

PLANKTON-CAUGHT ZOEAL STAGES AND MEGALOPA OF THE LOBSTER SHRIMP *AXIUS SERRATUS* (DECAPODA: AXIIDAE) FROM THE BAY OF FUNDY, CANADA, WITH A SUMMARY OF AXIIDEAN AND GEBIIDEAN LITERATURE ON LARVAL DESCRIPTIONS

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A B S T R A C T

Wild-caught larvae, attributed to the lobster shrimp *Axius serratus*, consisting of two zoeal stages and a decapodid (megalopa), are described in detail. Parentage of larvae was ascertained based on geographic distribution of axiideans and gebiideans (= former thalassinideans) within the study area and close morphological resemblance to other congeneric larval stages. Larvae of *A. serratus* represent the first described 'thalassinidean' larvae from Canadian Atlantic waters and the first for Axiidae within the northwest Atlantic. Among axiidean larvae, those of *A. serratus* most closely resemble larvae of *A. stirhynchus* from the eastern Atlantic. Distinct features include the spination of the pleon that set *A. serratus* zoeae apart from those of most other 'thalassinideans' but that, in combination with a telson very similar to *Homarus americanus*, contributes to the general resemblance of *A. serratus* larvae to those of the American lobster. The primary distinction between these taxa is the presence of a chela on the third pereopod in the latter that is not present in the former. In view of these appendages being prone to loss or damage, other characters that separate these taxa are listed and discussed. Given the uncertain status of some taxa within Axiidae and limited detailed information of larvae with certain parentage, difficulties in delineating the family based on larvae persist, as they do for cladistic analyses using adult morphology and molecular approaches.

KEY WORDS: Axioidea, *Axius serratus*, *Homarus americanus*, larval development, plankton, thalassinideans, systematics

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INTRODUCTION

Thalassinideans, even though recently recognized as paraphyletic and separated into the infraorders Axiidea and Gebiidea (Robles et al., 2009; Bracken et al., 2009), constitute a widely recognized group whose members are variously referred to as ghost shrimps (Callianassidae), mud shrimps (Upogebiidae), mud lobsters (Thalassinidae), or lobster shrimps (Axiidae) (McLaughlin et al., 2005). Herein collectively referred to as thalassinideans, these crustaceans occur in soft sediments primarily within intertidal and shallow subtidal waters, where they may reach high population densities (Dworschak, 1983, 1987; Tunberg, 1986; Candisani et al., 2001). Four axiidean species among two families are known to occur in Atlantic Canada: the axiids *Axius serratus* Stimpson, 1852; *Calocaris templemani* Squires, 1965; and the callianassids *Gilvossius setimanus* (Dekay, 1844) (= *Callianassa atlantica* Rathbun, 1926) and *Biffarius biformis* (Biffar, 1971) (= *Callianassa biformis*) (Squires, 1990). The presence of a reported fifth species (Nizinski, 2003; Heard et al., 2007), the gebiidean laomediid *Naushonia crangonoides* Kingsley, 1897 is possible but needs confirmation.

Axius serratus is found from off Delaware Bay as far north the Gulf of St. Lawrence and Nova Scotia, where, in the Strait of Canso, it is known to occur in high densities (Pemberton et al., 1976). It appears to be the most common thalassinidean in Canadian Atlantic waters, including the

Bay of Fundy (Squires, 1990). While known to occur at depths ranging from 18–220 m, most records are from the near-shore at depths less than 100 m (Kensley, 2001). *Axius armatus* Smith, 1881, a closely related and rarely recorded sympatric species (Kensley, 2001), has only been found in US waters, south of Cape Cod, offshore at depths of greater than 100 m.

Axius serratus is the only species known to occur in the immediate vicinity of where the larval specimens described herein were collected, including the occurrence of an inshore ovigerous female from 60 m depth held in the research collection at the Atlantic Reference Centre of the Huntsman Marine Science Centre. Other known larvae of that genus (Gurney, 1942; Kurata, 1965) in general also resemble those obtained in the present study much more than larvae of the other thalassinidean genera listed from the area. With only one species of *Axius* in the area, it is reasonable to assume that the larvae obtained here are those of *A. serratus*.

The purpose of this study was to describe the larvae of *A. serratus* and compare them to larvae of other thalassinideans and morphologically similar larvae of the sympatric lobster *Homarus americanus* H. Milne Edwards, 1837.

MATERIALS AND METHODS

Specimens examined are part of a collection set obtained in the Bay of Fundy during July to October 1989 using a 0.505 mm mesh bongo

Table 1. Dimensions (mm) of larval structures of *Axius serratus* Stimpson 1852. Note: Values are given as the mean \pm standard deviation, with range in parenthesis.

Stage	Rostral spine length	Carapace length	Pleonal length	Total length
Zoea 1	1.11 \pm 0.16 (0.88-1.47)	1.58 \pm 0.16 (1.32-1.97)	3.92 \pm 0.22 (3.52-4.18)	6.72 \pm 0.31 (5.99-6.92)
Zoea 2	1.19 \pm 0.07 (1.10-1.26)	1.60 \pm 0.19 (1.35-1.98)	4.32 \pm 0.35 (3.92-4.88)	7.13 \pm 0.39 (6.51-7.74)
Megalopa	0.59 \pm 0.08 (0.41-0.67)	1.78 \pm 0.17 (1.32-1.93)	4.39 \pm 0.26 (4.01-4.90)	6.76 \pm 0.44 (5.74-7.42)

plankton net deployed from near-surface to 131 m depth, mostly in an area about 5–10 km off Point Lepreau, New Brunswick (44°58'N, 66°28'W).

Whenever possible, a minimum of ten specimens were measured and at least five specimens of each stage were dissected for morphological description. For slide preparations polyvinyl lactophenol mounting medium was used with Acid Fuchsin and/or chlorazol black stains. Measurements (\pm 7 μ m) include total length (TL), measured in lateral view from the tip of the rostrum to the posterior midpoint of the telson; carapace length (CL), measured in lateral view from the base of the rostrum to the posterior midpoint of the carapace; and rostrum length (RL), measured in dorsal view from the distal end of the rostrum to the base of the rostrum above the eye.

The description of setae follows Pohle and Telford (1981), but here includes only analysis by light microscopy (LM), using an Olympus BH-2 microscope with Nomarski Differential Interference Contrast and camera lucida. Some of the setae designated as plumose herein may be plumodenticulate setae due to the lower resolution limits of LM as compared to scanning electron microscopy (SEM). Description guidelines of Clark et al. (1998) were generally followed. Specimens of larval stages have been deposited at the Atlantic Reference Centre of the Huntsman Marine Science Centre, under catalog numbers 64921, 64822 and 56319.

RESULTS

Larval development of *Axius serratus* consists of two zoeal stages and one megalopa. Larval morphometrics are given in Table 1.

First Zoea (Fig. 1)

Carapace (Fig. 1A).—Longer than wide; with long round rostral spine, about same length as remainder of cephalothorax, slightly upturned, adorned with minute spines dorsolaterally. Frontal margin with large antennal spine, followed by 4-6 spinules. Eyes fused to carapace.

Antennule (Fig. 1B).—With three-segmented peduncle, proximal segment bearing 1-2 short plumose setae medially, 3-4 distally on the outer margin and single inner plumose seta; middle segment with 3-5 plumose setae in outer margin and single inner plumose seta; distal segment with single outer and 3 long inner plumose setae. Unsegmented endopod with optional simple seta subterminally, 1 plumose and 2 reduced simple setae terminally; unsegmented exopod with 8 aesthetascs, 6 terminal, 2 subterminal, and 2 terminal simple setae.

Antenna (Fig. 1C).—Coxa and basis separated; basis with distal spine about 1/5 of endopod on outer margin, shorter spine on inner margin. Unsegmented endopod almost as long as exopod, with 3 small simple setae apically. Scaphocerite armed with distinct distolateral spine, 18-22 inner plumose setae.

Mandibles (Fig. 1D).—Symmetrical, molar region denticulated, incisor process bearing armed spinules; unarmed palp present.

Maxillule (Fig. 1E).—Coxal endite with 4 plumodenticulate setae and 4-5 developing setae, basal endite with 4-5 plumodenticulate cuspidate setae and 4 or more developing setae. Endopod unsegmented with 1 long and 2 shorter plumodenticulate setae proximally, 1 long and 1 short medially, 1 subterminal and 1-2 terminal plumodenticulate setae.

Maxilla (Fig. 1F).—Coxal endite distinctly bilobed, larger proximal lobe with 6-7 plumose and 2 developing setae; distal lobe with 3 plumodenticulate setae, 1 developing seta; basal endite strongly and equally bilobed, proximal and distal lobes each with 4 plumodenticulate setae and 1 developing seta. Endopod unsegmented, with 5 tiers, each bearing a pair of sparsely plumodenticulate setae. Scaphognathite with 35-40 marginal densely plumose setae.

Maxilliped 1 (Fig. 1G).—Coxa with 5-6 plumodenticulate setae, basis with 10-15 plumodenticulate setae. Endopod four-segmented, much shorter than exopod, with 4, 2, 2, 4 plumodenticulate setae. Incompletely bisegmented exopod with 7-8 plumose natatory setae. Bilobed epipod bud present.

Maxilliped 2 (Fig. 1H).—Coxa and basis with 1 and 7-8 sparsely plumodenticulate setae, respectively. Endopod four-segmented, much shorter than exopod segment, with 2, 0, 1, 6 plumodenticulate setae. Incompletely bisegmented exopod with 8-9 plumose natatory setae. Epipod and gill bud present.

Maxilliped 3 (Fig. 1I).—Coxa and basis without setae. Endopod four-segmented, longer than exopod, with 0-1, 1, 2-3, 4 plumodenticulate setae. Incompletely bisegmented exopod with 9 plumose natatory setae. Epipod and gill bud present.

Pereiopods 1 and 2 (Fig. 1J, K).—Endopod four-segmented, chela distinct; unsegmented exopod present. Setae absent. Epipod and gill bud present.

Pereiopod 3 (Fig. 1L).—Endopod with four segments, chela absent; unsegmented exopod present. Setae absent. Epipod and gill bud present.

Pereiopods 4 and 5.—Present as unextruded buds.

Pleon (1A).—Five somites, without setae, first somite with single ventrolateral spine, somites 2 and 3 with single dorsolateral and ventrolateral spines, fourth somite with single dorsolateral and two ventrolateral spines, last somite with two dorsolateral spines and two ventrolateral spines, lateral spines longest. Somites 1-5 with dorsal 'collar'.

Pleopods (Fig. 1A, M).—On somites 2-5, with endo- and exopod, no setae, no appendix interna.

Uropods.—Absent.

Telson (Fig. 1N).—Proximally undifferentiated from somite 6, distally subtriangular, posterior margin bearing

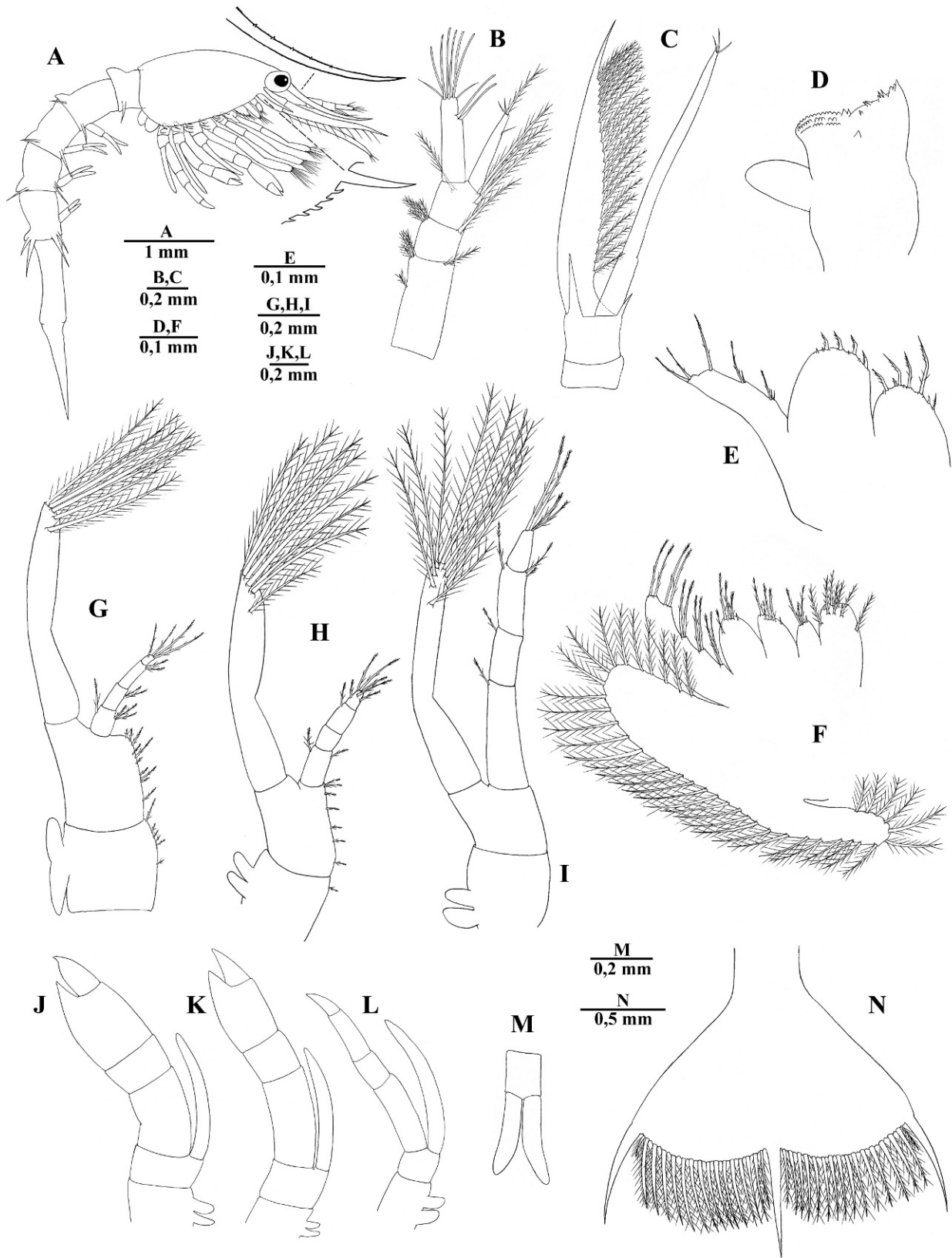


Fig. 1. First zoea of *Axis serratus* Stimpson, 1852. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, maxilliped 1; H, maxilliped 2; I, maxilliped 3; J-L, developing pereopods 1-3; M, first pleopod; N, telson.

central and lateral spines, and 15 marginal plumodenticulate setae and single plumose 'anomuran hair' on either side of central spine. Anal spine absent.

Second Zoea (Fig. 2)

Carapace (Fig. 2A).—With movable stalked eyes, spines on rostrum more developed, otherwise unchanged.

Antennule (Fig. 2B).—Three-segmented peduncle, proximal segment medially with 2-4 plumose setae, distally with 3-4 plumose setae on outer margin and single plumose seta on inner margin; second segment with 3-5 plumose setae on the outer margin and single inner plumose seta; distal segment with 1 long and short optional plumose seta on outer margin, 3 long plumose setae on inner margin. Endopod with subterminal simple seta, 1 long plumose seta and 3-5 simple setae apically. Exopod two-segmented, proximal segment with 2 distal aesthetascs, distal segment with 6 aesthetascs and 4 simple setae.

Antenna (Fig. 2C).—Distal spine of basis now about 1/6 of endopod length. Inner distal basal spine reduced. Endopod two-segmented, longer than exopod, proximal segment without setae, distal segment with 3-4 apical simple setae. Scaphocerite unchanged.

Mandible (Fig. 2D).—Palp enlarged, segmentation apparent.

Maxillule (Fig. 2E).—Coxal endite with 4 plumodenticulate setae and 3-4 developing setae; basal endite with 4 plumodenticulate cuspidate setae and 8-9 developing setae. Endopod unsegmented with 1 medial and 1 distal plumodenticulate seta. Epipod seta absent.

Maxilla (Fig. 2F).—Coxal endite proximal and distal lobes with 5 plumose and 4 plumodenticulate setae, respectively; basal endite with 3-5 and 5 plumodenticulate setae on proximal and distal lobe, respectively; endopod distally with 2-3 setae, otherwise unchanged; scaphognathite with 39-42 marginal densely plumose setae.

Maxilliped 1 (Fig. 2G).—Coxa and basis each with 3-4 plumodenticulate setae. Endopod smaller than in first zoea, four-segmented, with 3, 2, 2, 3-4 plumodenticulate setae. Incompletely bisegmented exopod with 8 plumose natatory setae. Bilobed epipod bud enlarged.

Maxilliped 2 (Fig. 2H).—Coxa with optional plumodenticulate seta; basis with no more than 2 plumodenticulate setae, 1 medially 1 distally. Endopod four-segmented with 2,2,2,3-4 plumodenticulate setae. Incompletely bisegmented exopod with 9 plumose natatory setae. Epipod and gill buds enlarged.

Maxilliped 3 (Fig. 2I).—Enlarged compared to maxillipeds 1 and 2. Coxa without setae; basis with optional seta distally on inner margin. Endopod five-segmented, longer than exopod, with 0,0,0-1,2-3,2-3 plumodenticulate setae. Incompletely bisegmented exopod with 9 plumose natatory setae. Epipod and gill buds bilobed.

Pereiopods 1 and 2 (Fig. 2J, K).—Exopod incompletely bisegmented, with 8 natatory plumose setae. Epipod bilobed, gill bud with incomplete lamellation.

Pereiopod 3 (Fig. 2L).—Endopod four-segmented with 0,1,2-3,0 plumodenticulate setae; exopod incompletely bisegmented, with 8 natatory plumose setae. Epipod bilobed, gill bud with incomplete lamellation.

Pereiopod 4 (Fig. 2M).—Coxa and basis without setae; four-segmented endopod with 0-1,1,2-3,0 plumodenticulate setae; exopod incompletely bisegmented, with 6 natatory plumose setae. Epipod bilobed, gill bud with incomplete lamellation.

Pereiopod 5 (Fig. 2N).—Slender, coxa and basis without setae; five-segmented endopod with 0,1,0,4,2 plumodenticulate setae; exopod bud reduced, without setae. Epipod and gill buds absent.

Pleon (Fig. 2A).—Longer than in zoea 1 (see Table 1), with 6th somite differentiated from telson; pleurites enlarged ventrodistally.

Pleopods (Fig. 2A, O).—On somites 2-5, with developing appendix interna.

Uropods.—Apparent internally in telson but not yet extruded.

Telson (Fig. 2P).—Posterior margin bearing central and lateral spines, and 14-16 marginal plumodenticulate setae, 3 additional small plumose setae on either side of central spine.

Megalopa (Figs. 3 and 4)

Carapace (Fig. 3A).—Rostrum shortened and blunt, slightly curved ventrally, adorned with spines dorsolaterally, plumodenticulate setae laterally. Antennal spine reduced. Lateral margins with 18-22 sparsely plumose setae.

Antennule (Fig. 3B).—Three-segmented peduncle, proximal segment with 9-12 plumose setae on outer margin, 4 plumose setae terminally, 28-32 plumose setae covering statocyst cavity; middle segment with 6-7 setae distally, 3-4 plumose and 3 simple; third segment with 5-6 simple setae. Endopod six-segmented, with 3,3-4,3,3,3-4,7-8 simple setae. Exopod seven-segmented, first four segments with 0,2,1,1-2 simple setae, fifth and sixth segments each with 2 aesthetascs and simple seta, distal segment with 6 simple setae.

Antenna (Fig. 3C).—Peduncle two-segmented, distal segment with longer outer and shorter inner spine, and optional simple seta; endopod with long flagellum, consisting of 20+ articles (all specimens with incomplete antenna), with setation as indicated in figure; exopod reduced to small lobe.

Mandible (Fig. 3D).—With denticulated molar process, incisor process armed with spinules; palp three-segmented, bearing 24-25 plumodenticulate cuspidate setae apically on terminal segment.

Maxillule (Fig. 3E).—Coxal endite with 27-30 setae, 25-28 plumodenticulate, 2 plumose on distal margin; basal endite with 22 terminal plumodenticulate cuspidate, 10-11

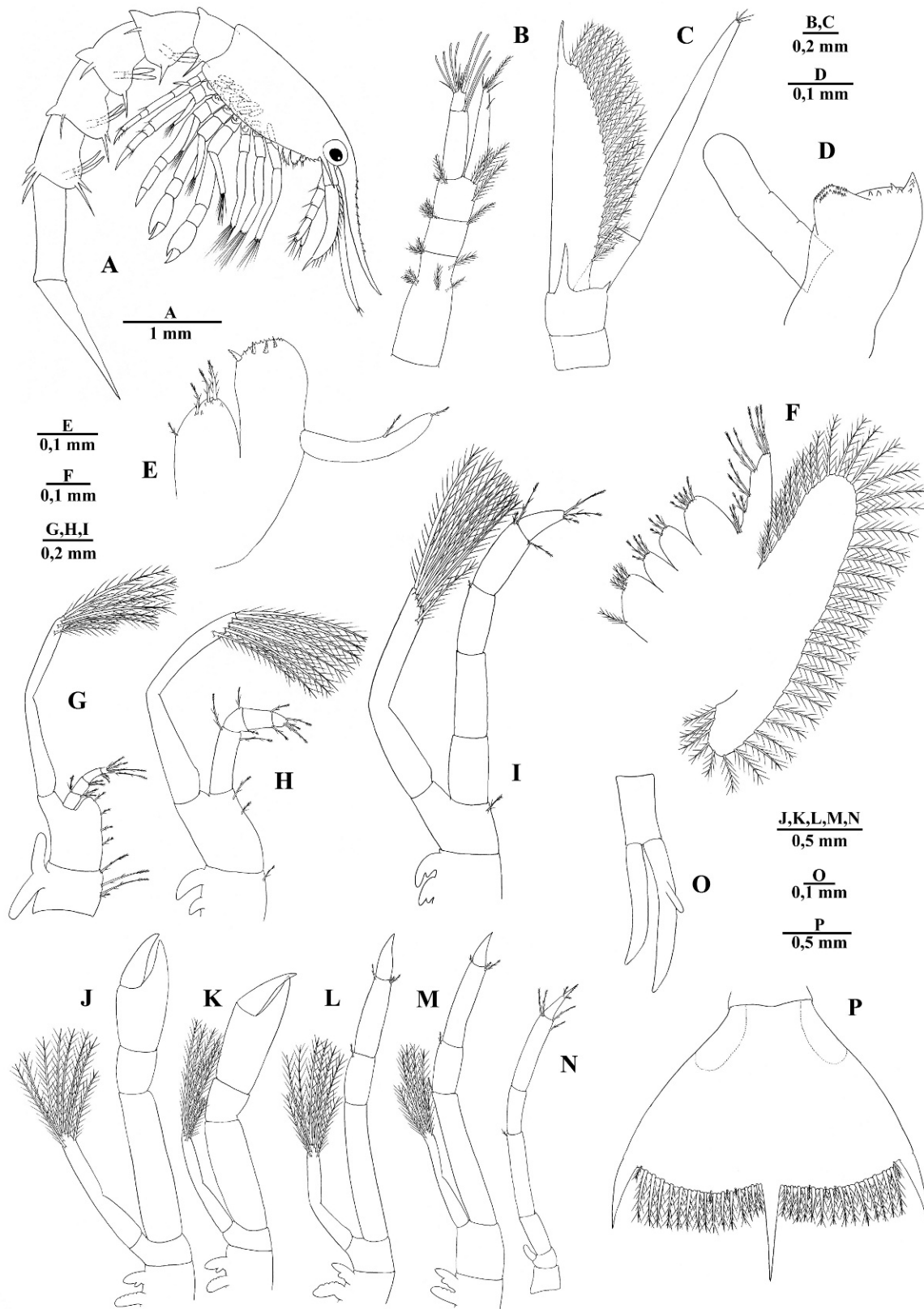


Fig. 2. Second zoea of *Axis serratus* Stimpson, 1852. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G-I, maxillipeds 1-3; J-N, pereiopods 1-5; O, first pleopod; P, telson.

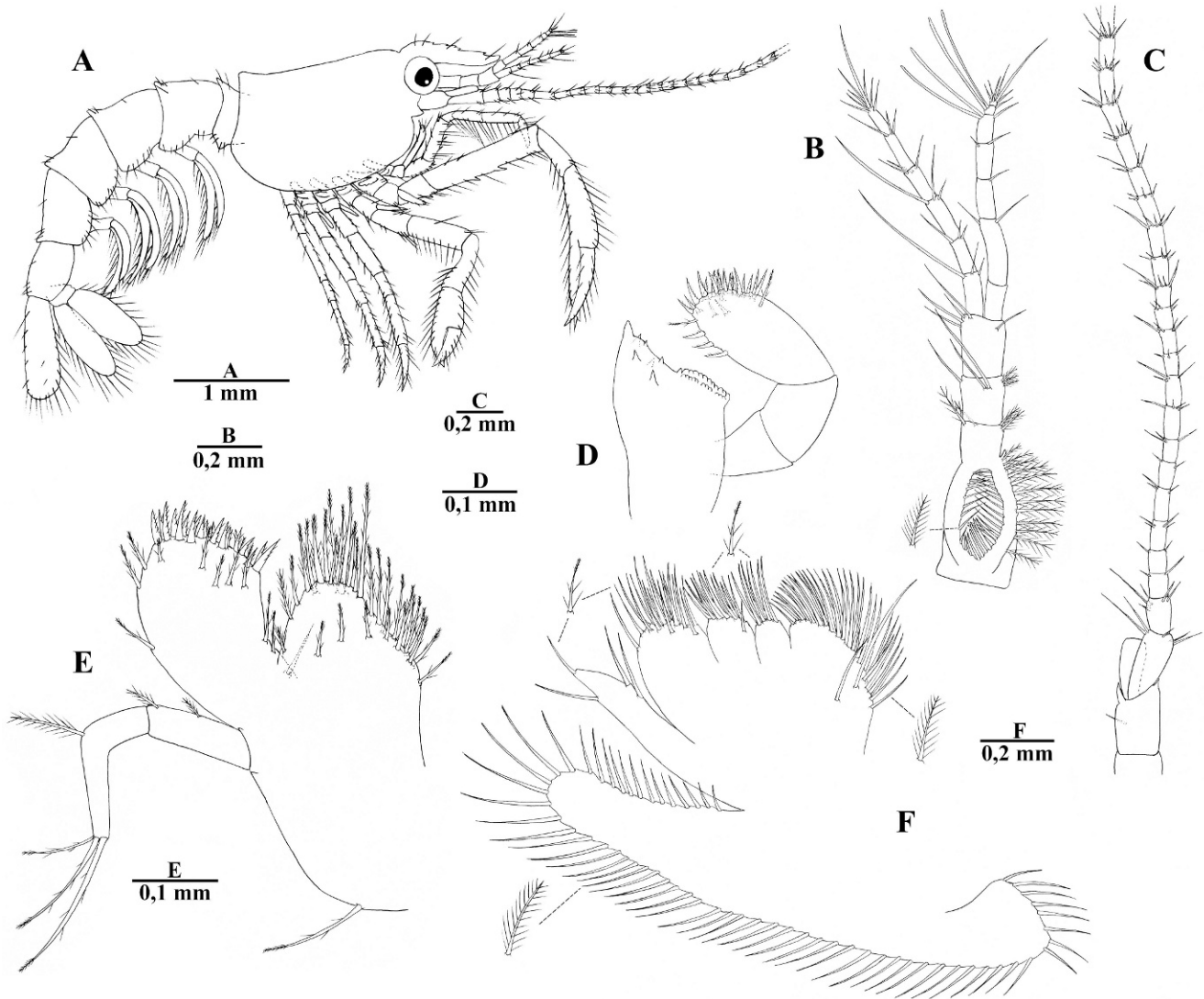


Fig. 3. Megalopa of *Axius serratus* Stimpson, 1852. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla.

subterminal plumodenticulate setae; endopod with 2 plumose setae on proximal segment, distal segment with single medial plumose seta and 2-3 terminal plumodenticulate setae; exopod plumodenticulate seta present.

Maxilla (Fig. 3F).—Coxal endite bilobed, enlarged proximal lobe with 34-36 plumose setae, 2 submarginal setae enlarged; distal lobe with 6-7 plumodenticulate setae; basal endite bilobed, with 11-13 and 18-19 plumodenticulate setae on proximal and distal lobes, respectively. Endopod with 4 plumodenticulate setae, scaphognathite with 61-66 marginal densely plumose setae.

Maxilliped 1 (Fig. 4A).—Coxa with 14-17 plumodenticulate setae, basis with 37-41 plumodenticulate setae; endopod without setae, reduced; exopod with 3-5 plumodenticulate setae medially and 6-7 apically; large bilobed epipod bud present.

Maxilliped 2 (Fig. 4B).—Coxa and basis with 4-8 and 8-11 sparsely plumodenticulate setae, respectively; endopod

four-segmented, proximal segment with 4-5 plumodenticulate setae on outer margin, 17-19 sparsely plumodenticulate and simple setae on inner margin, second segment with plumodenticulate seta, segments three and four with 12-14, and 7-10 mostly plumodenticulate setae, respectively; exopod unsegmented, bearing 6-8 plumose setae distally. Basally with arthrobranch bud and podo- and epipod buds, latter bearing 2-3 plumodenticulate setae.

Maxilliped 3 (Fig. 4C).—Coxa and basis with 5 plumodenticulate setae each; endopod five-segmented with 26-28, 20-25, 23-30, 30-35 and 13-15 mostly plumodenticulate setae of two types and few simple setae; crista dentata well developed on ischium, less developed on merus; exopod with 8-9 plumose setae. Basally with arthrobranch and epipod buds, latter bearing 4 plumodenticulate setae.

Pereiopod 1 (Fig. 4D).—Chelate, covered with mostly simple setae, some plumose and plumodenticulate as shown; basis and ischium with distal spine, merus with 3 spines on ventral margin; exopod reduced, bearing 7 simple

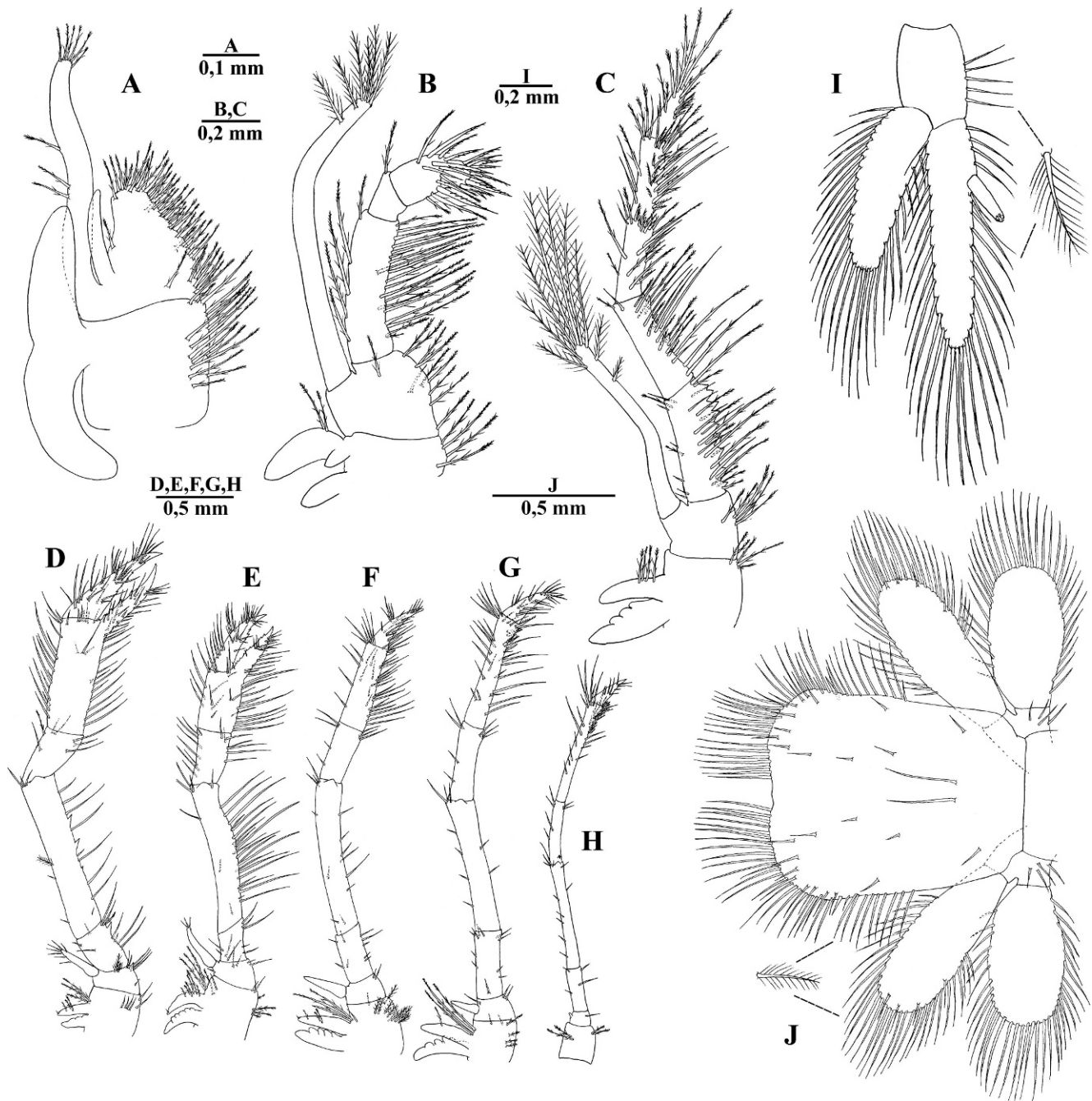


Fig. 4. Megalopa of *Axis serratus* Stimpson, 1852. A-C, maxillipeds 1-3; D-H, pereiopods 1-5; I, first pleopod; J, telson and uropods.

setae. Basally with epipod bearing 3-4 plumodenticulate setae, and partially lamellate gill.

Pereiopod 2 (Fig. 4E).—Chelate, covered with mostly simple setae, but without spines; coxa with several plumose and plumodenticulate setae; exopod reduced, bearing 3 simple setae. Basally with epipod bearing 7 plumodenticulate setae, and partially lamellate gill.

Pereiopod 3 (Fig. 4F).—Not chelate, covered with mostly simple setae, and without spines; coxa with several plumose and plumodenticulate setae; exopod reduced,

without setae. Basally with epipod bearing 4 plumodenticulate setae, and partially lamellate gill.

Pereiopod 4 (Fig. 4G).—Not chelate, covered with mostly simple setae, and without spines; coxa with several plumose and plumodenticulate setae, propodus also armed with plumodenticulate setae on ventral margin; exopod reduced, without setae. Basally with epipod bearing single plumodenticulate seta, and partially lamellate gill.

Pereiopod 5 (Fig. 4H).—Not chelate, covered with mostly simple setae; coxa with 4 plumodenticulate setae; carpus

with 3 short spines proximally; propodus armed with additional plumodenticulate setae on ventral margin; exopod minute, without setae. Epipod and gill absent.

Pleon (Fig. 3A).—Somites lacking spines, bearing plumose setae as shown. Dorsal ‘collar’ on somites 1-5 reduced.

Pleopods (Fig. 4I).—Protopod with 5 plumose setae; endopod with 32-34 and exopod with 28-30 plumose setae; enlarged appendix interna bearing 5-6 cincinnuli.

Uropods (Fig. 4J).—Fully developed; protopod with 4 simple setae, endopod and exopod marginally covered with plumose setae as shown.

Telson (Fig. 4J).—Subrectangular, spines absent; distally and sub-distally covered in 2 rows of plumose setae; dorsal surface with 2 long medial and several shorter simple setae as shown.

DISCUSSION

Thalassinidean Larval Knowledge and Identity of Larvae of *Axius serratus*

Recent phylogenetic investigations based on molecular evidence (Tsang et al., 2008a, b; Braken et al., 2009; Felder and Robles, 2009; Robles et al., 2009) concluded that thalassinideans are a paraphyletic group and proposed the separation into two infraorders, Axiidea and Gebiidea, as originally suggested by de Saint Laurent (1979) and followed by De Grave et al. (2009) in the most recent classification of decapods. Axiidea comprises the families Callianassidae, Callianadeidae, Ctenochelidae, Micheleidae, Strahlaxiidae, Thomassiniidae, and Axiidae, the latter now including the merged Eiconaxiidae and Calocarididae based on molecular evidence by Tsang et al. (2008a) and Robles et al. (2009); and Gebiidea comprising the families Axianassidae, Laomediidae, Thalassinidae, and Upogebiidae. A different arrangement of families within the grouping of former superfamilies Axioidea, Callianassoidea, and Thalassinioidea, which was in general use previously (Poore, 1994; Martin and Davis, 2001; McLaughlin et al., 2005), is no longer supported by molecular evidence. The new scheme has been adopted in the present study, even though the higher classification of thalassinideans is not conclusively resolved, as evidenced by discussions within the above publications and the limited taxa included in different analyses.

Presently, Axiidea and Gebiidea together are thought to comprise about 615 extant species among 117 genera (De Grave et al., 2009), compared to 556 species and 96 genera listed earlier by Dworschak (2005) and the 600 species among 99 genera of Robles et al. (2009). Taking into account the uncertain identity of some described larvae and the contentious status of a number of genera and species (see Table 2), larval information is available for about one eighth of the species and one quarter of known genera, *Upogebia* representing the genus with most known larvae. Only about one third of larval accounts comprise complete larval descriptions of species. Most of the species with larval information are callianassids, with the Axiidea

representing approximately 55% of the larval descriptions, and the Gebiidea the remaining 45% (Table 2). Larvae of the axiideans Callianadeidae, Ctenochelidae, Micheleidae, and Thomassiniidae are currently unknown.

Until the present study, larvae of the four axiidean species, recorded by Squires (1990) from Atlantic Canada, were unknown. Among genera found in that area, partial descriptions exist for *Axius stirhynchus* Leach, 1815 by Webb (1921), Gurney (1942) and Bourdillon-Casanova (1960), a species restricted to the northeast Atlantic, as well as for *Axius* sp. A (zoea I-III) and sp. B (zoea III-VI, decapodid) from the western Pacific (Kurata, 1965). Apart from larvae of unspecified Axiidae (Gurney, 1924, 1938; Wear, 1965), known larval information for other Axiidae is restricted to the first zoea of *Axiopsis serratifrons* (A. Milne-Edwards, 1873), a species widespread in tropical waters (Rodrigues, 1994); second zoea of *Calocarides coronatus* (Trybom, 1904) from the eastern Atlantic; first zoea of *Eiconaxius* spp. from the southwest Pacific; and late zoea and decapodid larvae possibly attributable to *Eutrichocheles* Wood-Mason, 1876 from Bermuda (see Table 2 for references). All but the larva of *A. serratifrons* were obtained from plankton-collected material. Thus, the larval description of *A. serratus* also represents the first complete one for Axiidae within the northwest Atlantic. Larvae of these taxa show morphological similarities, such as in a pronounced and even pleonal spination in most cases.

The other axiidean genus represented within the Canadian Atlantic is *Calocaris* Bell, 1846, as *C. templemani* Squires, 1965, of Calocarididae. Known larvae of this genus are of *C. macandreae* Bell, 1846 (Björck, 1913; Bull, 1934; Bourdillon-Casanova, 1960; Gurney, 1942), a species restricted to the eastern Atlantic. These larvae are clearly distinct from those obtained in the present study, particularly in a much less developed spination of the carapace, pleon, and telson.

The remaining verified taxa represented within Canadian Atlantic waters are callianassids, *B. biformis* and *G. setimanus*, in Squires listed as *Callianassa biformis* and *C. atlantica*, respectively. Sandifer (1973b) described zoal stages of plankton-collected larvae that he tentatively assigned to these two species. These larvae, and those of other axiideans (Table 2), are also morphologically very distinct from larvae collected in the present study, particularly in terms of more poorly developed pleonal and telson spination. Thus any callianassids have been excluded as possible parentage of the larvae in the present study.

In addition to the species reported by Squires (1990), Nizinski (2003), and Heard et al. (2007) report the laomediid *Naushonia crangonoides* from Canadian waters. While these records could not be verified, larvae of *Naushonia* Kingsley, 1897 have very distinct mandibles, and other than the rostral spine (Goy and Provenzano, 1978), have a more poorly developed spination of the carapace pleon and telson. Therefore this taxon is also excluded as possible parentage of the larvae in the present study.

Larval information on other axiideans is restricted to two species in the family Strahlaxiidae (Poore, 1994), with very

Table 2. Known described larvae of Axiidea and Gebiidea (= Thalassimidea). Note: despite reviews ranging from Axiidae (Sakai and de Saint Laurent, 1989) to Upogebiidae (Sakai, 2006), thalassimidean systematics are in a state of flux, with the taxonomic status of some taxa varying according to author(s). Here higher classification follows DeGrave et al. (2009), with inclusion of Eiconaxiidae and Calocarididae within Axiidae as per Tsang et al. (2008a) and Robles et al. (2009). While updating the taxonomy was attempted, the status of some taxa remains contentious, e.g., status of callianassid genera of Manning and Felder (1991), Heard and Manning (1998) versus Sakai (1999); following Strasser and Felder (2000), such taxa are herein referred to as sensu lato (s.l.), or include separate foot notes for species with conflicting taxonomic status. P, prezoa; Z, zoea; D, decapod (= megalopa), PL, post-larva; Z (var.), various zoal stages; ?, determination uncertain or not possible based on information provided. Definitions: (1) description: Incomplete = deficient description of listed larval stage(s); partially complete = more or less full description of listed larval stages; (complete) = all stages covered but detailed descriptions lacking; (complete, in combination) = complete description of all stages in combination of all sources but details lacking; complete = more or less full description of all larval stages. (2) Source: ♀ lab-reared = laboratory-reared specimens hatched from identified ovigerous female(s); plankton: wild-caught specimens of unproven parentage; plankton (lab-reared): live wild-caught specimens that were lab-reared. Taxa with conflicting taxonomic status: ¹ resuscitated family as per Tudge and Cunningham (2002); * *Biffarius* was synonymized with *Callianassa* by Sakai (1999), but not others (Poore, 1994; Tudge et al., 2000); ** *C. kevaltramanii*, not analyzed by Tudge et al. (2000), justifiably synonymized with *C. masoomi* and removed to new genus *Podocallichirus* by Sakai (1999), removal contentious as per Tudge et al. (2000); *** removed from *Callianassa* to new genus *Necallianassa* by Heard and Manning (1998), was subsequently synonymized with *Callianassa truncata* by Ngoc-Ho (2003), recognized by some (Sakai, 1999; Tudge et al., 2000) but not others (e.g., de Grave, 2009); † *Callianassa atlantica* is a junior synonym of *Gonodactylus setimanus*, recognized as *Callianassa setimanus* by Manning (1987), later placed in the newly erected genus *Gilvossius* by Manning and Felder (1992), recognized by Poore (1994), Tudge et al. (2001) and De Grave et al. (2009), but not Sakai (1999, as *Callianassa setimana*); †† removed from *Callianassa* to *Neotrypaea* by Manning and Felder (1991), recognized e.g., by Poore (1994) and Tudge et al. (2001), but latter genus synonymized with *Callianassa* by Sakai (1999) due to taxa with perceived intermediate morphology that do not allow a clear-cut distinction; ††† removed from *Callianassa* to *Nilomonotrypaea* by Manning and Tamaki (1998), recognized by Tudge et al. (2001), but synonymized with *Callianassa* by Sakai (1999) due to varying interpretation of appendix interna morphology; + removed to *Pestarella* by Ngoc-Ho (2003) but listed elsewhere as *Callianassa*; ++ removed from *Neocallichirus* Sakai, 1988 to *Sergio* by Manning and Lemaitre (1993), supported by analyses of Tudge et al. (2001) and Poore (1994), but all species in *Sergio* were synonymized with *Neocallichirus* by Sakai (1999) based on perceived intermediate forms that prevent clear separation; +++ removed from *Callianassa* to re-established genus *Trypaea* Dana, 1852 by Manning and Felder (1991), supported by analyses of Tudge et al. (2001) and Poore (1994), but synonymized with *Callianassa* by Sakai (1999) because of perceived lack of distinctive characteristics.

Taxon	Distribution	Source	Stage(s)	Description	Reference(s)
Axiidea, Axiidae:					
Axiidae sp(p).	Southwest Pacific	plankton	Z1?	incomplete	Gurney (1924); Wear (1965)
Axiidae spp.	Southwest Pacific	plankton	Z (var.)	incomplete	Gurney (1938) "Group I"; Lindley and Hernández (1999)
<i>Axiopsis serratifrons</i> (A. Milne-Edwards, 1873)	Tropical West Atl., Pac. & Ind. Oceans	♀, lab-reared	Z1	partially complete	Rodrigues (1994)
<i>Axius stirlinchus</i> Leach, 1815	East Atlantic	plankton (lab-reared); plankton	P, Z1-Z2, D	(complete, in combination)	Webb (1921); Gurney (1942); Kurian (1956); Bourdillon-Casanova (1960); Barnich (1996)
<i>Axius</i> s.l. sp. A	West Pacific	plankton	Z1-Z3	incomplete	Kurata (1965)
<i>Axius</i> s.l. sp. B	West Pacific	plankton	Z3-Z6, D	incomplete	Kurata (1965)
<i>Calocarides coronatus</i> (Trybom, 1904)	East Atlantic	plankton	Z2	partially complete	Elofsson (1959)
<i>Calocaris macandreae</i> Bell, 1846	East Atlantic	plankton & ♀, lab-reared	Z1-Z3, D	(complete, in combination)	Sars (1884); Björck (1913); Bull (1934); Gurney (1942); Bourdillon-Casanova (1960); Barnich (1996)
<i>Eiconaxius</i> spp.	Southwest Pacific	plankton	Z1, Z3	incomplete	Gurney (1924); Wear (1965) as <i>Iconaxiopsis</i>
<i>Eutrichocheles</i> sp.?	Northwest Atlantic	plankton	Late Z, D	incomplete	Gurney (1938); Dakin and Colefax (1940) as Thalassinid D.I.; Lebour (1941) as <i>Axiopsis</i> subgenus <i>Paraxiopsis</i>
Axiidea, Callianassidae:					
Callianassidae spp.	East Atlantic	plankton	Z?, Z1	incomplete	Seridji (1995); Lindley and Hernández (1999)
<i>Biffarius biformis</i> (Biffar, 1971)*	Northwest Atlantic, incl. Canada	plankton	Z1-Z4	partially complete	Sandifer (1973b) as <i>Callianassa biformis</i> ?
<i>Callianassa filholi</i> A. Milne-Edwards, 1878	West Pacific	♀, lab-reared	Z1+	incomplete	Wear (1965)
<i>Callianassa</i> s.l. <i>masoomi</i> (Tirmizi, 1970)**	North Indian	♀, lab-reared	Z1-Z2, D, PL	complete	Sankolli and Shenoy (1975) as <i>Callianassa (Callichirus) kevaltramanii</i>
<i>Callianassa</i> s.l. <i>maxima</i> A. Milne-Edwards, 1870	Indian Ocean	plankton	Z1-Z2, D	complete	Menon (1933) as <i>Callianassa</i> sp.; Daniel (1981) as <i>Callianassa (Callichirus) maxima</i>

Table 2. Continued.

Taxon	Distribution	Source	Stage(s)	Description	Reference(s)
<i>Callianassa</i> s.l. sp.	Red Sea	plankton (lab-reared)	Z1-Z4, D	(complete?)	Al-Kholy and Fikry-Mahmoud (1967)
<i>Callianassa</i> s.l. sp.	Red Sea	plankton	Z?	incomplete	Williamson (1970)
<i>Callianassa</i> s.l. sp.	North Indian	plankton	Z?	incomplete	Menon (1940)
<i>Callianassa</i> s.l. sp. C	Northwest Atlantic	plankton	Z1	partially complete	Sandifer (1973b)
<i>Callianassa</i> s.l. sp.?	Southwest Pacific	plankton	Z1-Z5	incomplete	Dakin and Colefax (1940)
<i>Callianassa</i> s.l. sp.	Mediterranean	plankton	Z?	incomplete	Williamson (1967)
<i>Callianassa subterranea</i> (Montagu, 1808)	East Atlantic, Mediterranean	plankton (lab-reared); plankton	Z1-Z5, D	(complete)	Sars (1884) as <i>Calocaris macandreae</i> ; Webb (1921); Lutze (1938); Gurney (1942)
<i>Callianassa truncata</i> Girard and Bomier, 1890***	East Atlantic, Mediterranean	plankton?	Z1-Z4, D	incomplete	Cano (1891) as <i>Axius stirrhynchus</i> ; Dolgopolskaia (1969); dos Santos (1999) in dos Santos and Gonzales-Gordillo (2004)
<i>Callincherus seilacheri</i> (Bott, 1955)	East Pacific	♀, lab-reared	P, Z1-Z5, D	complete	Aste and Retamal (1983) as <i>Callianassa garthi</i>
<i>Callincherus islagrande</i> (Schmitt, 1935a)	West Atlantic (Gulf of Mexico)	♀, lab-reared	Z1-Z4 (Z5), D	complete	Strasser and Felder (2000)
<i>Callincherus kraussi</i> (Stebbing, 1900)	Off South Africa	♀, lab-reared	Z1-Z2, D	(complete)	Forbes (1973) as <i>Callianassa kraussi</i>
<i>Callincherus major</i> (Say, 1818)	Western Atlantic	♀, lab-reared	Z1-Z4 (Z5), D	complete	Strasser and Felder (1999)
<i>Callincherus</i> sp.	Southwest Atlantic	♀, lab-reared	Z1-Z3	partially complete	Rodrigues (1976) as <i>C. major</i> ; see Strasser and Felder (1999)
<i>Gilvossius setimanus?</i> (De Kay, 1844) †	Northwest Atlantic, incl. Canada	plankton	Z1-Z2	partially complete	Sandifer (1973b) as <i>Callianassa atlantica?</i>
<i>Glypturus armatus</i> (A. Milne-Edwards, 1870)	South Pacific, Indian Ocean, Red Sea	♀, lab-reared	P, Z1	incomplete	Vaugelas et al. (1986) as <i>Callincherus armatus</i> ; Setidji (1995) as <i>Callincherus laurae</i>
<i>Lepidophthalmus louisianensis</i> (Schmitt, 1935b)	West Atlantic (Gulf of Mexico)	♀, lab-reared	Z1-Z2, D	complete	Nates et al. (1997)
<i>Lepidophthalmus sinuensis</i> Lemaitre and Rodrigues, 1991	Caribbean Sea	♀, lab-reared	Z1-Z2, D	complete	Nates et al. (1997)
<i>Lepidophthalmus sirihoa</i> Felder and Rodrigues, 1993	Southwest Atlantic	♀, lab-reared	Z1-Z3, D	complete	Abrunhosa et al. (2005)
<i>Neotrypaea biffari</i> †† (Holthuis, 1991)	East Pacific	plankton	Z1	partially complete	Lebour (1938) as <i>Callianassa affinis</i>
<i>Neotrypaea uncinata</i> (H. Milne Edwards, 1837) ††	Southeast Pacific	♀, lab-reared	P, Z1-Z5	partially complete	Aste and Retamal (1984) as <i>Callianassa uncinata</i>
<i>Nihonotrypaea ?harmandi</i> (Bouvier, 1901) †††	West Pacific	♀, lab-reared	Z1-Z5, D	complete	Konishi et al. (1999) as <i>Callianassa</i> sp. Note: assignment to <i>N. harmandi</i> based on Manning and Tamaki (1998) information
<i>Nihonotrypaea japonica</i> (Ortmann, 1891) †††	West Pacific	♀, lab-reared; plankton	Z1-Z5, D	complete	Miyazaki (1937); Kurata (1965) as <i>Callianassa japonica</i> or <i>C. subterranea japonica</i> ; Miyabe et al. (1998)
<i>Nihonotrypaea petalura</i> (Stimpson, 1860) †††	West Pacific	♀, lab-reared	Z1-Z6, D	complete	Konishi et al. (1990) as <i>Callianassa petalura</i>
<i>Pestarella candida</i> (Olivieri, 1792) †	Mediterranean	?	Z1-Z3, D	?	Dolgopolskaia (1969) as <i>Callianassa pestai</i>

Table 2. Continued.

Taxon	Distribution	Source	Stage(s)	Description	Reference(s)
<i>Pestarella tyrhena</i> (Petagna, 1792) +	East Atlantic, Mediterranean	♀, lab-reared; plankton	Z1-Z3, D	(complete, in combination)	Cano (1891) as <i>C. subterranea</i> ; Gurney (1942) as <i>C. laticauda</i> ; Heegaard (1963) as <i>C. strebbingi</i> ; Thessalou-Legaki (1990); Martin (2001); dos Santos and González-Gordillo (2004) as <i>Callianassa tyrhena</i>
<i>Sergio mirim</i> (Rodrigues, 1971) ++	Southwest Atlantic	♀, lab-reared	Z1-Z2, D	complete	Rodrigues (1984) as <i>Callichirus mirim</i>
<i>Trypaea australiensis</i> (Dana, 1852) +++	Southwestern Pacific	♀, lab-reared (Z1-Z2), plankton (Z3-Z6, D)	Z1-Z6, D	(complete)	Dakin and Colefax (1940)
Axiidea, Strahlaxiidae:					
<i>Neaxius vivesi</i> (Bouvier, 1895)	Northeast Pacific	♀, lab-reared	Z1	incomplete	Berril (1975)
<i>Strahlaxius plectrorhynchus</i> (Strahl, 1862)	West Pacific	from eggs	P	incomplete	Hale (1927) in Gurney (1938) as <i>Axius plectrorhynchus</i>
Gebiidea, Axianassidae¹:					
<i>Axianassa australis</i> Rodrigues and Shimizu 1992	Southwest Atlantic	♀, lab-reared	Z1-Z8, D	partially complete	Rodrigues and Shimizu (1992); Strasser and Felder (2005)
<i>Axianassa</i> sp.A	West Atlantic (Gulf of Mexico)	plankton	Z1-Z4, Z6 or Z7	partially complete	Ngoc-Ho (1981)
Gebiidea, Laomedidae:					
<i>Jaxea nocturna</i> Nardo, 1847	East Atlantic, Mediterranean	plankton	Z1-Z6	incomplete	Caroli (1924); Gurney (1942); Kurian (1956); Bourdillon-Casanova (1960); Barnich (1996); Martin (2001)
<i>Jaxea novaecelandiae</i> Wear and Yaldwyn, 1966	Southwest Pacific	plankton	Z1-Z6(Z7), D	(complete)	Gurney (1924); Wear and Yaldwyn (1966)
<i>Jaxea</i> sp. A	Southwest Pacific	plankton (lab-reared); plankton	Z1-Z6	incomplete	Wear (1965); Dakin and Colefax (1940)
<i>Jaxea</i> sp. B	Southwest Pacific	plankton	Z1	incomplete	Gurney (1938)
<i>Jaxea</i> sp. C	Mediterranean	plankton	Z6	incomplete	Kurian (1956); Thirirot (1974)
<i>Laomedia astacina</i> De Haan, 1849	Northwest Pacific	♀, lab-reared	Z1-Z5	partially complete	Fukuda (1982)
Laomedidae sp.	Southwest Pacific	plankton	Z3	incomplete	Gurney (1924)
Laomedidae sp.	North Indian	plankton	Z1-Z5, D	(complete?)	Menon (1933) as Upogebinae (see Ngoc-Ho, 1981)
<i>Naushonia crangonoides</i> Kingsley, 1897	Northwest Atlantic	plankton, (lab-reared); plankton	Z1-Z6(Z7), D	complete	Thompson (1903); Goy and Provenzano (1978)
<i>Naushonia portoricensis</i> (Rathbun, 1901)	West Atlantic	plankton, (lab-reared)	Z1, Z2, Z5, D, PL	incomplete	Gurney and Lebour (1939)
<i>Naushonia</i> sp. A	Northwest Pacific	plankton	Z1	partially complete	Konishi (2001)
<i>Naushonia</i> sp. B	Southwest Pacific	plankton	Z1-Z6	incomplete	Dakin and Colefax (1940)
<i>Naushonia ?perrieri</i> (Nobili, 1904)	Southwest Pacific	plankton	Z1, Z4, Z5	incomplete	Gurney (1938); as <i>Naushonia</i> sp.; Sendji (1995)
<i>Naushonia</i> sp. C?	Southwest Atlantic	plankton	Z2-Z6	partially complete	Fernandes and Bonecker (2008)
Gebiidea, Thalassinidae:					
<i>Thalassinia anomala</i> (Herbst, 1804)	North Indian	♀, lab-reared	P, Z1-Z2	incomplete	Sankolli (1967)
Gebiidea, Upogebidae:					
<i>Acutigebia danai</i> (Miers, 1876)	Southwest Pacific	plankton	Z1-Z4, D	(complete)	Gurney (1924) as <i>Upogebia danai</i>

Table 2. Continued.

Taxon	Distribution	Source	Stage(s)	Description	Reference(s)
<i>Upogebia affinis</i> (Say, 1818)	Northwest Atlantic	plankton	Z1-Z4, Z5?, D	(complete, in combination)	Sandifer (1973a); Ngoc-Ho (1981); Andryszak (1986)
<i>Upogebia darwini</i> (Miers, 1884)	West Pacific, Indian	♀, lab-reared	Z1-Z3, D	complete	Ngoc-Ho (1977)
<i>Upogebia deltaura</i> (Leach, 1815)	Northeast Atlantic, Mediterranean	plankton (lab-reared); ♀, lab-reared	Z1-Z4, D, PL	complete	Webb (1919); Heegaard (1963); Williamson (1967); Martin (2001)
<i>Upogebia edulis</i> Ngoc-Ho and Chan, 1992	Northwest Pacific	♀, lab-reared	Z1-Z2, D	complete	Shy and Chan (1996)
<i>Upogebia kempi</i> Sankolli, 1972	Northeast Indian; NW Pacific	♀, lab-reared	Z1-Z4, D, PL	complete	Shenoy (1967)
<i>Upogebia major</i> (De Haan, 1841)	Northwest Pacific	♀, lab-reared; plankton	Z1-Z3, D; Z1-Z3; Z1	complete; partially complete	Miyazaki (1937); Kurata (1965); Konishi (1989)
<i>Upogebia paraffinis</i> Williams, 1993	Southwest Atlantic	♀, lab-reared;	Z1-Z5; D	complete	Melo and Brossi-Garcia (2000)
<i>Upogebia pugeitensis</i> (Dana, 1852)	Northeast Pacific	plankton	Z1-Z3, D	incomplete	Hart (1937)
<i>Upogebia pusilla</i> (Petagna, 1792)	Northeast Atlantic, Mediterranean	♀, lab-reared; plankton	Z1-Z4, D	complete	Cano (1891) as <i>Gebia littoralis</i> ; ?Bourdillon-Casanova (1960); Heegaard (1963) as <i>U. littoralis</i> ; Dolgopolskaia (1969); Martin (2001); dos Santos and Paula (2003)
<i>Upogebia quidustiae</i> Tirmizi and Ghani, 1978	North Indian	♀, lab-reared	Z1-Z3, D	complete	Siddiqui and Tirmizi (1995)
<i>Upogebia savignyi</i> (Strahl, 1862)	Red Sea, South Africa	♀, lab-reared	Z1	(complete)	Gurney (1937)
<i>Upogebia</i> s.l. sp. A	North Indian	plankton	Last Z, D	incomplete	Menon (1940)
<i>Upogebia</i> s.l. sp. B	West Atlantic (Gulf of Mexico)	plankton	Z1-Z5	partially complete	Ngoc-Ho (1981)
<i>Upogebia</i> s.l. sp. C	West Atlantic (Gulf of Mexico)	plankton	Z2-Z5	partially complete	Ngoc-Ho (1981)
<i>Upogebia</i> s.l. sp. D	Southwest Pacific	plankton	various	incomplete	Gurney (1938); Dakin and Colefax (1940)
<i>Upogebia</i> s.l. sp. E	Red Sea	plankton	Z2, Z3	incomplete	Seridji (1995)
<i>Upogebia</i> s.l. sp. F	Mediterranean	plankton	Z4	incomplete	Williamson (1967)
<i>Upogebia stellata</i> (Montagu, 1808)	Northeast Atlantic	plankton, (lab-reared)	Z1-Z4, D, PL	(complete)	Webb (1919); Heegaard (1963); Williamson (1967); Martin (2001)

limited information on the prezoa of *Strahlaxius plectorhynchus* (Strahl, 1862) (cf. Gurney, 1938) and the first zoea of *Neaxius vivesi* (Bouvier, 1895) (cf. Berrill, 1975), from the western and northeast Pacific, respectively (Table 2).

Comparison With Other Thalassinidean Larvae

Comparisons are hampered not only by few known descriptions but also by the lack of details and missing stages for many, particularly older works, as well as the uncertainty of stage equivalency. However, a comparison of larvae of *A. serratus* with those of *A. stirhynchus*, while missing details for the latter, confirms the close relationship of these taxa: gross morphologically with very similar carapace armature and proportions, and similarly distinct telson shape and spination that is unlike in any other axiid zoeae; and in details, such as the segmentation and setal grouping of the maxilla endopod. The primary distinction between the two species is the presence of additional spines dorsally and more developed ventrolateral spines in *A. serratus* compared to the already well armed pleon of *A. stirhynchus*. In the Pacific, the presumed *Axius* sp. A and B of Kurata (1960) are distinct from the two Atlantic species, such as in the greater number of zoeal stages and telson shape and spination, but do share a similarly armed rostrum, strong carapace antennal spine, paired large and small spines on the basis of the antenna, and pleonal spination to warrant close affiliation.

As for a comparison with other Axiidae, Gurney (1942: 242) considered his Group I larvae from the SW Pacific (Gurney, 1938), "in all probability belonging to the Axiidae," to be characterized by a long, flat and armed rostrum; usually antenna 2 basis with very large spine, in addition to a smaller spine; and an outer plumose seta near the base of the antennal 'scale' (actually no seta in 1/3 of cases); maxillule with 2-3 segmented palp, maxilla 3-segmented palp; pereopod 5 with exopod, epipods on all pereopods; pleomeres with "relatively small dorsal spines" and, usually, pointed pleura; telson with large median spine, in late stages parallel-sided and with 3-4 lateral spines. *Axius serratus* shares a number of these character states but not a flat rostrum or outer plumose scale seta, has a different maxillule and maxilla endopod segmentation, and a telson of different shape armed with a single lateral spine. While not sharing all the same distinctions with *A. serratus*, *A. stirhynchus* shares the same distinct endopod segmentation and telson spination.

Gurney (1942) summarized knowledge on larvae of *Calocaris macandreae*. While having exopods on all pereopods, that Gurney considered an important unifying character, these larvae differ markedly from other Axiidae, such as in carapace and pleonal spination. Based on adult characteristics *Calocaris macandreae* was moved to Calocarididae, a family resurrected by Kensley (1989) based on hermaphroditism, eye reduction, and second pleopods having enlarged appendices masculinae along with loss of the distal endopod. However, this view has been abandoned in the light of molecular evidence, with Eiconaxiidae and Calocarididae remerged into Axiidae (Tsang et al., 2008a; Robles et al., 2009). The subsequent description of a

presumed second zoea of *Calocarides coronatus* is in many respects very similar to the zoeae of *Calocaris macandreae*, as noted by Elofsson (1959), and if of correct parentage, might justify removal to Calocarididae, as for *Calocaris macandreae*. Differences between these larvae do not seem to warrant assignment to different families from a zoeal perspective but are distinctive from other known Axiidae, corroborating the molecular evidence. That said, larvae of known parentage with more detailed descriptions are necessary to further investigate such matters.

The first zoea of *Axiopsis serratifrons*, as noted by Rodrigues (1994), also differs widely from other axiids, including those of *Axius* and Gurney's presumed Axiidae larvae, having a telson similar to "Species A" assigned to a "axiid-callianassid" group by Lebour (1941). The remaining axiid larvae include those tentatively attributed to *Eutrichocheles* (see Rodrigues, 1994), listed among the Group I larvae of Gurney (1938), while those of *Eiconaxius*, now considered within Axiidae (Robles et al., 2009) morphologically differ in poor pleonal spination (Gurney, 1924; Wear, 1965).

As for larvae of other taxa now considered outside Axiidae but within Axiidea, there is very limited evidence for Strahlaxiidae (Table 2), based on the prezoa of *Strahlaxius plectorhynchus* and the figured but undescribed first zoea of *Neaxius vivesi*. The latter indicates a lack of pleonal spination and a deeply cleft telson without a median spine, a combination of character states that set it apart from any known larvae of Axiidae.

In summary, among axiidean larvae, those of *A. serratus* most closely resemble larvae of *A. stirhynchus* from the eastern Atlantic, validating the deduced *A. serratus* parentage and same generic status of these two species from a larval perspective. However, overall knowledge on axiid larvae, when compared to other families such as Upogebiidae and Callianassidae (Table 2), is at present too scant in species coverage, morphological details, and certainty of parentage to deduce clear morphological patterns. While the most recent advances in phylogenetic studies of thalassinideans (Tsang et al., 2008a; Felder and Robles, 2009; Robles et al., 2009) concluded that this group is paraphyletic, none of these studies used morphology of adults or larvae as evidence. Given the diversity of characters and character states among thalassinidean larvae and adults, the inclusion of morphological data with certain parentage and detailed descriptions would be very useful but has not been undertaken to date.

Konishi (1989) attempted a family characterization of thalassinidean larvae based on zoeal stages, for Axiidae, Callianassidae, Laomediidae, Upogebiidae, and Thalassinidae. This has brought to light useful information in characterizing some families, such as Laomediidae with asymmetrical mandibles and Upogebiidae with unsegmented antennule protopod. However, for Axiidae, a number of characters listed have states other than ones listed, when considering larvae described since, such as those of *Axius serratus*, *Axiopsis serratifrons*, e.g., maxillule and maxilla endopod segmentation, and for some larvae known at the time, e.g., *Calocarides coronatus*, maxilliped 3 endopod segmentation. Thus, while this comparison is informative,

and has shown the potential importance, difficulties in characterizing Axiidae persist.

Comparison With Larvae of *Homarus americanus*

As members of separate infraorders, Gebiidea and Axiidea are not considered to be phylogenetically close relatives of Astacidea (formerly Nephropoidea), that includes the sympatric American lobster, *H. americanus*. Yet, some thalassinidean larvae share considerable morphological similarities with those of astacideans, such as *Homarus* Weber, 1795 (Hadley, 1906; Herrick, 1909; Factor, 1995). It has been long recognized that larvae of thalassinideans can be separated into two distinct types, those of Upogebiidae and Laomedidae resembling larvae of Anomura, while larvae of Callianassidae and Axiidae, constitute a “homarine group” that is considerably more like those of Astacidea (Gurney, 1938, 1942; Kurata, 1965). As pointed out by Robles et al. (2009) this larval grouping supports the new molecular-based phylogenetic hypothesis of two separate infraorders, where Upogebiidae and Laomedidae, together with Thalassinidae, now constitute Gebiidea, with Callianassidae and Axiidae members of Axiidea, as originally suggested by de Saint Laurent (1979) based on zoeal morphology. Larvae of typical Axiidae in particular, unlike most other thalassinidean larvae, share well-developed pleonal spines with zoeae of *Homarus*. However, it is the triangular telson of *Axius*, with its distinct median and lateral spines, that is particularly similar to that of *Homarus*. Within *Axius*, ventrolateral spines in *A. serratus* are more developed than in *A. stirhynchus*, resulting in even greater resemblance of the former to zoeae of *H. americanus*.

The primary characteristic used to separate larvae of astacidean lobsters from those of thalassinideans is whether, respectively, pereopod 3 is chelate or not (Williamson, 1957). Given that wild-caught larvae are frequently damaged, including missing appendages such as pereopods, this primary differentiating criterion may not always be useable, and, with no other similar larvae known from the Bay of Fundy area, this can, and in some cases has led to the initial confusion of larvae of *A. serratus* with those of *H. americanus*. Morphometrically the first and second zoeal stages of *H. americanus* and *A. serratus* are also similar. With average carapace lengths of 1.74 and 2.62 mm, and total lengths of 2.64 (7.50-8.03) and 9.2 (8.3-10.2) mm, respectively (Factor, 1995), small larvae of *H. americanus* overlap or approximate those of larger individuals of *A. serratus* (Table 1). With an additional third zoeal stage, missing in *A. serratus*, the decapodid or postlarval stage of *H. americanus*, with a mean carapace and total length of 3.75 of 12.6 (11-14) mm, respectively, is about twice the size *A. serratus*. With morphological details apparently not available for the decapodid of *H. americanus*, a detailed comparison with that stage was not undertaken here.

For zoeal stages, a closer examination of thoracic appendages reveals differences other than the presence or absence of a chela on the third pereopod: In *A. serratus*, the antennal carapace spine is relatively longer, in contrast to *H. americanus*, reaching beyond the eye and the base of

the antennal scale; the exopods of *H. americanus* bear natatory setae along most of the margin, while being restricted to the apex in *A. serratus*; the latter has all three maxillipeds with exopods longer than endopods, the opposite being the case in *H. americanus*; the pleon of the zoeae of *H. americanus* has a single mid-dorsal spine and no dorsolateral spines on all but the first and last somites, compared to a rounded mid-dorsal process and a pair of dorsolateral spines in *A. serratus*; the first somite of *H. americanus* is naked and partially obscured by the carapace, while that of *A. serratus* is more exposed and bears a ventrolateral spine; the zoeae of *H. americanus* bear no more than a single ventrolateral spine, while somites 4–5 in *A. serratus* bear two such spines on each side; dorsolaterally on somite 5, *A. serratus* bears two pairs of spines compared to the single pair in *H. americanus*.

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