 morphological characters: both alone and in combination with the molecular data. The separate morphological, molecular, and **combined cladograms** were all but identical for the thalassinidean clade and differed from the arrangement shown in Dixon et al. (2003) in that the laomeidiid, *Jaxea*, was no longer basal to the entire thalassinidean clade, but grouped as a sister taxon to the thalassinid, *Thalassina*, with the callianassids and strahlaxiids now being sister taxa in one clade and upogebiids, laomeidiids, and thalassinids grouped in a second clade.

The first **molecular phylogenetic analysis** of the thalassinideans was by Tudge & Cunningham (2002), who used two genes (18S nuclear and 16S mitochondrial ribosomal genes) to investigate relationships between 14 thalassinidean shrimp species from six families. They concluded, based on their limited taxonomic and gene sampling, that the previously suggested monophyly of Thalassinidea (cf. Borradaile, 1903; Poore, 1994) was only weakly supported and that a strong **dichotomy of the infraorder** was apparent, in contrast to the three monophyletic clades indicated by Poore (1994). The two main clades recovered with the molecular data grouped upogebiids, thalassinids, and axianassids (a suggested resurrection of this family came from the same data) in one, and strahlaxiids and callianassids in the other. A **dichotomous Thalassinidea** (*sensu* Gurney, 1938; de Saint Laurent, 1979b) was thereafter more strongly supported by molecular phylogenetic analyses targeted specifically to an ever broader representation of thalassinidean taxa, in independent analyses that led to very similar conclusions (Tsang et al., 2008a, b; Robles et

al., 2009). These recent molecular analyses have provided an ever more robust coverage of both thalassinidean taxa and genes, and direct comparisons of the results were undertaken in Robles et al. (2009). The Tsang et al. (2008a) paper used partial nuclear (18S and 28S rDNA) and mitochondrial (16S rDNA) genes to examine interrelationships between 27 species of thalassinidean shrimps from 12 of the current 13 recognized families. Resolution of this large dataset split the infraorder into two clades (each ranked as a superfamily, Callianassoidea and Thalassinoidea, by the authors) with eight families in one (Strahlaxiidae, Axiidae, Eiconaxiidae, Calocarididae, Micheleidae, Callianideidae, Ctenochelidae, and Callianassidae) and four (Upogebiidae, Laomediidae, Axianassidae, and Thalassinidae) in the other. The Robles et al. (2009) study in turn applied 18S nuclear and 16S mitochondrial gene sequence data to a larger set of thalassinidean taxa (34 genera and 50 species), and also resulted in division of the group into large clades of the same composition (fig. 69.32). As in the present synthesis, the latter authors applied the previous terminology of de Saint Laurent (1979b) in the course of establishing the **separate infraorders Gebiidea and Axiidea** (cf. Robles et al., 2009), and they therewith abandoned the taxon Thalassinidea. Sakai (2005b) in his paper comparing gastric mill morphology also postulated a diphyletic Thalassinidea (but based on a single character only), with his two superfamilies Thalassinoidea and Callianassoidea, later also being suggested to represent separate infraorders (Sakai & Sawada, 2006), and thus holding equivalent rank to Gebiidea and Axiidea that we have herein applied.

It then appears that present evidence supports **separation of thalassinidean taxa** into **two major clades**, and that characters previously used to group them into a single monophyletic infraorder were based largely upon **convergent adaptations** to independently derived **burrowing lifestyles**. Further evaluation of the separate infraordinal status for gebiidean and axiidean thalassinideans, as we herein adopt, is pending with ever more robust, taxonomically rich, multigene analyses of the decapods overall. However, in even their earliest iterations, this subdivision appears to be supported by such analyses (Bracken et al., 2009, 2010).

Besides studies dealing with morphological or molecular phylogeny of the thalassinideans overall, several have focused on **relationships** within and between **individual families**. Callianassidae was the focus of a morphological cladistic analysis (Tudge et al., 2000) and subsequently of a molecular analysis based upon two mitochondrial genes (Felder & Robles, 2009). The morphological study by Tudge et al. (2000) investigated phylogenetic relationships on the basis of 93 adult morphological characters among members of just two families, Callianassidae and Ctenochelidae, in an analysis that included 106 representative species from the 25 recognized genera. Resultant cladograms confirmed monophyly of the two families but showed a need for major revisions of subfamilies and genera of Callianassidae. The more recent paper of Felder & Robles (2009) examined relationships of 46 species from 18 genera historically treated within Callianassidae, based upon fragments of the 16S and 12S rDNA mitochondrial genes. They also included two genera in the related Ctenochelidae and five axiids as an out-group. The analysis retrieved a monophyletic Ctenochelidae and Callianassidae, but

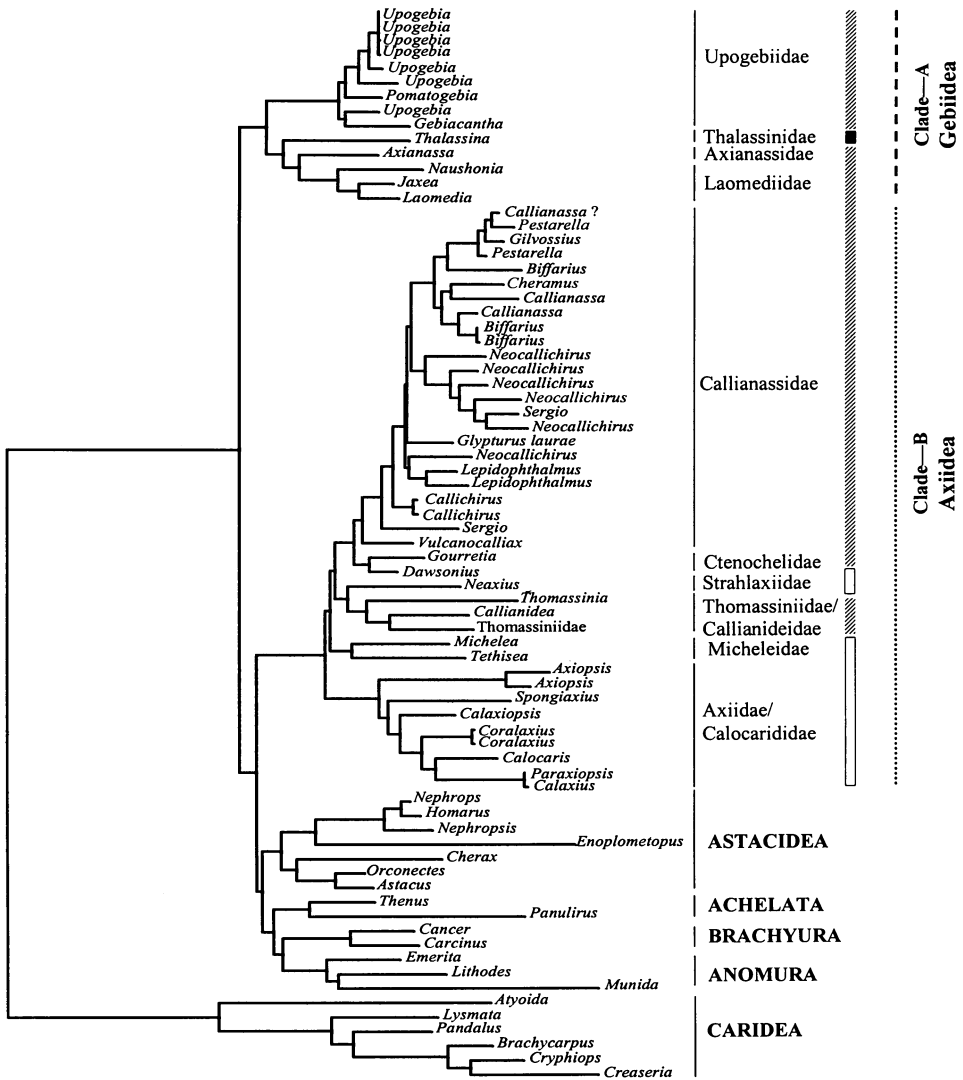


Fig. 69.32. Phylogenetic relationships among 12 "thalassinidean" families inferred from a Bayesian analysis of 16S and 18S rDNA. "?" next to a *Callianassa* indicates a questionable identity of a GenBank sequence. Vertical bar indicates assignments to rejected superfamilies Axioida (open), Thalassinoida (solid), and Callianassoidea (hatched) [modified from Robles et al., 2009, fig. 1].

excluded the callianassid subfamily Eucalliinae (placed basal to them both). It suggested a monophyletic, but not well resolved, Callichirinae and nested Cheraminae within Callianassinae. Both studies, despite the different datasets, showed a family in serious need of a major taxonomic revision, especially among members of the type genus *Callianassa* s.l., but also among other genera. Both these analyses also contradicted markedly the controversial systematic revisions of Callianassidae (and closely allied Ctenochelidae and

Gourettiidae) by Sakai (1999a, b, 2002, 2004, 2005a). The substantial revisions suggested by Sakai (summarized in his 2005 monograph) involve abundant synonymies, appear to ignore natural groupings suggested by more voluminous datasets, and have not been well received by other workers (Dworschak, 2007b). Although heavily criticized, Sakai's continued efforts have at the very least generated much interest and diverse analyses of systematic relationships within this large thalassinidean grouping.

Some examples where one or more representative thalassinideans have been used in larger **decapod molecular phylogenetic analyses** include Morrison et al. (2002); Ah Yong & O'Meally (2004); Porter et al. (2005); Tsang et al. (2008b); Toon et al. (2009); Chu et al. (2009); and Bracken et al. (2009). The latest consensus molecular **phylogeny of the Decapoda** provided by Bracken et al. (2009, 2010) uses four genes (16S, 18S, 28S, and H3) and multiple search methods and includes 18 thalassinidean species (from a total of 128 species of Decapoda). The representatives from 10 thalassinidean families are diphyletic and not surprisingly are basal to the remainder of the reptant decapod infraorders (placing between the stenopodidean shrimps and Anomura). Within the thalassinidean families the more basal clade is comprised of Upogebiidae, Thalassinidae, and Laomeidiidae (Gebiidea of Robles et al., 2009) while the larger clade includes Strahlaxiidae, Axiidae, Calocarididae, Ctenochelidae, Micheleidae, Callianideidae, and Callianassidae (Axiidea of Robles et al., 2009).

In summary, the present molecular and morphological evidence supports separation of thalassinidean taxa into two major clades. Recent comprehensive multigene analyses (Bracken et al., 2009, 2010) continue to further support this basic separation and the separate infraordinal status for gebiidean and axiidean thalassinideans, and provide robust dates for the ancient emergence of these **independent burrowing lineages**.

Biogeography

The biogeography and global **biodiversity patterns** of thalassinidean mud shrimps were first summarized by Dworschak (2000a) and then updated later by the same author (Dworschak, 2005). In these papers, he presented a census of the known species within Thalassinidea and then provided latitudinal, regional, and depth distributions. The total number of thalassinidean species and genera in 2004 was 556 and 96, respectively (now 631 and 108, as of February 2010). Latitudinal distribution on a global scale shows a clear gradient with the low latitudes having the greatest diversity of species and the higher latitudes showing the least. The current northernmost record is 71°N (Norway) and corresponding southernmost species record is 55°S (Beagle Channel, Chile) (Dworschak, 2005). Regionally, the Indo-West Pacific dominates with 36.5% of the species diversity, and then the southwest Atlantic (particularly the Caribbean and Gulf of Mexico) has 21.6% of the species diversity, with the next highest (16.7%) found in the Indian Ocean. Some regional biota are particularly rich, with the Australian axiid fauna alone, for example, recently described as 30 species (Poore & Collins, 2009).

SYSTEMATICS

Axiidea and Gebiidea: our classification of the decapods formerly treated as the infraorder Thalassinidea follows recently proposed revisions that have partitioned this paraphyletic group into two separate infraorders, which were originally proposed by de Saint Laurent (1979a, b) as “sections”, her Axiidea and Gebiidea, each with families as reflected in the listings that follow. As reviewed in the genetically-based revision by Robles et al. (2009), both morphological observations (Gurney, 1938, 1942; de Saint Laurent, 1979a, b; Sakai, 2004; Sakai & Sawada, 2005) and previous genetic studies (Tsang et al., 2008a; Tsang et al., 2008b) lend support to this arrangement. No genetic support can be found for retention of the former superfamilies Axioidea, Thalassinidea, and Callianassoidea as previously applied by Poore (1994) and Martin & Davis (2001). Within Axiidea, Thomassiniidae does not appear to represent a distinct family, and the formerly separated Eiconaxiidae and Calocarididae appear to be imbedded within Axiidae, no longer warranting separate family rank (Robles et al., 2009). However, for now, these three families continue to be included in our list. It should also be noted that many lower level taxonomic revisions within these infraorders proposed by Sakai (1999, 2005, 2006, 2011) are not incorporated into this list, especially in cases of obvious errors or lack of adequate justification (see Dworschak, 2007; Poore, 2008a, b).

Note. – The diagnosis for the former families Calocarididae, Eiconaxiidae, Gourretiidae, and Thomassiniidae (currently unsupported; see Introduction) are still included in this systematic section (in order to reduce confusion) but are appended (in parentheses and italics) to the end of the diagnosis for the recognized family they have been subsumed into.

Infraorder GEBIIDEA de Saint Laurent, 1979a

First pereiopod chelate or subchelate (rarely almost simple); second pereiopod subchelate or simple. [Modified from de Saint Laurent, 1979a.]

AXIANASSIDAE Schmitt, 1924

Linea thalassinica present; cervical groove distinct; rostrum of moderate size; antennular flagella of moderate length; well developed, mobile antennal scale; first pereiopod unequal, chelate; second-fourth pereiopods simple; fifth pereiopod imperfectly subchelate; gills trichobranchiate with slender filaments; pleura of pleomeres very poorly developed; pleopods without appendix interna; exopod of uropods unjointed, without trace of a suture (except in one species). [Modified from Schmitt, 1924.]

LAOMEDIIDAE Borradaile, 1903

Linea thalassinica present; cervical groove distinct; posterior margin of carapace with lateral lobes; cephalothorax with posterior margin separate from thickened margins of posterolateral extensions of branchial region; rostrum minute, or at least as long as eyestalks; eyestalks cylindrical; antenna with acicle or broad antennal scale; first antenna with third article as long as or longer than second article; second maxilla scaphognathite with several thickened setae on posterior lobe; third maxilliped pediform, epipod with serrate margin; first pleomere with anterolateral lobes, chitinized; first pereiopod chelate or subchelate, equal; second

pereiopod simple; third pereiopod simple, propodus linear with few spiniform setae on lower margin; fourth pereiopod simple or subchelate, propodus with few spiniform setae on lower margin; coxa cylindrical; fifth pereiopod chelate or subchelate; seventh thoracic sternite slender; male first pleopod absent; female first pleopod uniramous; second pleopod similar to third-fifth pleopods, rami lanceolate; pleopods without appendix interna; uropodal exopod ovate; second-fourth pereiopods and pleomeres without setal rows. [Modified from Poore, 1994, 2004; Davie, 2002.]

THALASSINIDAE Latreille, 1831

Linea thalassinica present; posterior margin of carapace with lateral lobes; eyestalks cylindrical; first antenna with third article about as long as second article; second maxilla scaphognathite with thickened setae on posterior margin; pleuron of first pleomere produced; gill elements irregular, filamentous proximally and plate-like distally; first and second pereiopod subchelate; second pereiopod always with dense row of long setae on lower margin; third and fourth pereiopods simple, propodus with spiniform seta; second pleopod similar to third-fifth pleopods; third-fifth pleopods without appendix interna (vestigial on male second pleopod); uropodal rami linear; second-fourth pereiopods and pleomeres without setal rows. [Modified from Poore, 1994; Davie, 2002.]

UPOGEBIIDAE Borradaile, 1903

Linea thalassinica present, diverse; posterior margin of carapace evenly curved; cephalothorax with distinct cervical groove; rostrum usually broad, spinose, and dorsally setose; eyestalks cylindrical, cornea large and terminal; first antenna with third article as long as or longer than second article; second maxilla scaphognathite without long seta on posterior lobe; first pleomere without anterolateral lobes, chitinized, pleuron weak; first pereiopod chelate or subchelate (rarely almost simple), equal; second pereiopod simple with dense row of long setae on lower margin; third pereiopod simple, propodus linear; fourth pereiopod simple or subchelate, coxa cylindrical; third and fourth pereiopods dactyli more or less spatulate, propodus without spiniform setae on lower margin; fifth pereiopod subchelate; seventh thoracic sternite slender; first pleopod absent in male, simple in female; second pleopod similar to third-fifth pleopods, rami lanceolate; pleopods without appendix interna; uropodal exopod triangular, suture absent; second-fourth pereiopods and pleomeres without setal rows. [Modified from Poore, 1994, 2004; Davie, 2002.]

Infraorder AXIIDEA de Saint Laurent, 1979a

First and second pereiopod chelate. [Modified from de Saint Laurent, 1979a.]

AXIIDAE Huxley, 1879

Carapace posterior margin with lateral lobes; rostrum conspicuous, usually spinose, apically acute; eyestalks cylindrical; eye usually pigmented; linea thalassinica absent; cervical groove distinct; first antenna with third article about as long as second article; scaphocerite strong; second maxilla scaphognathite with

1-2 long setae on posterior margin (rarely without); pleuron of first pleomere produced; second pleomere less than twice as long as first; first and second pereopods chelate; third-fifth pereopods simple; propodus of third and fourth pereopods linear or broadened; coxa of fourth pereopod more or less cylindrical; male first pleopod present or absent; male second pleopod endopod foliaceous with small appendix masculina attached mesially; exopods of second-fifth pleopods not laterally lobed; third-fifth pleopods with or without appendix interna; uropodal endopod ovate; second-fourth pereopods without setal rows, sixth pleomere with longitudinal setal row. [Modified from Poore, 1994, 2004; Davie, 2002; Sakai & Ohta, 2005.]

[CALOCARIDIDAE Ortmann, 1891

Rostrum usually spinose, apically acute; eye usually not pigmented; linea thalassinica absent; second maxilla scaphognathite with spinulose whip; pleuron of first pleomere produced; second pleomere less than twice as long as first; third-fifth pereopods dactyli simple; propodus of third and fourth pereopod more or less linear; coxa of fourth pereopod more or less cylindrical; male second pleopod endopod simple, with terminal enlarged appendix masculina; exopods of second-fifth pleopods not laterally lobed; uropodal endopod ovate; uropodal exopod with transverse suture; second-fourth pereopods and pleomeres without setal rows. [Modified from Poore, 1994; Sakai & Ohta, 2005.]

EICONAXIIDAE Sakai & Ohta, 2005

Rostrum conspicuous, concave on dorsal surface; cervical groove indistinct; linea thalassinica absent; scaphocerite strong; third-fifth pereopods dactyli rounded, ventral margins spinulate; male first pleopod absent, second-fifth pleopods slender, biramous, second pleopod with appendix interna and appendix masculina, third-fifth pleopods all with appendix interna; female first pleopod uniramous, second-fifth pleopods slender, biramous, all with appendix interna. [Modified from Sakai & Ohta, 2005.]]

CALLIANASSIDAE Dana, 1852

Linea thalassinica present, complete, lateral to antennae; posterior margin of carapace evenly curved, rarely with cardiac prominence; rostrum obsolete or a spike; eyestalks flattened, rarely cylindrical; first antenna with third article as long as or longer than second article; second maxilla scaphognathite without long seta on posterior lobe; first pleomere without anterolateral lobes, weakly chitinized; first pereopod unequal or equal, chelate; first pereopod merus with straight or toothed lower margin; second pereopod chelate; third pereopod simple, propodus with or without distal spiniform seta on lower margin, with proximal heel on lower margin; fourth pereopod simple or subchelate, coxa flattened, mobile; fifth pereopod chelate or subchelate; seventh thoracic sternite narrow; second pleopod different from third-fifth pleopods, sexually modified; third-fifth pleopods with broad interacting rami, endopod with appendices internae in both

sexes; uropodal exopod with thickened anterodorsal setose margin (dorsal plate); only sixth pleomere with setal rows. [Modified from Poore, 1994, 2004; Davie, 2002.]

CALLIANIDEIDAE Kossman, 1880

Linea thalassinica absent or very short; posterior margin of carapace evenly curved; rostrum reduced; eyestalks flattened; second maxilla scaphognathite with 1 long seta on posterior lobe; first pleomere with anterodorsal dome; first pereopod unequal; first pereopod merus with convex lower margin; second pereopod chelate; third and fourth pereopods propodus with single distal spiniform seta on lower margin; third pereopod propodus ovate; coxa of fourth pereopod flattened, immobile; seventh thoracic sternite narrow; second pleopod similar to third-fifth pleopods, rami lanceolate, with marginal filaments; uropodal exopod simply ovate; second-fourth pereopods and first and sixth pleomeres with setal rows. [Modified from Poore, 1994.]

[THOMASSINIIDAE de Saint Laurent, 1979b

Cephalothorax, rostrum, pleon, telson, and limbs without armature; linea thalassinica complete or incomplete, starting immediately lateral to eyes; posterior margin of carapace evenly curved; rostrum minute or a spike; eyestalks flattened; first antenna peduncle first article as long as second and third; second antenna with minute, barely articulating, scaphocerite; second maxilla scaphognathite with one long seta on posterior lobe; first pleomere without anterolateral lobes, almost as long as second pleomere, with broadly rounded pleuron; first pereopod unequal, fingers shorter than proximal part; first pereopod merus with convex lower margin; second pereopod chelate; third pereopod (and sometimes fourth) propodus with single distal spiniform seta on lower margin; second-fourth pereopods propodi flattened, broad, or ovate; coxa of fourth pereopod flattened, immobile; seventh thoracic sternite broad, visible between coxae of fourth pereopod only as a flat plate, no condyle with flattened, immobile fourth coxae; male first pleopod absent; second pleopod not modified, similar to third-fifth pleopods, second-fifth pleopods rami lanceolate with well developed appendix interna; uropodal endopod more or less ovate; uropodal exopod simply ovate without transverse suture; anterior carapace and first and sixth pleomeres with weak lateral setal rows. [Modified from Poore, 1994, 1997; Davie, 2002.]]

CTENOCHELIDAE Manning & Felder, 1991

Linea thalassinica present, lateral to antennae; posterior margin of carapace evenly curved, with cardiac prominence; rostrum obsolete or a spike; eyestalks flattened; first antenna with third article as long as or longer than second article;

second maxilla scaphognathite without long seta on posterior lobe; first pleomere without anterolateral lobes, weakly chitinized; first pereopod chelate, unequal, merus with straight or toothed lower margin; second pereopod chelate; third pereopod simple, propodus without distal spiniform seta on lower margin, propodus linear or weakly ovate; fourth pereopod simple or subchelate, coxa flattened, mobile; fifth pereopod simple or subchelate; seventh thoracic sternite narrow; second pleopod similar to third-fifth pleopods, rami lanceolate; uropodal exopod simply ovate; only sixth pleomere sometimes with setal rows. [Modified from Poore, 1994, 2004; Davie, 2002.]

[*GOURRETIIDAE* Sakai, 1999

Carapace lacking dorsal oval, cardiac prominence with a mid-pit present or absent; rostral carina absent; linea thalassinica entire; third maxilliped with or without exopod, distal margin of merus with or without distal spine; first pereopod unequal, larger with proximal meral hook, smaller elongate; third pereopod propodus with broadened heel; first pleopod uniramous; second pleopod biramous, foliaceous with appendix interna (male and female) and appendix masculina (male only); third-fifth pleopods biramous and foliaceous with appendix interna, larger than second pleopod; uropodal exopod with or without lateral notch. [Modified from Sakai, 1999a.]]

MICHELEIDAE Sakai, 1992

Cephalothorax laterally compressed, ending midposteriorly as a median lobe separate from produced posterolateral margins of carapace, which are thickened to form a marginal ridge; cephalothorax, rostrum, pleon, telson, and limbs without armature; linea thalassinica absent; rostrum present, flat, or obsolete, apically acute, with lateral carinae; eye usually pigmented; first antenna, first article longer than second article; second antenna with scaphocerite articulating and prominent; second maxilla scaphognathite with 1-2 long setae extending into branchial chamber; pleuron of first pleomere obsolete (obscure); second pleomere twice as long as first, pleuron overlaps first pleomere; first pereopod chelate, unequal, fingers as long as proximal part; second pereopod chelate; propodus of third and fourth pereopods more or less broadened; coxa of fourth pereopod flattened; seventh thoracic sternite visible between coxae of fourth pereopods only as a narrow ridge, condyle with flattened and mobile fourth coxae functional; male first pleopod with triangular second article, appendix interna represented by hooks, appendix masculina free; male second pleopod not modified, similar to third-fifth pleopods, endopod foliaceous without appendix masculina; exopods of second-fifth pleopods laterally lobed; uropodal exopod without transverse suture; uropodal endopod ovate to triangular; carapace, anterior cephalothorax, second-fourth pereopods, and first-sixth pleomeres with some lateral setal rows. [Modified from Poore, 1994, 1997, 2004; Davie, 2002.]

STRAHLAXIIDAE Poore, 1994

Linea thalassinica absent; rostrum usually spinose, apically bifid; eyestalks cylindrical; eye usually pigmented; first antenna, first article as long as second article, third article as long as second; second maxilla scaphognathite with or without 1-2 long setae on posterior margin; pleuron of first pleomere not produced; second pleomere twice as long as first; first pereopod chelate; second pereopod chelate, always with dense row of long setae on lower margin; third pereopod simple, propodus broadened; fourth pereopod simple or subchelate; propodus broadened; coxa more or less flattened; fifth pereopod chelate or subchelate; pleopods with appendix interna, second pleopod similar to third-fifth pleopods; male second pleopod endopod foliaceous without appendix masculina; exopods of second-fifth pleopods laterally lobed; uropodal rami lamellate; uropodal endopod triangular; second-fourth pereopods and pleomeres with some setal rows. [Modified from Poore, 1994, 2004; Davie, 2002.]

APPENDIX

Taxa at species level (and occasionally at genus level), mentioned in this chapter, with authorities and dates of their description

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- Ambiaxius surugaensis* Sakai & Ohta, 2005
Argyrosomus hololepidotus (Lacépède, 1801)
Austinogebia edulis (Ngoc-Ho & Chan, 1992)
Austinogebia narutensis (Sakai, 1986)
Austinogebia wuhsienweni (Yu, 1931)
Axianassa australis Rodrigues & Shimizu, 1992
Axianassa intermedia Schmitt, 1924
Axiopsis serratifrons (A. Milne-Edwards, 1873)
Axiorygma nethertoni Kensley & Simmons, 1988
Axius stirhynchus Leach, 1815
Biffarius arenosus (Poore, 1975)
Biffarius biformis (Biffar, 1971)
Bornia sebetia (O. G. Costa, 1829)
Calaxius acutirostris Sakai & de Saint Laurent, 1989
Callianassa ceramica Fulton & Grant, 1906
Callianassa filholi A. Milne-Edwards, 1878
Callianassa subterranea (Montagu, 1808)
Callianassa rathbunae Schmitt, 1935
Callianassa subterranea (Montagu, 1808)
Callianassa truncata (Giard & Bonnier, 1890)
Callianidea laevicauda Gill, 1859
Callianidea tya H. Milne Edwards, 1837
Calaxius oxypleura (Williams, 1974)
Callichirus adamas (Kensley, 1974)
Callichirus islagrande (Schmitt, 1935)
Callichirus kraussi (Stebbing, 1900)

- Callichirus major* (Say, 1818)
Callichirus masoomi (Timirzi, 1970)
Callichirus seilacheri (Bott, 1955)
Calocaris caribbaeus Kensley, 1996
Calocaris macandreae Bell, 1853
Catoptrophorus semipalmatus (Gmelin, 1789)
Chaenogobius macrognathus (Bleeker, 1860)
Coenemertes caravalas Corrêa, 1966
Coralaxius abelei Kensley & Gore, 1981
Corallianassa coutierei (Nobili, 1904)
Corallianassa hartmeyer (Schmitt, 1935)
Corallianassa longiventris (A. Milne-Edwards, 1870)
Corallianassa xutha Manning, 1988
Crassostrea gigas (Thunberg, 1793)
Crosniera minima (Rathbun, 1901)
Ctenocheles balssi Kishinouye, 1926
Ctenocheles holthuisi Rodrigues, 1978
Ctenocheles serrifrons LeLoeuff & Intès, 1974
- Dawsonius*
Dasyatis akajei (Müller & Henle, 1841)
- Eiconaxius albatrossae* Kensley, 1996
Eiconaxius cristagalli (Faxon, 1893)
Eiconaxius farreae (Ortmann, 1891)
Eiconaxius hakuhou Sakai & Ohta, 2005
Elops machnata (Forsskål, 1775)
Enteromyces callianassae Lichtwardt, 1966
Eschrichtius robustus Lilljeborg, 1861
Eucalliax aequimana (Baker, 1907)
- Fordonia leucobalia* (Schlegel, 1837)
- Gebiacantha acutispina* de Saint-Laurent & Ngoc-Ho, 1979
Gebiacantha laurentae Ngoc-Ho, 1989
Gebiacantha talismani (Bouvier, 1915)
Gilvossius setimanus (DeKay, 1844)
Glypturus acanthochirus Stimpson, 1866
Glypturus armatus (A. Milne-Edwards, 1870)
Glypturus laurae (de Saint Laurent, 1984)
Glypturus motupore Poore & Suchanek, 1988
Gouretia coolibah Poore & Griffin, 1979
- Jaxea nocturna* Nardo, 1847
- Laomedia astacina* De Haan, 1849
Laomedia healyi Yaldwyn & Wear, 1972
Laomedia paucispinosa Ngoc-Ho, 1997
Lepidophthalmus bocourti (A. Milne-Edwards, 1870)
Lepidophthalmus louisianensis (Schmitt, 1935)
Lepidophthalmus tridentatus (Von Martens, 1868)
Lepidophthalmus turneranus (White, 1861)
Lepidophthalmus sinuensis Lemaitre & Rodrigues, 1991

- Leptocottus armatus* Girard, 1854
Lightiella incisa Gooding, 1963
Lithognathus lithognathus (Cuvier, 1829)
Marcusiarius colpos Kensley & Heard, 1991
Marcusiarius lemoscastroi Carvalho & Rodrigues, 1973
Michelea leura (Poore & Griffin, 1979)
Michelea novaecaledoniae Poore, 1997
Michelea paraleura Poore, 1997
Michelea pillsburyi Kensley & Heard, 1991
Mictaxius dentatus Lin, 2006
Monodactylus falciformis Lacépède, 1801
Mustelus mustelus (Linnaeus, 1758)
Naushonia carinata Dworschak, Marin & Anker, 2006
Neaxius acanthus (A. Milne-Edwards, 1878)
Neaxius frankeae Lemaitre & Ramos, 1992
Neaxius mclaughlinae Ngoc-Ho, 2006
Neaxius trondlei Ngoc-Ho, 2005
Neaxius glyptocercus (Von Martens, 1868)
Neaxius vivesi (Bouvier, 1895)
Neocallichirus audax (De Man, 1911)
Neocallichirus cacahuete Felder & Manning, 1995
Neocallichirus grandimana (Gibbes, 1850)
Neocallichirus jousseaumei (Nobili, 1904)
Neocallichirus lemaitrei Manning, 1993
Neocallichirus maryae Karasawa, 2004
Neotrypaea biffari (Holthuis, 1991)
Neotrypaea californiensis (Dana, 1854)
Neotrypaea uncinata (H. Milne Edwards, 1837)
Neotrypaea (as *Callianassa*) *gigas* (Dana, 1852)
Nihonotrypaea harmandi (Bouvier, 1901)
Nihonotrypaea japonica (Ortmann, 1891)
Nihonotrypaea petalura (Stimpson, 1860)
Numenius americanus Bechstein, 1812
Numenius phaeopus (Linnaeus, 1758)
Paratrypaea bouvieri (Nobili, 1904)
Peregrinamor ohshimai Shoji, 1938
Peregrinamor gastrochaenans Kato & Itani, 2000
Pestarella candida (Olivi, 1792)
Pestarella tyrrhena (Petagna, 1792)
Pestarella whitei (Sakai, 1999)
Phacoides pectinatus (Gmelin, 1791)
Phoronis pallida (Schneider, 1862)
Pisodonophis cancrivorus (Richardson, 1848)
Platycephalus indicus (Linnaeus, 1758)
Pluvialis squatarola (Linnaeus, 1758)
Pomadasyz commersoni (Snyder, 1909)
Pomatogebia operculata (Schmitt, 1924)
Pomatogebia rugosa (Lockington, 1878)
Prochristianella hispida (Linton, 1890)

Pseudopythina rugifera (Carpenter, 1864)
Raja miraletus Linnaeus, 1758
Raja clavata Linnaeus, 1758
Rayllianassa amboinensis (De Man, 1888)
Saintlaurentiella
Scyliorhinus canicula (Linnaeus, 1758)
Sergio guassutinga (Rodrigues, 1971)
Sergio mericeae Manning & Felder, 1995
Sergio mirim (Rodrigues, 1971)
Sestrostoma balssi (Shen, 1932)
Sestrostoma toriumii (Takeda, 1974)
Sillaginodes punctatus (Cuvier, 1829)
Squalus fernandinus Molina, 1792
Strahlaxius plectrorhynchus (Strahl, 1862)
Stylocus ellipticus (Loosanoff, 1956)
Tachysurus feliceps Valenciennes, 1840
Takifugu niphobles (Jorsan & Snyder, 1901)
Thalassina anomala (Herbst, 1804)
Thalassina emerii Bell, 1844
Thalassina krempfi Ngoc-Ho & de Saint Laurent, 2009
Thalassina squamifera De Man, 1915
Thomassinia gebioides de Saint Laurent, 1979
Trypaea australiensis Dana, 1852
Typhlogobius californiensis Steindachner, 1879
Upogebia acanthura Coelho, 1973
Upogebia affinis (Say, 1818)
Upogebia africana (Ortmann, 1894)
Upogebia aristata LeLoeuff & Intès, 1974
Upogebia carinicauda (Stimpson, 1860)
Upogebia deltaura (Leach, 1815)
Upogebia issaeffi (Balss, 1913)
Upogebia major (De Haan, 1839)
Upogebia mediterranea Noël, 1992
Upogebia pugettensis (Dana, 1852)
Upogebia pusilla (Petagna, 1792)
Upogebia quddusiae Tirmizi & Ghani, 1978
Upogebia stellata (Montagu, 1808)
Upogebia synagelas Williams, 1987
Upogebia tipica (Nardo, 1869)

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