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Larval development of *Apiomithrax violaceus* (A. Milne Edwards, 1868) (Decapoda: Brachyura: Majoidea: Pisidae) reared in laboratory conditions, and a review of larval characters of Pisidae

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Apiomithrax violaceus (A. Milne Edwards, 1868) is a pisid majoid crab occurring in tropical and subtropical coastal waters of the eastern and western South Atlantic. Larval development consists of two zoeal stages and a megalopa. Beginning with the first zoea, the duration of each larval stage at 24°C was 3–8 (5 ± 1), 3–5 (4 ± 0.5) and 9–15 (11 ± 2) days, the megalopa and first crab instar appearing 9–11 (10 ± 1) and 20–27 (23 ± 2) days after hatching, respectively. Larval characters agree with those proposed for the Majoidea, in having nine or more setae on the scaphognathite in the first zoea and well-developed pleopods in the second zoea. However, larvae of *A. violaceus* do not fit larval pisid features. Zoeal stages differ from most other Pisidae in having lateral spines, a long rostral spine extending beyond the antenna, two spines per telson fork and a dorsolateral process on the third abdominal somite. The megalopa differs in having a spine dorsally on the carapace and on the basial segment of the second pereiopod. Two characters that are potentially unique to *Apiomithrax* include a zoeal antenna with an exopod that is much longer than the protopod, and a rostral spine that is longer than the dorsal spine. These characters should facilitate the identification of this taxon and could also be useful for phylogenetic studies. A review of larvae of 28 species among 14 genera indicated that there is no apparent single larval character that differentiates the Pisidae, with more limited phylogenetic analyses suggesting that this is a paraphyletic group. *Apiomithrax*, *Eurynolambrus*, *Pisoides*, *Rochinia* and *Scyra* have the most divergent morphological characters within the family. The analysis and inclusion of additional taxa is likely to shed more light on the sister-group relationships of the Pisidae. However, based on the extent of morphological interspecific variability of known larvae it is likely that the group, as presently defined by adult morphology, is not monophyletic.

KEYWORDS: Larval development, systematics, Majoidea, Pisidae, *Apiomithrax violaceus.*

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Introduction

Among the 45 genera of Majoidea (*sensu* Martin and Davis, 2001) from Brazilian waters (Pohle *et al.*, 1999), the family Pisidae Dana, 1851 is represented by 11 genera (Melo, 1996). This includes the genus *Apiomithrax* Rathbun, 1897, comprised of two South Atlantic species (Manning and Holthuis, 1981), of which only *A. violaceus* (A. Milne Edwards, 1868) occurs in south-western waters. In that area this species is apparently restricted to Brazilian waters, ranging from the states of Paraiba to Rio Grande do Sul. However, *A. violaceus* also occurs in the Eastern Atlantic from Cape Verde and Cape Branco Islands to Angola, and at Ascension Island in the Central Atlantic. *Apiomithrax violaceus* is generally found on muddy or sandy bottoms, in shallow water to 50 m deep (Melo, 1996).

The family Pisidae contains the largest number of genera and species of any of the Majoidea families (Griffin and Tranter, 1986). However, larval information is available only for 13 genera (table 1), with descriptions of three species among two genera applying to Brazilian waters. This comprises *Libidoclaea granaria* H. Milne Edwards and Lucas, 1843, *Libinia ferreirae* Brito Capello, 1871 and *L. spinosa* H. Milne Edwards, 1834. Larval pisid descriptions are not only pertinent for identification purposes but also for phylogenetic analysis in view of the fact that there is presently no support for the monophyly of this 'problematic' family (Pohle and Marques, 2000; Marques and Pohle, 2003). The purpose of the present paper is to present a detailed description of all larval stages of *Apiomithrax violaceus* and to compare them to those of other Pisidae in particular and majoids in general.

Materials and methods

Specimens of *Apiomithrax violaceus* were collected in February 2001 at a depth of 45 m in the Bay of Ubatuba of São Paulo State (44°43′N, 23°32′W), Brazil. Specimens were held in an aquarium until hatching, in a temperature-controlled room (24 ± 2°C, close to natural heat conditions), which occurred at night. After hatching, 50 of the most active, positively phototactic larvae were separated into 100-ml acrylic jars containing 50 ml of filtered seawater. The remaining larvae were raised in mass culture for use as specimens in morphological description.

Newly hatched larvae were fed *ad libitum* with *Artemia* nauplii. Seawater was changed, and specimens were inspected and fed daily. All acrylic ware was washed in fresh water and air-dried before re-use with fresh seawater the following day. Average salinity was 32‰. Natural photoperiod was maintained ($\cong$14 light:10 dark).

Whenever possible, a minimum of 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. 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.* (1998a) were generally followed. Taxonomic rankings follow Martin and Davis (2001) in which majid subfamilies were raised to the family level within the Majoidea.

Specimens of larval stages and a spent female crab have been deposited at the Museu de Zoologia da Universidade de São Paulo, MZUSP, São Paulo, Brazil, accession number MZUSP # 15849.

Table 1. Species of the Pisidae with known larval descriptions, indicating source and stages described.

Species	Authors	Stages described
Doclea gracilipes	Chhapgar, 1956; Krishnan and Kannupandi, 1988	M, C1; Z1, Z2, M
D. hybrida	Sankolli and Shenoy, 1975	Z1, Z2, M
D. ovis	Mohan and Kannupandi, 1985	Z1, Z2, M
D. muricata	Krishnan and Kannupandi, 1987	Z1, Z2, M
Eurynolambrus australis	Webber and Wear, 1981	Z1, Z2, M
Eurynome aspera	Kinahan, 1858; Kinahan, 1860; Gurney, 1924; Lebour, 1928; Bourdillon-Casanova, 1960; Salman, 1982; Wear and Fielder, 1985	PZ; Z1; PZ, Z1; Z1, Z2, M; M; Z1, Z2, M; Z2, M
E. spinosa	Salman, 1982; Hong, 1988	Z1; Z1, Z2, M
Herbstia condyliata†	Cano, 1893; Bourdillon-Casanova, 1960	Z2, M; Z1
Hyastenus diacanthus†	Kurata, 1969	Z1, M
H. elongatus†	Terada, 1983; Ko, 1997	Z1, Z2; Z1
Libidoclaea granaria	Fagetti, 1969a	Z1, Z2, M
Libinia dubia	Sandifer and van Engel, 1971	Z1, Z2, M
L. emarginata	Johns and Lang, 1977	Z1, Z2, M
L. erinacea†	Yang, 1967	Z1, Z2, M
L. ferreirae	de Bakker *et al.*, 1990	Z1, Z2, M
L. setosa†	Rathbun, 1923	M
L. spinosa	Boschi and Scelzo, 1968; Clark *et al.*, 1998b	Z1, Z2, M; Z1, Z2, M, C1
Lissa chiragra†	Cano, 1893 (*Lissa* sp.); Boraschi, 1921; Bourdillon-Casanova, 1960; Heegaard, 1963; Guerao *et al.*, 2003	Z1, Z2, M; Z1; Z1; Z1; Z1, Z2, M, C1
Naxioides histrix†	Kurata, 1969	Z1
N. serpulifera†	Rathbun, 1914	(direct development) C1, C2

Table 1. (*Continued*).

Species	Authors	Stages described
Pisa armata	Heegaard, 1963; Ingle and Clark, 1980	Z1; Z1, Z2, M, C1
P. corallina†	Gourret, 1884	Z1
P. nodipes†	Heegaard, 1963	Z1
P. tetraodon	Heegaard, 1963; Rodríguez, 1997	Z1; Z1, Z2, M, C1
Pisoides edwardsi	Fagetti, 1969b	Z1, Z2, M
P. ortmanni†	Kurata, 1969; Terada, 1983	Z1, M; Z1, Z2
Rochinia carpenteri	Ingle, 1979	Z1, Z2, M
Scyra compressipes	Kim and Hong, 1999	Z1, Z2, M

†Not included in comparison; PZ, prezoea; Z1, zoea 1; Z2, zoea 2; M, megalopa; C1, first crab instar).

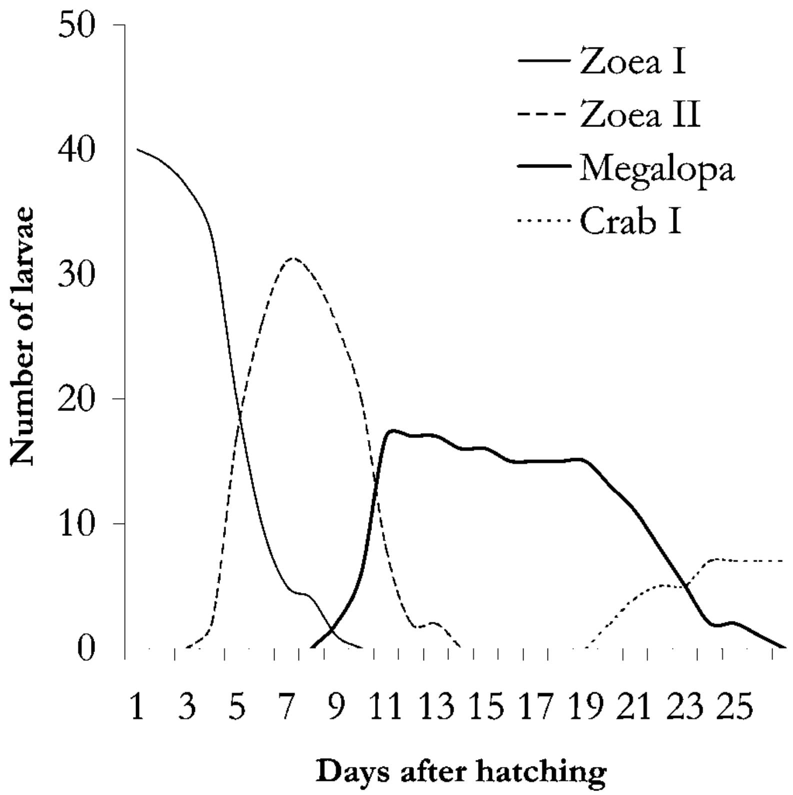

FIG. 1. Rearing record of larval stages and first crab instar of *Apiomithrax violaceus* (A. Milne Edwards, 1868).

Results

Larval development and description

Larval development of *Apiomithrax violaceus* consists of two zoeal stages and one megalopa. Figure 1 shows the rearing record for the three stages cultured at 24 ± 2°C. The duration of each larval stage was 3–8 (5 ± 1), 3–5 (4 ± 0.5) and 9–15 (11 ± 2) days, the megalopa and first crab instar appearing 9–11 (10 ± 1) and 20–27 (23 ± 2) days after hatching, respectively. Larval morphometrics are given in table 2. Only morphological changes are described for the second zoea.

Apiomithrax violaceus (A. Milne Edwards, 1868)

First zoea (figure 2)

Carapace (figure 2A). With long slightly curved dorsal and rostral spines, latter extending beyond antennule, and short straight lateral spines; ventral margin with densely plumose 'anterior seta' (Clark *et al*., 1998a) posterior to scaphognathite notch, followed by four sparsely plumose setae, and optional plumodenticulate seta. Eyes sessile, with small papilla on peduncle. Frontal area between dorsal and rostral spine possesses a small protuberance with dorsal organ (*sensu* Martin and Laverack, 1992). Additional small knob with dorsal

Table 2. Dimensions (mm) of larval structures of *Apiomithrax violaceus* (A. Milne Edwards, 1868).

Stage	Rostral spine length	Dorsal spine length	Lateral spine length	Carapace length	Carapace width	Antenna length
Zoea 1	0.54 SD 0.008 (0.54–0.56)	0.52 SD 0.02 (0.48–0.54)	0.16 SD 0.02 (0.14–0.18)	0.74 SD 0.02 (0.72–0.78)	0.53 SD 0.04 (0.46–0.56)	0.42 SD 0.02 (0.40–0.46)
Zoea 2	0.64 SD 0.03 (0.60–0.74)	0.56 SD 0.03 (0.52–0.60)	0.20 SD 0.03 (0.16–0.24)	0.92 SD 0.03 (0.88–0.96)	0.71 SD 0.05 (0.64–0.76)	0.42 SD 0.04 (0.36–0.46)
Megalopa	0.35 SD 0.04 (0.32–0.40)	0.31 SD 0.04 (0.28–0.36)	–	1.03 SD 0.05 (0.98–1.08)	0.90 SD 0.07 (0.84–0.98)	0.62 SD 0.05 (0.56–0.66)

Values are given as the mean and standard deviation, with range in parentheses.

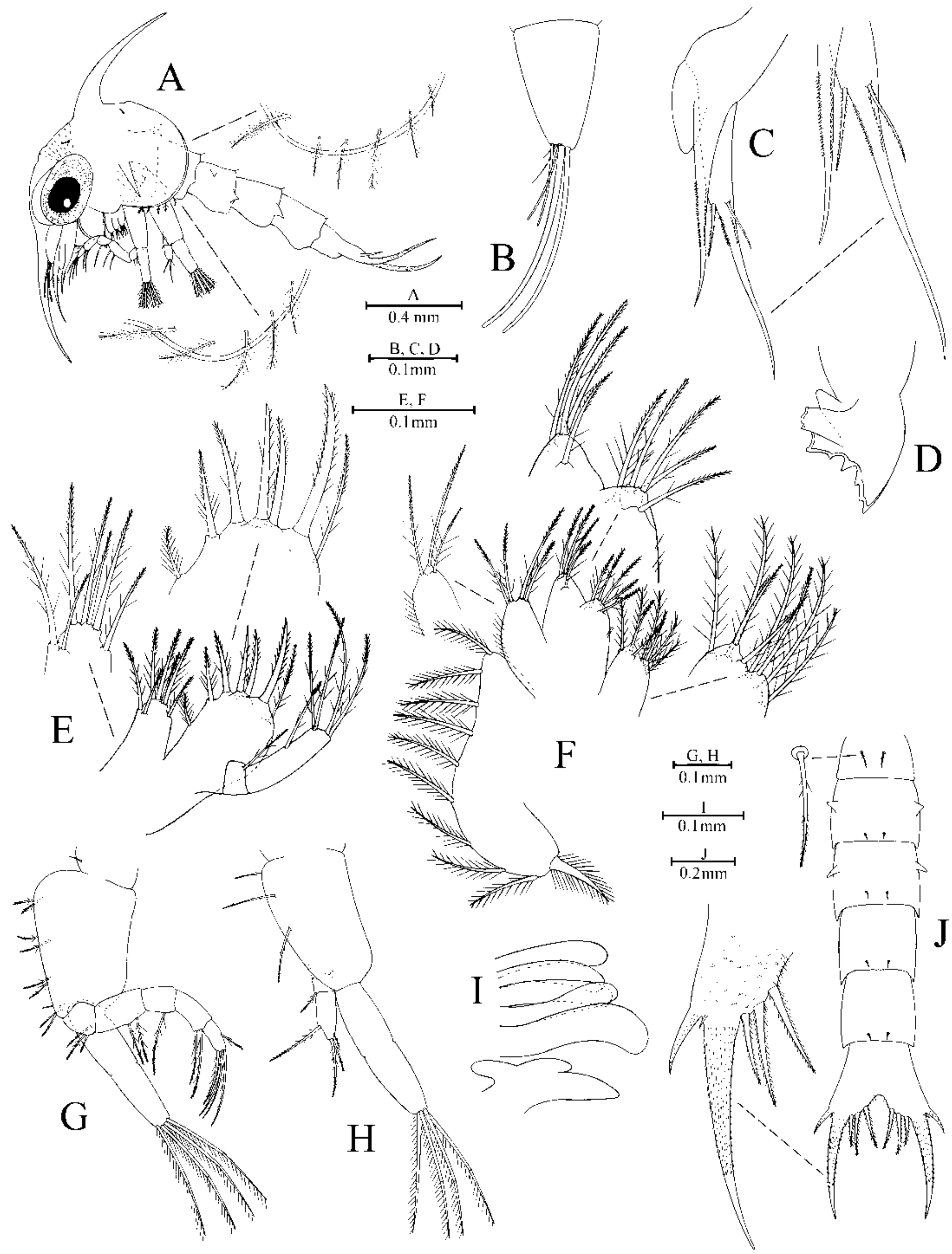

FIG. 2. First zoea of *Apiomithrax violaceus* (A. Milne Edwards, 1868). (A) Lateral view; (B) antennule; (C) antenna; (D) mandible; (E) maxillule; (F) maxilla; (G) maxilliped 1; (H) maxilliped 2; (I) developing maxilliped 3 and pereiopods; (J) dorsal view of abdomen and telson.

organ posterior to dorsal spine. Two pairs of simple setae present, one between eyes and dorsal spine, another posterior to dorsal spine.

Antennule (figure 2B). Unsegmented, smooth, conical. Terminally bearing two long aesthetascs, two shorter aesthetascs and two short setae.

Antenna (figure 2C). Biramous, protopod pointed, shorter than exopod, about half the length of rostral spine, bearing two rows of sharp spinules; endopod bud present; one-segmented exopod with pair of serrulate setae about two-thirds from tip, spinulations restricted to one-quarter of distal process beyond setae.

Mandible (figure 2D). Asymmetrical, with irregular medial toothed molar process and enlarged lateral incisor process bearing marginal teeth. Palp absent.

Maxillule (figure 2E). Coxal endite bearing seven setae, three terminal graded plumodenticulate, and subterminally four plumodenticulate setae. Basial endite with four terminal plumodenticulate cuspidate setae and three subterminal setae, two plumodenticulate and one plumose. Two-segmented endopod with proximal segment bearing plumodenticulate seta, distal segment bearing single plumodenticulate seta subterminally and two pairs of plumodenticulate setae apically. Exopod seta absent.

Maxilla (figure 2F). Coxal endite incipiently bilobed, 4+4 setae, three plumose, one plumodenticulate, and two plumodenticulate and two plumose setae, respectively. Basial endite bilobed, proximal lobe with five plumodenticulate setae and microtrichia on proximal margin, distal lobe bearing four plumodenticulate setae. Unsegmented endopod distally with three (rare) or four (common) terminal plumodenticulate setae; microtrichia on lateral margin. Scaphognathite marginally with 10 densely plumose setae, including distal process.

Maxilliped 1 (figure 2G). Coxa with developing seta. Basis with nine plumodenticulate setae arranged 2, 2, 2, 3. Endopod five-segmented with 3, 2, 1, 2 and 4+1 plumodenticulate setae. Incompletely bisegmented exopod with four terminal plumose natatory setae.

Maxilliped 2 (figure 2H). Coxa naked. Basis with three plumodenticulate setae. Endopod three-segmented; first segment naked, second with plumodenticulate seta, distal segment with four plumodenticulate setae. Incompletely bisegmented exopod with four terminal plumose natatory setae.

Maxilliped 3 (figure 2I). Present as small endo-, exo- and epipod buds.

Pereiopods (figure 2I). Present as small buds, chela enlarged.

Abdomen (figure 2A, J). Five somites. Somite 1 with pair of dorsal plumodenticulate setae, somites 2–5 each with pair of shorter simple setae. Posterolateral spines on somites 2–4 increasing in length distally; somites 2 and 3 with pair of dorsolateral processes. Pleopods absent.

Telson (figure 2J). Bifurcated, distinct median notch with microtrichia, three pairs of plumodenticulate setae on inner margin; each furcal shaft proximally bearing two lateral spines, longer spine with spinules, shorter spine naked; furcal shafts covered in rows of spinules for three-quarters length. Grouped denticulettes present.

Second zoea (figure 3)

Carapace (figure 3A). Eyes mobile. Additional pair of simple setae just above eyes. Lateral margin with additional plumose seta.

Antennule (figure 3B). With eight long aesthetascs and two simple setae, one shorter than other; endopod bud present.

Antenna (figure 3C). Endopod bud enlarged to middle of protopodite.

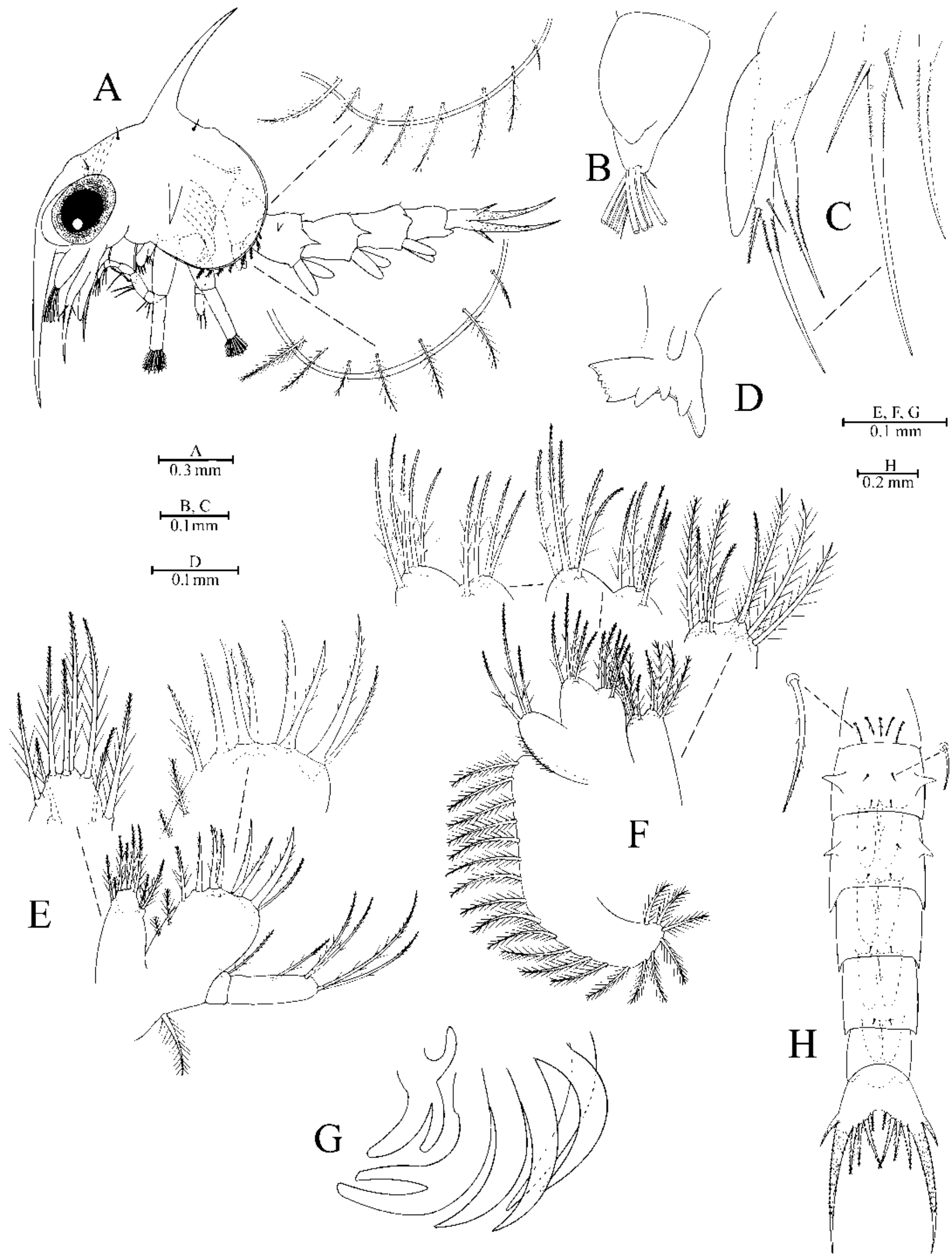

FIG. 3. Second zoea of *Apiomithrax violaceus* (A. Milne Edwards, 1868). (A) Lateral view; (B) antennule; (C) antenna; (D) mandible; (E) maxillule; (F) maxilla; (G) developing maxilliped 3 and pereiopods; (H) dorsal view of abdominal somites 1–6, showing ventral pleopods as stippling.

Mandible (figure 3D). With palp bud.

Maxillule (figure 3E). Coxal endite with an additional plumodenticulate seta subterminally; basial endite additionally with two terminal plumodenticulate cuspidate setae and subterminal plumose seta; exopod plumose seta present.

Maxilla (figure 3F). Proximal basial lobe with four to five plumodenticulate setae, distal basial lobe bearing additional plumodenticulate seta. Scaphognathite with 20 marginal plumose setae.

Maxilliped 1 (figure 3A). Exopod with six plumose natatory setae.

Maxilliped 2 (figure 3A). Exopod with six plumose natatory setae.

Maxilliped 3 (figure 3G). Endo-, exo- and epipod buds enlarged.

Pereiopods (figure 3G). Longer, segmentation not apparent, chela distinct.

Abdomen (figure 3A, H). Additional sixth somite. Somite 1 with five dorsal plumodenticulate setae. Additional pair of mid-dorsal simple setae on somites 2 and 3. Somites 2–5 with pair of unsegmented biramous pleopods, endopods distinct.

Megalopa (figures 4, 5)

Carapace (figure 4A, B). Sub-rectangular, bearing conspicuous straight rostral spine, recurved dorsal spine present, lateral spines absent; mediolateral lobes anterior to central elevations, sloping anteroventrally; flanked by lateral ridges; ventrolateral expansion posterior to eyes. Surface covered with simple setae as shown, posterolateral margin with few plumodenticulate setae.

Antennule (figure 4C). Three-segmented peduncle with one seta on proximal, two setae on middle and single seta on distal segment, all simple type; unsegmented endopod with one subterminal and two terminal simple setae; three-segmented exopod with naked proximal segment, simple seta and 10 aesthetascs on middle segment, and distal segment with four subterminal aesthetascs and aesthetasc-like seta.

Antenna (figure 4D). Segments 1–7, progressing proximally to distally, each with 1, 2, 3, 0, 0, 4, 3 simple setae, respectively; all terminal setae long.

Mandible (figure 4E). Scoop-shaped process with cutting edge and two-segmented palp bearing five to six apical plumodenticulate setae.

Maxillule (figure 4F). Coxal endite with 10–11 apical plumodenticulate setae and basal seta; basial endite with 16 plumodenticulate apical setae and three subterminal plumose setae; exopod seta plumodenticulate; unsegmented endopod with two simple setae.

Maxilla (figure 4G). Coxal endite incipient proximal and distal lobes with five (four plumose, one plumodenticulate) and three (two plumose, one plumodenticulate) setae, respectively; basial endite with five to six plumodenticulate setae each on proximal lobe and distal lobe, latter with additional subterminal seta; endopod unsegmented, naked, marginal microtrichia present; scaphognathite with 37–40 marginal plumose setae, blade with three simple setae.

Maxilliped 1 (figure 5A). Coxa with six to eight plumodenticulate setae; basis bearing 12–14 plumodenticulate setae; endopod unsegmented, bearing optional subterminal simple seta; exopod with pappose or plumose seta distally on proximal segment and four plumose setae on distal segment; epipod with seven plumodenticulate setae.

Maxilliped 2 (figure 5B). Coxa and basis not clearly differentiated; four endopod segments proximally to distally with 0, 1, 2–3 and 5–6 plumodenticulate setae, respectively; exopod with naked proximal segment and four plumose setae on distal segment; epipod not present on examined specimens.

Maxilliped 3 (figure 5C). Coxa with six to seven plumodenticulate setae; endopod proximally to distally with 13, 9 or 11, 4–5, 7 and 4 mostly plumodenticulate

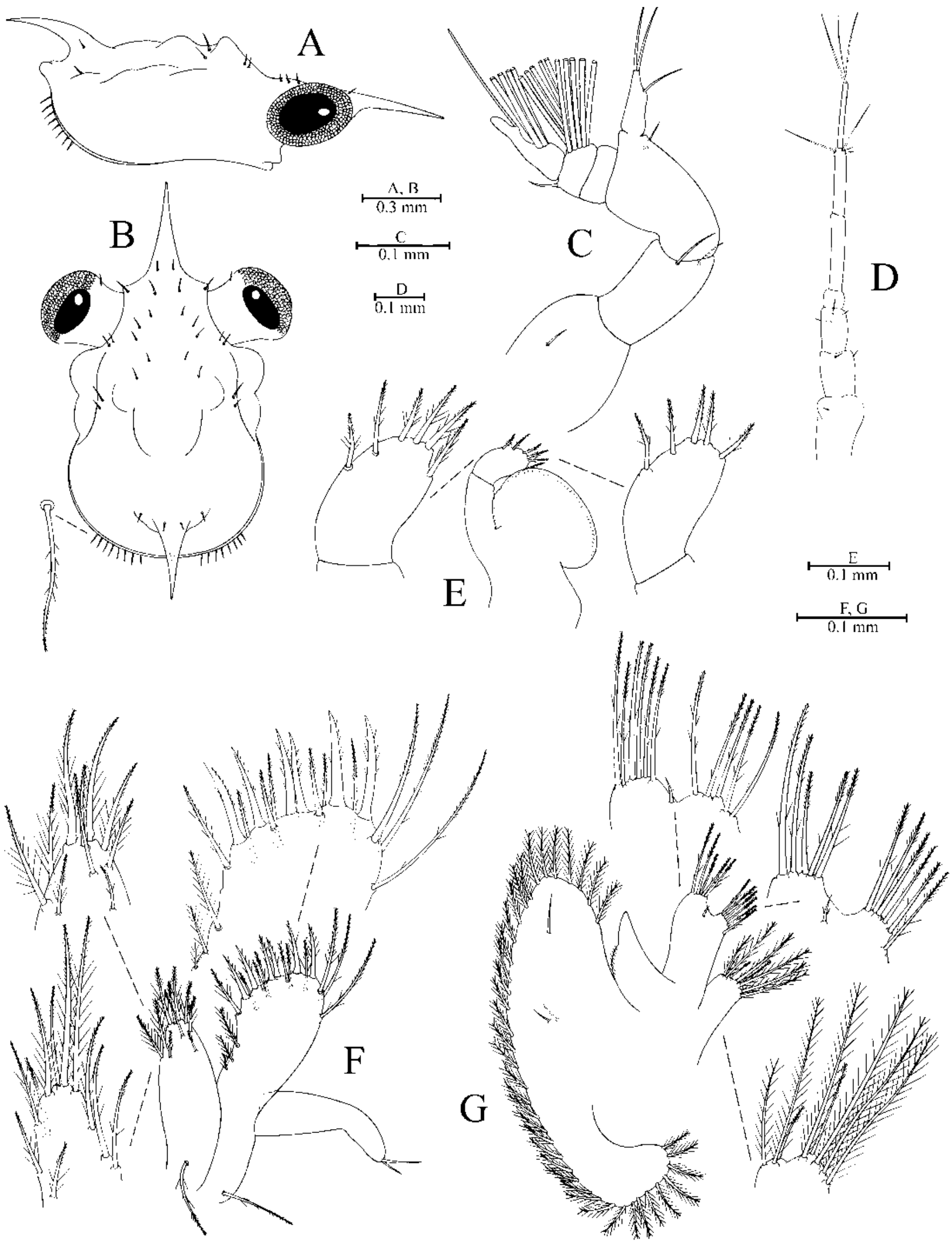

FIG. 4. Megalopa of *Apiomithrax violaceus* (A. Milne Edwards, 1868). (A) Lateral view; (B) dorsal view, (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla.

setae; basischium with undeveloped crista dentata; bisegmented exopod with naked proximal segment and four to five reduced plumose setae apically on distal segment; epipod with two plumodenticulate setae proximally, five distally.

Pereiopods (figure 5D, E). Covered with mostly simple setae; dactyl of pereiopods 2–5 with spinules as shown and 4, 4, 3, 3 serrate setae, respectively; propodus

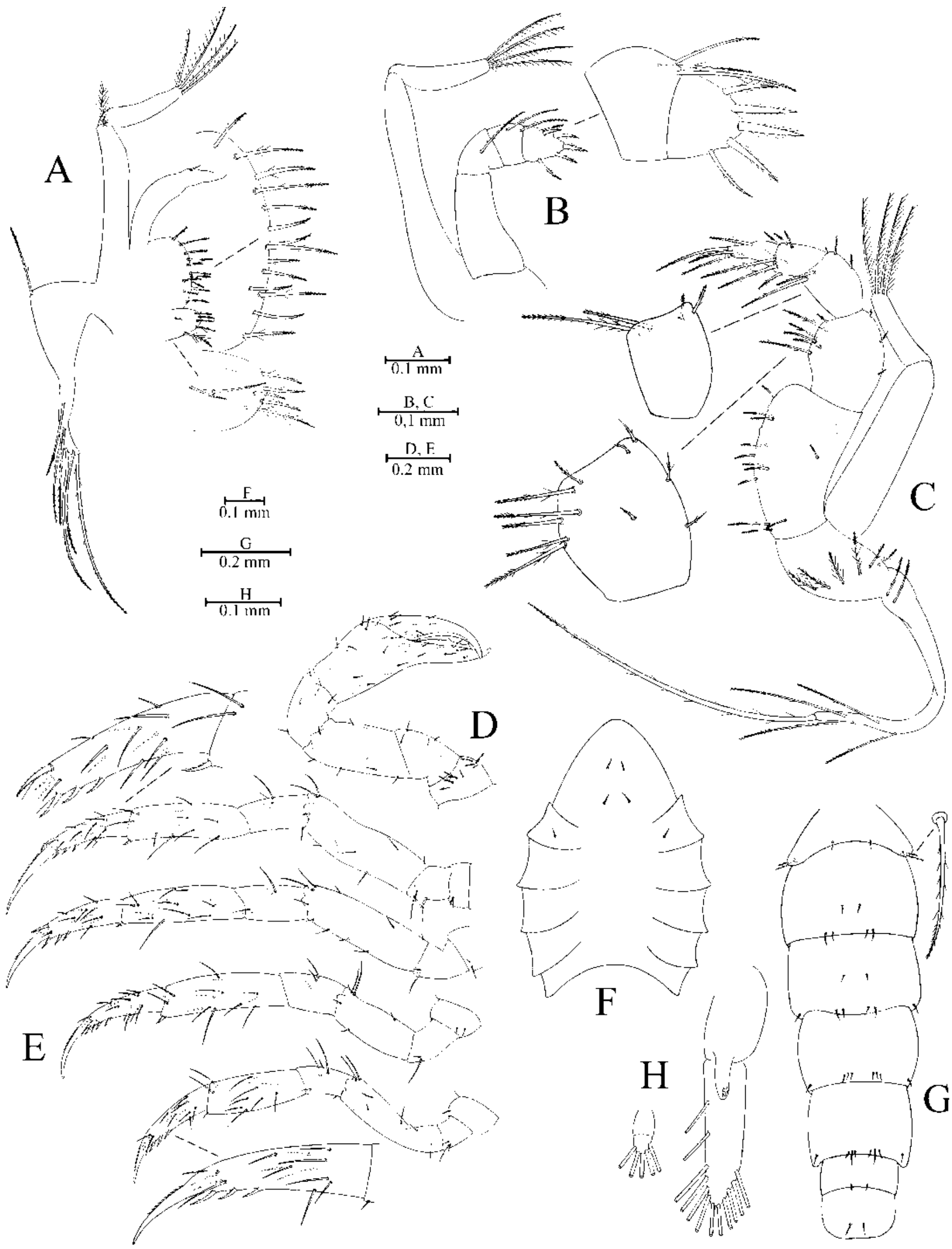

FIG. 5. Megalopa of *Apiomithrax violaceus* (A. Milne Edwards, 1868). (A) Maxilliped 1; (B) maxilliped 2; (C) maxilliped 3; (D) cheliped; (E) pereiopods; (F) sternum; (G) dorsal view of abdomen and telson; (H) first and fifth pleopods.

of pereiopods 2–4 with serrate setae; coxa of pereiopod 2 with spine, coxa of cheliped with plumodenticulate setae.

Sternum (figure 5F). Projecting anteriorly, with three pairs of simple setae as illustrated.

Abdomen (figure 5G, H). Posterolateral margins of all somites rounded, proximally to distally with 6, 6, 8, 8, 8 and 2 setae, all simple except for two pairs of lateral plumodenticulate setae on first somite; exopod of pleopods 1–5 on somites 2–6 with 11–12, 11–12, 11, 9 and 5 plumose setae, respectively; endopod of pleopods 1–4 with three cincinnuli each, pleopod 5, i.e. uropod, lacking endopod.

Telson (figure 5G). Rounded posteriorly, bearing pair of simple dorsal setae.

Discussion

Identification and larval affinities of Apiomithrax violaceus

The larval characters of *Apiomithrax violaceus* agree with those proposed by Rice (1980, 1983) for the Majoidea (cf. Martin and Davis, 2001), in having nine or more setae on the scaphognathite in the first zoea and well-developed pleopods in the second zoea. However, the larval characters of Pisidae, defined by Ingle (1979) based on the genera *Eurynome*, *Herbstia*, *Hyastenus*, *Libidoclaea*, *Libinia*, *Lissa*, *Naxioides*, *Pisa* and *Pisoides*, are not shared by *A. violaceus*. The zoeal stages of the latter differ from the others in having lateral spines, a long rostral spine that extends beyond the antenna, two spines per telson fork and a dorsolateral process on the third abdominal somite (latter present in *Herbstia*). In the megalopa *A. violaceus* differs in having a spine on the basial segment of the second pereiopod and a dorsal spine on the carapace (also in *Libinia spinosa*). Other pisid larvae, such as *Rochinia*, also do not fully correspond to the group definition, showing oregoniid affinities that question the pisid status of that genus (Ingle, 1979).

Apiomithrax violaceus is also morphologically distinct in comparison to other majoids. In zoeal stages the antenna is very distinct in having an exopod that is much longer than the protopod and a rostral spine that is longer than the dorsal spine (figures 2, 3). These characters should facilitate the identification of this taxon in plankton material and could also be useful for phylogenetic studies. Based on initial work by Kurata (1969) relating to the armature of the antennal exopod, Clark and Webber (1991) postulated ancestral and derived states for majoids, an approach that was also used in a modified form in more recent phylogenetic analyses (Marques and Pohle, 1998; Pohle and Marques, 2000). However, the relative length of the antennal exopod and protopod represents an additional and apparently new character in elucidating majoid relationships. The relative size of rostral and dorsal spines has a similar potential.

Zoeal stages of *A. violaceus* are also easily distinguishable from other Pisidae in having a rostral spine that is longer than the dorsal spine, a dorsolateral process on the second and third abdominal somites, and by the five setae on the first abdominal somite in the second zoeal stage (tables 3, 4). However, the last two characters are also found among other majoids. The paired dorsolateral process on the second and third abdominal somites is present in oregoniids (Pohle, 1991), some inachids (Yang, 1976; Paula and Cartaxana, 1991), the epialtid *Taliepus* (Fagetti and Campodonico, 1971) and in *Macrocheira* (Clark and Webber, 1991). The latter also has five setae on the first abdominal somite. In addition, *A. violaceus* shares the presence of lateral carapace spines with oregoniids, some inachids and *Macrocheira*, and some majids (Pohle and Marques, 2000). Other characters shared with oregoniids include two lateral spines on the telson fork and four pairs of telson setae in the second zoea.

The megalopa of *Apiomithrax violaceus* has a distinct set of characters that

Table 3. Comparison of larval characters of the first zoeal stage for Pisidae genera.

Zoea 1	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
Carapace	RS: long; (RS > DS); LS present; 5–6 s ventral margin	RS: short or absent; LS absent; 5–8 s ventral margin	RS: intermediate; LS absent; 7 s ventral margin	RS: intermediate; LS absent; 4 s ventral margin	RS: long; (RS < DS); LS absent; 6 s ventral margin	RS: short; LS absent; 6–8 s ventral margin	RS: short; LS absent; 6–7 s ventral margin	RS: short; LS absent; 6–7 s ventral margin	RS: long (RS < DS); LS present; $4^{\dagger}$ s ventral margin	RS: intermediate; LS absent; 6 s ventral margin
Antennule	4 aes, 2 s	4 aes, 0–2 s	4 aes, 2 s	4 aes, 1–2 s	3 aes, 2 s	2–4 aes, 1–2 s	4–6 aes, 0 or 2 s	4 aes, 2 s	2 aes, 1 s	5 aes, $1^{\dagger}$ s
Antenna	exo > pro	exo ≤ pro	exo < pro	exo < pro;	exo = pro	exo ≤ $\text{pro}^{\dagger}$	exo = pro	exo ≥ pro	exo ≥ pro	exo < pro
Maxillule	cox: 7; bas: 7; end: 1, 5	cox: 7; bas: 7; end: 0–1, 6–7	cox: 7; bas: 7; end: 1, 6	cox: 7; bas: 7; end: 1, 6	cox: 7; bas: $7^{\dagger}$; end: 1, 5	cox: 7; bas: 7; end: 1, 5	cox: 7; bas: 7; end: 1, 6	cox: 8; bas: 7; end: 1, 6	cox: 7; bas: 7; end: 1, 6	cox: 7; bas: 7; end: 1, 4
Maxilla	cox: 4, 4; bas: 5, 4; end: 3–4; sca: 10	cox: 3–5, 3–5; bas: 2–5, 3–4; end: 4–5; sca: 11–16	cox: 3, 4; bas: 5, 4; end: 5; sca: 13	cox: 5, 4; bas: 4–5, 4; end: 5; sca: 9–10	cox: 4, 5; bas: 4, 5; end: 3, 3; sca: 15	cox: 4, 4; bas: 4, 4–5; end: 4–5; sca: 10–11	cox: 5–6, 4; bas: 4–5, 4; end: 5; sca: 11–13	cox: 5, 4; bas: 4, 4; end: 5; sca: 13	cox: 5, 4; bas: 5, 4; end: 6; sca: 12	cox: 4, 4; bas: 5, 4; end: 4; sca: 9–10
Mxpd 1	cox: 1; bas: 2, 2, 2, 3; end: 3, 2, 1, 2, 5	cox: $0^{\dagger}$; bas: 2, 1–2, 2, 3; end: 3–4, 2, 1–2, 2–3, 5	cox: 1; bas: 2, 2, 2, 3; end: 3, 2, 1, 2, 5	coxa 0–1; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: $0^{\dagger}$; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: 0–1; bas: 2, $2^{\dagger}$, 3, 3; end: 3, 2, 1, 2, 5	cox: $0^{\dagger}$; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: $0^{\dagger}$; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: $0^{\dagger}$; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: $0^{\dagger}$; bas: 2, 2, 2, 3; end: 3, 2, 1, 2, 5
Mxpd 2	bas: 3; end: 0, 1, 4	bas: 2–4; end: 0, 1, 3–4	bas: 3; end: 0, 1, 6	bas: 3; end: 1, 1–2, 5	bas: 3; end: 0, 1, 5	bas: 3; end: 0, 1, 4–5	bas: 3; end: 0–1, 1–2, 5 or 3	bas: 3; end: 1, 1, 4	bas: 3; end: 0, 1, 5	bas: 3; end: 0, 1, 4

Table 3. (*Continued*).

Zoea 1	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
Abdomen	S1: 2; S2–5: 2; dlp: S2–3	S1: 2–3; S2–5: 0 or 2; dlp: S2	S1: 2; S2–5: 2; dlp: S2	S1: 2; S2–5: 2; dlp: S2	S1: ?; S2–5: 2†; dlp: S2	S1: 2; S2–5: 2; dlp: S2	S1: 2; S2–5: 2; dlp: S2	S1: 2; S2–5: 2; dlp: S2	S1: 2; S2–5: 2; dlp: S2	S1: 2; S2–5: 2; dlp: S2
Telson	furca: 2 sp; spi present; 6 s	furca: 0 sp; spi absent; 6 s	furca: 3 sp; spi present; 6 s	furca: 2–4 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s

RS, rostral spine; DS, dorsal spine; LS, lateral spine; dlp, dorsolateral process; cox, coxa or coxal endite; bas, basis or basial endite; end, endopod; exo, exopod; sca, scaphognathite; epi, epipod; pro, protopod; ped, peduncle; S, somite; s, setae; aes, aesthetasc; sp, spine; spi, spinules.

†Observation from figure.

Table 4. Comparison of larval characters of second zoeal stage for Pisidae genera.

Zoea 2	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
Carapace	RS: long; (RS > DS); LS present; 7–8 s ventral margin	RS: short or absent; LS absent; 6–10 s ventral margin	RS: intermediate; LS absent; 8 s ventral margin	RS: intermediate; LS absent; 4–6 s ventral margin	RS: long; (RS < DS); LS absent; 7 s ventral margin	RS: short; LS absent; 7–10 s ventral margin	RS: short; LS absent; 7 s ventral margin	RS: short; LS absent; 11 s ventral margin	RS: long; (RS < DS); LS present	RS: intermediate; LS absent; 6 s ventral margin
Antennule	8 aes, 2 s	5–8 aes, 0–2 s	8 aes	5–7 aes, 1 s	7 aes	6 or 8 aes, 1–2 s	6 or 8 aes, 0 or 2 s	6 aes	5 aes, 1 s	8 aes, 2 s
Antenna	exo > pro	exo ≤ pro†	exo < pro	exo < pro	exo < pro†	exo ≤ pro†	exo = pro	exo > pro	exo > pro	exo = pro
Maxillule	cox: 8;	cox: 6–8;	cox: 7;	cox: 7;	cox: 7;	cox: 7–8;	cox: 7–8;	cox: 7† or 8 (text);	cox: 6–7;	cox: 7;
	bas: 10; end: 1, 5;	bas: 8–10; end: 0–1, 6–7;	bas: 9; end: 1, 6;	bas: 9†; end: 1, 6;	bas: 10†; end: 1, 5;	bas: 9–10; end: 1, 5;	bas: 8–9; end: 1, 6;	bas: 9; end: 1, 6;	bas: 10; end: 1, 6;	bas: 10; end: 1, 4;
	exo: 1	exo: 0–1	exo: 1	exo: 1	exo: 1	exo: 1	exo: 1	exo: 0†	exo: 1	exo: 1
Maxilla	cox: 4, 4;	cox: 4–6, 3–5;	cox: 3, 4;	cox: 5, 4;	cox: 4, 5;	cox: 4, 3–4;	cox: 5, 4;	cox: 4 (text) or 5†, 4†;	cox: 5, 4;	cox: 4, 4;
	bas: 4–5, 5;	bas: 4–5, 3–4;	bas: 5, 5;	bas: 5, 5;	bas: 5, 5†;	bas: 5, 4–5;	bas: 5, 4–5;	bas: 5, 4;	bas: 5, 8;	bas: 5, 5;
	end: 3–4; sca: 20	end: 4–5; sca: 25–30	end: 5; sca: 23–25	end: 5; sca: 16–19	end: 5; sca: 29	end: 5; sca: 16 or 20	end: 5; sca: 20–23	end: 5; sca: 21	end: 7; sca: 21–23	end: 4; sca: 16
Mxpd 1	cox: 1; bas: 2, 2, 2, 3; end: 3, 2, 1, 2, 5	cox: 0–1; bas: 1–2, 2, 2–3, 3; end: 2–4, 2, 1–2, 2–3, 5	cox: 1, bas: 2, 2, 2, 3; end: 3, 2, 1, 2, 5	cox: 0–1; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: 0†; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: 0–1; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: 0; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: 0†; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: 0†; bas: 2, 2, 3, 3; end: 3, 2, 1, 2, 5	cox: 0†; bas: 2, 2, 2, 3; end: 3, 2, 1, 2, 5

Table 4. (*Continued*).

Zoea 2	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
Mxpd 2	bas: 3; end: 0, 1, 4	bas: 2–6; end: 0, 1, 3–5	bas: 3; end: 0, 1, 6	bas: 3; end: 1, 1–2, 5	bas: 3; end: 0, 1, 5	bas: 3; end: 0, 1, 4–5	bas: 3; end: 0–1, 1–2, 3 or 5	bas: 3; end: 1, 1, 4	bas: 3; end: 0, 1, 5	bas: 3; end: 0, 1, 4
Abdomen	S1: 5;	S1: 3;	S1: 2;	S1: 3;	dlp: S2; S1: ?; S2–5: ?	S1: 3;	S1: 2;	S1: 4;	S1–2: 2;	S1: 2†;
	S2–3: 4;	S2–5: 0 or 2 (5 or 6 S);	S2–5: 2;	S2–5: 2;		S2–3: 4;	S2: 4;	S2: 4;	S3–4: 4;	S2–3: 4;
	S4–5: 2; dlp: S2–S3	dlp: S2	dlp: S2	dlp: S2		S4–5: 2†; dlp: S2	S3–5: 2; dlp: S2	S3–5: 2; dlp: S2	S5: 2 or 4; dlp: S2	S3–5: 2; dlp: S2
Telson	furca: 2 sp; spi present; 8 s	furca: 0 sp; spi absent; 6 s	furca: 3 sp; spi present; 8 s	furca: 2–4 sp†; spi present; 8 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s	furca: 1 sp; spi present; 6 s

See table 3 for abbreviations.

separates it from other Pisidae, consisting of a long rostral spine, presence of dorsal spine, ventrolateral carapace expansions posterior to eyes, 19 setae on basial endite of maxillule and discrete abdominal setation (table 5). Also, the setal formula of the antenna is a distinctive character that is shared only with *Libinia dubia* (Sandifer and van Engel, 1971). However, the latter, unlike *A. violaceus*, is restricted to the North Atlantic.

Comparison among Pisidae genera

A comparison of larval descriptions of the family Pisidae shows substantial differences among the genera of this group (tables 3, 4, 5). These morphological differences can be distinct, such as for *Doclea* that lacks furcal telson spines in zoeal stages, and *Pisoides*, characterized by a second maxilliped with a completely developed epipod in the megalopa (tables 3, 4, 5). This demonstrates the heterogeneity of Pisidae, the largest majoid group (Griffin and Tranter, 1986).

A more detailed generic-level comparison of described pisid larvae is complicated by fragmented or incomplete information (table 1), such as for *Herbstia condyliata* (Cano, 1893; Bourdillon-Casanova, 1960), *Libinia erinacea* (Yang, 1967), *L. setosa* (Rathbun, 1923), *Pisa nodipes* (Heegaard, 1963) and *P. ortmanni* (Kurata, 1969; Terada, 1983) that were not used in this comparison. In total, 18 species among 10 genera, for which there is information on all larval stages, were considered for the comparison (table 1). Among these taxa there may also be some lack of congruence in larval morphology. Intraspecific variation, such as for species of *Doclea*, suggests a need for re-evaluation of certain taxa because of inadequate descriptions. Thus, the results should be viewed with some caution.

Both zoeal stages of species of the following genera have distinctive features (tables 3, 4): for *Doclea* it is the setation of the basis of the second maxilliped; for *Eurynolambrus* and *Eurynome* the number of spines on the telson furca; for *Scyra* the endopod setation of the maxillule; and for *Rochinia* the endopod setation of the maxilla.

The first zoeal stage of *Libidoclaea* and *Rochinia* has a distinct number of aesthetascs. The same stage of *Pisoides* has a characteristic number of setae on the coxal endite of the maxillule and endopod of second maxilliped (table 3).

The second zoeal stage of *Doclea* is characterized by a distinct number of setae on the endopod of maxillule, and the number of somites in *Doclea gracilipes* may also be distinctive; in *Eurynolambrus* the setation of the coxal endite of the maxilla is distinct; *Pisa* and *Pisoides*, *Rochinia* and *Scyra* have a distinct abdominal setation; and *Rochinia* differs in the setation of the coxal endite of the maxillule, basial endite and endopod of maxilla (table 4).

In the megalopa, the distinctive characters are: for *Eurynolambrus* the lack of a rostral spine, segmentation and setation of the antennule, setation of the basial endite of the maxillule, coxal endite and blade of the maxilla and exopodite of third maxilliped; for *Eurynome* the setation of the exopod of the third maxilliped; for *Libidoclaea* the setation of the epipod of the first maxilliped; for *Pisoides*, segmentation of the endopod of the maxillule and the setation of the coxa of the third maxilliped; for *Rochinia*, setation of the peduncle of the antennule, antenna, endopod of maxillule and coxa of maxilla; for *Scyra*, setation of the peduncle of the antennule and coxa of maxilla. Also, the abdominal setation in each of *Eurynolambrus*, *Pisoides*, *Rochinia* and *Scyra* is different (table 5).

Table 5. Comparison of larval characters of the megalopa stage for Pisidae genera.

Megalopa	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
Carapace	RS: long;	RS: short or two-horned;	RS: absent;	RS: short;	RS: short;	RS: short or long (*L. spinosa*);	RS: short;	RS: intermediate;	RS: long;	RS: short;
	DS: present; 7–8 s	DS: absent; 0† s	DS: absent; 5† s	DS: absent; 0 s	DS: absent; 0 s	DS: present (*L. spinosa*); 6–7† or 15† s	DS: absent; 0† s	DS: absent; 5 s	DS: present; 0† s	DS: absent; 0† s
	posterior margin	posterior margin	posterior margin	posterior margin	posterior margin	posterior margin	posterior margin	posterior margin	posterior margin	posterior margin
Antennule	ped: 1, 2, 1;	ped: 0 or 4, 0, 1–2;	ped: 0, 1, 1;	ped: 0–1, 2, 0 or 2;	ped: 0, 1, 1†;	ped: 0, 1–2, 1–2;	ped: 0, 1, 1;	ped: 0, 2, 1;	ped: 0, 2, 0;	ped: 1, 1, 1;
	end: 3;	end: 2–3;	end: 3;	end: 3–4;	end: 3;	end: 3;	end: 3;	end: 3;	end: 3;	end: 2;
	exo: 10+1 s, 5 aes	exo: 0 or 5, 3–4, 2–3, 0–1 aes+1s	exo: 10+1s, 4, 1 aes	exo: 4 or 6, 3 aes	exo: 8+1s†, 4+1† aes	exo: 5–6 or 10+0−1s, 3–4 or 6+1† aes	exo: 6 or 8+1s, 4+0−1 aes	exo: 10+1s, 4+1 aes	exo: 6+1s, 4, 3, 1+1 aes	exo: 6, 5+1 aes
Antenna	seg 1–7: 1, 2, 3, 0, 0, 4, 3	seg 1–7: 0, 0 or 2, 1 or 3, 0, 0–1, 2–3, 1 or 4	seg 1–7: 0, 1, 1, 3, 0, 4, 3†	seg 1–7: 2, 1–2, 2–3, 0–1, 0, 3, 3–4	seg 1–7: 0, 2, 3, 0, 0, 4, 4	seg 1–7: 0–1, 1–2, 1–3, 0, 0, 3–4, 3–4†	seg 1–7: 0, 2, 3, 0, 0, 4, 4	seg 1–7: 0, 2, 3, 0, 0, 3, 4†	seg 1–7: 0, 2, 2, 0, 0, 3, 3	seg 1–7: 0, 2, 3, 0, 0, 3, 4
Mandible	palp 5–6	palp 4–5	palp 4	palp 6	palp 5	palp 5	palp 5	palp 4	palp 5	palp 5
Maxillule	cox: 10–11+1;	cox: 7 or 9–10;	cox: 8;	cox: 9–10;	cox: 11†;	cox: 10–11;	cox: 9–10;	cox: 10;	cox: 10;	cox: 10;
	bas: 19;	bas: 12 or 17;	bas: 11;	bas: 15–16;	bas: 18;	bas: 16–18;	bas: 17;	bas: 17;	bas: 11–12†;	bas: 15;
	end: 2;	end: 2–3 or 5;	end: 2;	end: 1–2;	end: 1;	end: 0–4†;	end: 2–3;	end: 0, 2;	end: 4;	end: 2;
	epi: 1	epi: 0	epi: 1	epi: 0	epi: 0†	epi: 0	epi: 0†	epi: 0†	epi: 0†	epi: 0

Table 5. (*Continued*).

Megalopa	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
Maxilla	cox: 5, 3;	cox: 5–7, 2 or 4 or 6–7;	cox: 5, 5;	cox: 6, 3;	cox: 7, 3;	cox: 5–6, 3;	cox: 7, 3;	cox: 5, 2;	cox: 9, 3–4;	cox: 6, 2;
	bas: 5–6, 6–7;	bas: 3 or 5 or 7, 4–5 or 7;	bas: 6, 6;	bas: 3–5, 5;	bas: 6, 6;	bas: 6–7, 5–7;	bas: 4–5, 6;	bas: 5, 6;	bas: 6, 6;	bas: 6, 7;
	end: 0; sca: 37–40, 3	end: 0; sca: 36–45, 0 or 6	end: 0; sca: 36–37, 4	end: 0; sca: 30–34, 0 or 3	end: 0; sca: 51, 0†	end: 0–2; sca: 31–36, 2	end: 0; sca: 30–32, 0† or 3	end: 0; sca: 42, 0†	end: 0; sca: 40†, 0†	end: 0; sca: 31–32, 2
Mxpd 1	cox: 6–8;	cox: 4–5 or 8;	cox + bas?: 16;	cox: 5–7;	cox: 7†;	cox: 5–7;	cox: 7–8;	cox: 7†	cox: 6;	cox: 7;
	bas: 12–14;	bas: 7 or 12–13;	end: 0;	bas: 9–11;	bas: 12†;	bas: 8–12;	bas: 11 or 16;	bas: 8†;	bas: 10;	bas: 11;
	end: 0–1;	end: 1–2 or 4;	exo: 1, 4;	end: 1;	end: 0†;	end: 0–3;	end: 0 or 4;	end: 0†;	end: 0;	end: 0;
	exo: 1, 4;	exo: 0–2, 4;	epi: 6	exo: 0†–1, 4;	exo: 1, 4†;	exo: 1, 4–6;	exo: 1, 4–5;	exo: 1, 4†;	exo: 1, 4;	exo: 0, 4;
	epi: 7	epi: 4–6		epi: 0† or 2–4	epi: 14†	epi: 3–5 or 7	epi: 5–6	epi: 6†	epi: 6	epi: 0†
Mxpd 2	end: 0, 1, 2–3, 5–6;	end: 0, 0 or 2, 0 or 3–4, 4–5 or 7;	end: 0, 1, 3, 5;	end: 0, 1, 3, 5–6;	end: 0, 1, 4, 6†;	end: 0, 1, 3, 6;	end: 0, 1, 3, 6;	cox: 5†	end: 0, 1, 4, 7;	end: 0, 1, 3, 6;
	exo: 0, 4	exo: 0, 5–6	exo: 0, 4	exo: 0, 4	exo: 0, 4†	exo: 0, 4–6	exo: 0, 4–5	end: 0, 1, 4, 6† exo: 0, 4† epi: 6†	exo: 0, 4	exo: 0, 4

Table 5. (*Continued*).

Megalopa	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
Mxpd 3	cox: 6–7;	cox: 3–4?;	cox: 9;	cox: 5–6 or 11;	cox: 8†;	cox: 6 or 8†–10;	cox: 6–7;	cox: 3†;	cox: 8†;	cox: 5;
	end: 13, 9–11, 4–5, 7, 4;	end: 0 or 9 or 12, 5–6 or 8–9, 2 or 4–5, 2–3 or 5–6, 3–5;	end: 13, 6, 4, 7, 5;	end: 12–14, 5, 1–2, 4–5, 5;	end: 12, 9, 5, 5, 4†;	end: 9–13, 7–9, 4–6, 5–6, 4;	end: 11–12, 8–9, 5–6, 6, 4;	end: 8, 4, 4, 4, 4†;	end: 13–15, 6–7, 5, 5, 4;	end: 13, 8, 5, 6, 4;
	exo: 4–5; epi: 7	exo: 4; epi: 4 or 8?	exo: 2, 4; epi: 13†	exo: 1, 4–5; epi: 5†–6	exo: 0, 5†; epi: 11†	exo: 0, 5–6; epi: 7–9†	exo: 0, 5; epi: 9–10	exo: 0†; epi: 6†	exo: 0, 6–7; epi: 5	exo: 0, 4; epi: 0†
Abdomen	S1–6: 6, 6, 8, 8, 8, 2	n/a	S1–6: 6, 10, 8, 8, 8, 2	S1–6: 6†–10, 4 or 6, 4 or 6, 4 or 6, 4 or 6, 0	S1–6: 4, 2, 2, 2, 0, 0†	S1–6: 6 or 8, 6, 6 or 8, 4 or 6 or 8, 6 or 8, 0 or 2†	S1–6: 6 or 8, 8, 6, 6, 6 or 8, 0 or 2†	S1–6: 4†, 2, 2, 2, 2, 2†	S1–6: 8, 6, 4, 4, 6, 2†	S1–6: 6, 8, 8, 8, 8, 2†

See table 3 for abbreviations. n/a, not available; seg, segment.

Taken together these differentiating characters indicate that *Apiomithrax*, *Eurynolambrus*, *Pisoides*, *Rochinia* and *Scyra* have the most divergent morphological characters within the family. Moreover, abdominal setation appears to be a good character to differentiate some genera within Pisidae. However, the apparent differences in the number of abdominal somites and mouthpart setation for *Doclea* are suspect, since these are known to vary little within a genus. Similarly suspect are, for *Eurynome spinosa*, the highly divergent number of setae on the exopod of the antenna and the lack of epipod in the first maxilliped, and for *Scyra*, the lack of epipods in the first and third maxillipeds.

Larval characters of several genera, including species of *Apiomithrax*, *Doclea* and *Rochinia*, no longer fit the proposed set of larval definitions of the Pisidae by Ingle (1979). Presently, the most homogeneous pisid characters in the first zoeal stage are the number of setae on the coxal and basial endite of the maxillule (excluding *Pisoides*) and the endopod of first maxilliped (excluding *Doclea*) (table 3). In the second zoeal stage it is the presence of the exopod seta on the maxillule (excluding Pisoides) (table 4). Morphologically, the megalopa appears more heterogeneous than zoeal stages since we found no shared characters (table 5). It is also important to realize that some of the differentiating characters for zoeal stages are present in other families and are therefore not considered distinctive among Majoidea.

Larval information in phylogenetic analysis

Larval information has been increasingly used for phylogenetic studies (Rice, 1980, 1983; Clark and Webber, 1991; Marques and Pohle, 1995, 1998; Pohle and Marques, 1998, 2000), as an alternative to adult-based or genetic studies. These efforts are presently hindered by the availability of appropriate larval descriptions. This is particularly so for the Pisidae, Clark and Webber's (1991) pioneering analysis being limited to *Pisa* and *Rochinia*, and even the most recent efforts by Marques and Pohle (2003) including only three additional genera, *Doclea*, *Libinia* and *Notolopas*.

All larval analyses presently suggest that the Pisidae is a paraphyletic group (Clark and Webber, 1991; Marques and Pohle, 1998, 2003; Pohle and Marques, 2000). The analysis and inclusion of additional pisid taxa is likely to shed more light on the sister-group relationships of this group. However, based on the extent of morphological interspecific variability of known larvae it is likely that the group, as presently defined by adult morphology, is not monophyletic.

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