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***Ciplakastacus* gen. nov., a primitive genus of Leptastacidae (Copepoda, Harpacticoida) from the Mediterranean coast of Turkey**

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Both sexes of *Ciplakastacus mersinensis* gen. et sp. nov. (Copepoda, Harpacticoida, Leptastacidae) are described in detail based on intertidal material collected from the Mediterranean coast of Turkey (Mersin Province). Plesiomorphic character states displayed by the antenna and P1–P2 indicate *Ciplakastacus* diverged before the crown group Leptastacidae diversified. The new genus is placed in a basal clade (currently encompassing *Archileptastacus* and *Meloriastacus*) defined by eight synapomorphies: (1) caudal ramus with strongly developed seta I flanked by two elongate spinules; (2) caudal ramus with posteriorly directed spinous outgrowth of outer distal corner; (3) caudal ramus seta III vestigial; (4) P5 exopod and baseopod forming single plate in both sexes; (5) P2–P4 exp-3 with one outer spine; (6) dorsal posterior margin of anal somite bilaterally serrate; (7) rostrum triangular or bell-shaped, and (8) sexually dimorphic ornamentation on the anal somite. Within this clade *Ciplakastacus* appears most closely related to *Meloriastacus* on account of the shared presence of the extremely elongate second antennular segment, an allobasis on the antenna, the strongly reduced accessory seta on the maxillipedal endopod, the subcylindrical sternal process between the maxillipeds and P1, and paired laterodorsal, posteriorly directed, serrate extensions on the anal somite. Both genera can be distinguished from each other by P5 morphology (both sexes), armature of P4 enp-2 and abdominal hyaline frill structure. The phylogenetic relationships between the basal taxa of the Leptastacidae are briefly outlined.

Keywords: taxonomy; phylogeny; *Ciplakastacus*; Leptastacidae; Turkey

Introduction

Members of the harpacticoid family Leptastacidae are exclusively mesopsammic, typically inhabiting the interstitial environment of temperate sandy beaches and shallow subtidal habitats (Hicks and Coull 1983). Many species are capable of colonizing sandy sediments with a substantial silt–clay content where other interstitial copepods can no longer survive (Huys 1992; Huys et al. 1992). Leptastacids often represent the dominant harpacticoids in temperate beaches where their zonation can extend from the infralittoral to the supralittoral zone (e.g. Mielke 1976; Whybrew 1984). Some species of *Paraleptastacus* Wilson, 1932 are occasionally found in freshwater lakes (Noodt 1954; Štěrba 1973).

The classification of the Leptastacidae Lang, 1948 was extensively revised by Huys (1992) who raised the cylindropsyllid subfamily Leptastacinae to family rank

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and disintegrated the polyphyletic genera *Leptastacus* T. Scott, 1906, *Psammastacus* Nicholls, 1935 and *Neopsammastacus* Cottarelli and Venanzetti, 1989 into natural species groups, resulting in the recognition of 15 valid genera. Since this revision, the family has witnessed the addition of three more monotypic genera: *Meloriastacus* Huys and Todaro, 1997, *Aquilastacus* Huys and Conroy-Dalton, 2005 and *Stereoxiphos* Huys and Conroy-Dalton, 2005. These recent additions (Huys and Todaro 1997; Huys and Conroy-Dalton 2005) and the revision of *Psamathea* Cottarelli and Venanzetti, 1989 by Huys et al. (1996a) have raised the number of valid genera and species in the Leptastacidae to 18 and 56, respectively (Wells 2007).

Leptastacidae are widely distributed in the western Mediterranean with published records from France (Božić 1965; Soyer 1971; Bodiou and Soyer 1973; Kunz 1975; Bodiou 1976; Nodot 1978; Huys 1992; Huys et al. 1996a), Spain (Sabater 1986), Italy (Chappuis 1954a, 1954b; Delamare Deboutteville 1953, 1960; Cottarelli and Venanzetti 1989; Huys and Todaro 1997) and Algeria (Chappuis 1954a; Delamare Deboutteville 1953). Conversely, the family has only been recorded twice from the eastern Mediterranean basin. *Leptastacus operculatus*, originally described by Masry (1970) but recently designated as the type of *Stereoxiphos* (Huys and Conroy-Dalton 2005), is known from a sandy beach in northern Israel. Although Noodt (1954) described *Paraleptastacus trisetata* Noodt, 1954 from the freshwater Lake İznik (İznik-Gölü) in the Bursa Province in Turkey, the only truly marine leptastacid record from the vast Turkish coastline is that by Karaytuğ and Sak (2006) who reported *Paraleptastacus kliei* (Gagern, 1923) from Küçükuyu beach in the Aegean Sea.

Extensive sampling of sandy beaches along the Turkish coasts of the entire Black Sea, the Mediterranean and most of the Sea of Marmara and the Aegean Sea revealed several species of *Paraleptastacus*. In addition, an undescribed primitive genus was found exclusively at İncekum beach in the Mersin Province on the Mediterranean coast (southern Turkey). The genus is most closely related to *Meloriastacus*, originally described from the Meloria Shoals, Tuscany (Italy) by Huys and Todaro (1997), but differs from it primarily in the morphology of leg 5.

Material and methods

Samples were collected using the Karaman–Chappuis method (Delamare Deboutteville 1953). Before dissection, the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid and the dissected parts were mounted in lactophenol mounting medium. Broken glass fibres were added to prevent the animal and appendages from being compressed by the coverslip and to facilitate rotation and manipulation, allowing observation from all angles. Preparations were subsequently sealed with Entellan® (Merck, Darmstadt, Germany). All drawings were prepared using a camera lucida on Olympus BX-50 or BX-51 differential interference contrast microscopes. Total body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. Measurements were made with an ocular micrometer. Scale bars in illustrations are in µm. The descriptive terminology is adopted from Huys et al. (1996b). Abbreviations used in the text are: ae, aesthetasc; P1–P6, for swimming legs 1–6; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segments of a ramus. Material was deposited in the Mersin University Zoology Museum (MUZM) in

Table 1. Physical and chemical parameters of interstitial water on different sampling dates at the type locality.

Date	10 April 2007	27 July 2007	27 November 2007
pH	8.19	7.85	7.78
Temperature (°C)	22.1	32.5	19.3
Conductivity (ms)	49.6	53.2	54.0
Salinity (ppt)	34.6	34.8	35.8
Oxygen (mg/l)	—	—	5.78

Mersin and the Natural History Museum in London (NHM). Physical and chemical parameters of the interstitial water in the sampling pit are summarized in Table 1. Parameters were measured with a YSI 85 Handheld Dissolved Oxygen and Conductivity Instrument (YSI Inc., Yellow Springs, WA), with the exception of the pH, which was measured with an Orion 3-star (Thermo Fisher Scientific Inc., Waltham, USA) Portable pH meter.

Systematics

Order **HARPACTICOIDA** Sars, 1903
 Family **LEPTASTACIDAE** Lang, 1948
 Genus *Ciplakastacus* gen. nov.

Diagnosis

Leptastacidae. Integument smooth. Hyaline frills of abdominal somites well developed, consisting of rectangular lappets. Anal opening flanked by conspicuous serrate extensions. Caudal ramus long, with distal outer corner acutely produced posteriorly; seta I very long, flanked by two elongate spinules; setae III and VI vestigial. Sexual dimorphism in antennule, P5, P6, abdominal spinulation and genital segmentation.

Rostrum triangular. Antennule with very long segment 2; seven-segmented in ♀, with aesthetasc on segment 4 and as part of apical acrothek on segment 7; haplocer and nine-segmented in ♂, with geniculation between segments 7 and 8 and aesthetascs on segment 5 and as part of apical acrothek on segment 9. Antenna with basis and proximal endopod segment completely fused forming allobasis; exopod with one lateral and two distal setae. Labrum with few long spinules medially; without frontal spinous process; not distinctly trilobate. Mandibular palp two-segmented; basis with one seta, endopod with one lateral and four apical setae. Maxillule with endopod and exopod represented by three and two setae, respectively; arthrite only slightly rotated relative to coxa and basis. Maxilla with two well-developed cylindrical endites on syncoxa; endopod short. Maxilliped with seta on syncoxa; accessory seta of endopod reduced.

P1 basis with both outer and inner seta. P1 exopod three-segmented; exp-3 with four setae/spines. P1 endopod three-segmented; enp-2 without seta; enp-3 with one vestigial and two geniculate setae; not prehensile. P2–P4 bases with outer seta; endopods two-segmented; outer distal element of enp-2 fused to segment. Armature formulae for P1–P4 are shown in Table 2.

Table 2. Armature formula of swimming legs 1 to 4 (P1 to P4).

	Exopod	Endopod
P1	0.0.022	1.0.120
P2	0.0.121	1.120
P3	0.1.221	1.020
P4	0.1.221	0.020

P5 with baseopod and exopod forming a common plate in both sexes; in ♀ with six setae and two spines; in ♂ with five setae and two spines. Sixth pair of legs asymmetrical in ♂, with three setae each; represented by opercula closing off gonopores in ♀, with three setae each.

Type and only species. *Ciplakastacus mersinensis* sp. nov.

Etymology

The genus is named in honour of Prof. Battal Çıplak (Akdeniz University, Antalya, Turkey) in recognition of his significant contributions to the taxonomy of Turkish Orthoptera.

Gender. Masculine.

Ciplakastacus mersinensis sp. nov.

(Figures 1–5)

Type locality

Turkey, Mediterranean coast, Mersin Province; İncekum beach, 400 m east of the NATO harbour (36°17.094'N, 33°49.928'E); for chemical and physical parameters see Table 1.

Material examined

Holotype ♀ dissected on seven slides (NHM reg. no. 2008.620). Paratypes: (1) collected on 10 April 2007: two ♀♀ dissected on four and nine slides, respectively (MUZM), one ♂ dissected on eight slides (NHM reg. no. 2008.621), 20 ♀♀ and four ♂♂ preserved in alcohol (NHM reg. no. 2008.622–645), 50 ♀♀ and five ♂♂ preserved in alcohol (MUZM); (2) collected on 27 July 2007: 15 ♀♀ and 30 ♂♂ preserved in alcohol (NHM reg. no. 2008.646–690), 45 ♀♀ and 47 ♂♂ preserved in alcohol (MUZM); (3) collected on 27 November 2007: four ♀♀ and 60 ♂♂ preserved in alcohol (NHM reg. no. 2008.691–754), three ♀♀ and 105 ♂♂ preserved in alcohol (MUZM). All material collected from the type locality by S. Sak, A. Alper and S. Sönmez.

Description of female

Body (Figure 1A, B). Total body length from tip of rostrum to posterior margin of caudal rami 548 µm (holotype NHM reg. no. 2008.620) (458–565 µm; mean 500 µm; $n=20$).

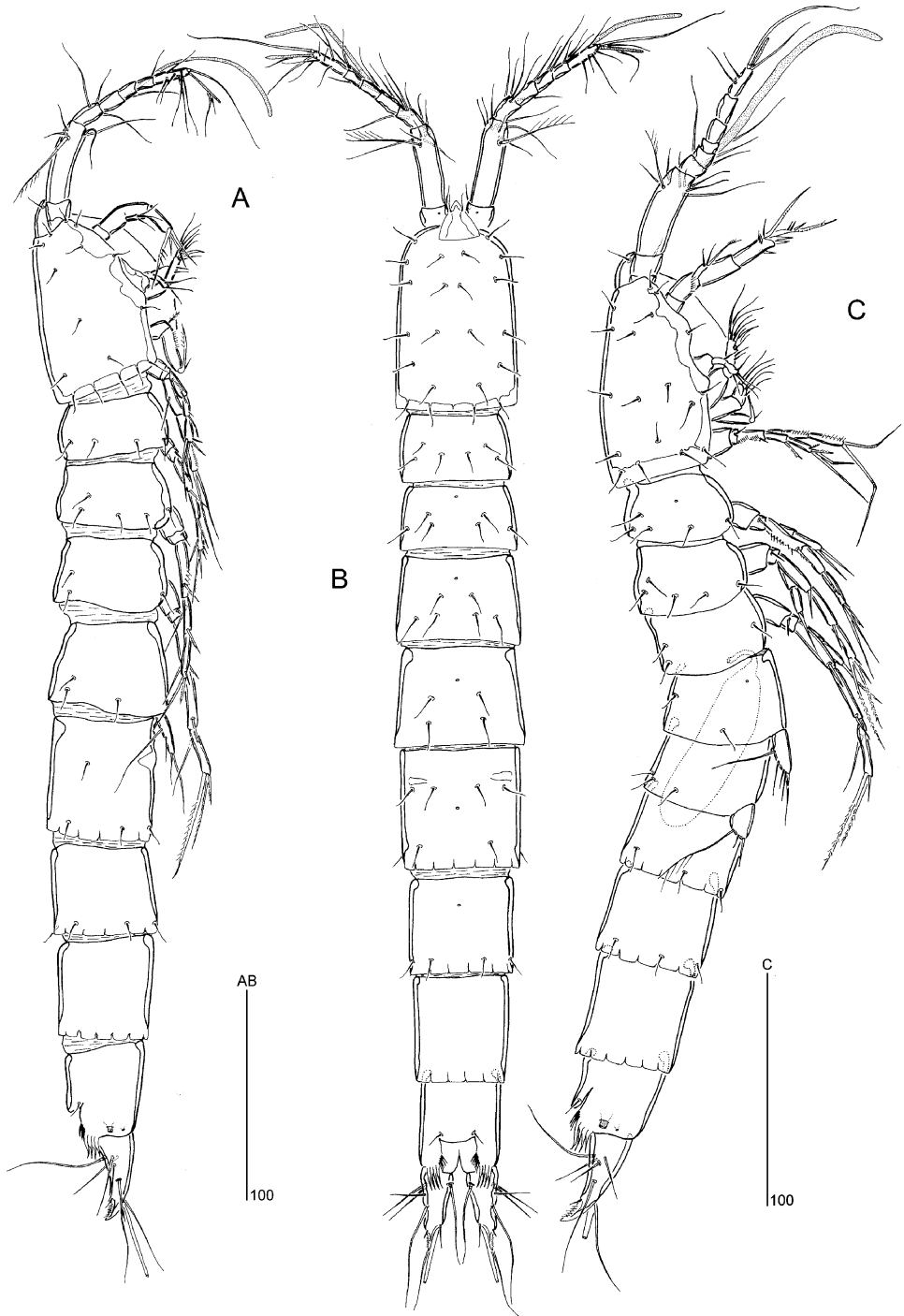


Figure 1. *Ciplakastacus mersinensis* gen. nov. sp. nov.: (A) habitus ♀, lateral, (B) habitus ♀, dorsal, (C) habitus ♂, lateral [(A), (B) holotype ♀, NHM reg. no 2008.620; (C) paratype ♂, NHM reg. no 2008.621].

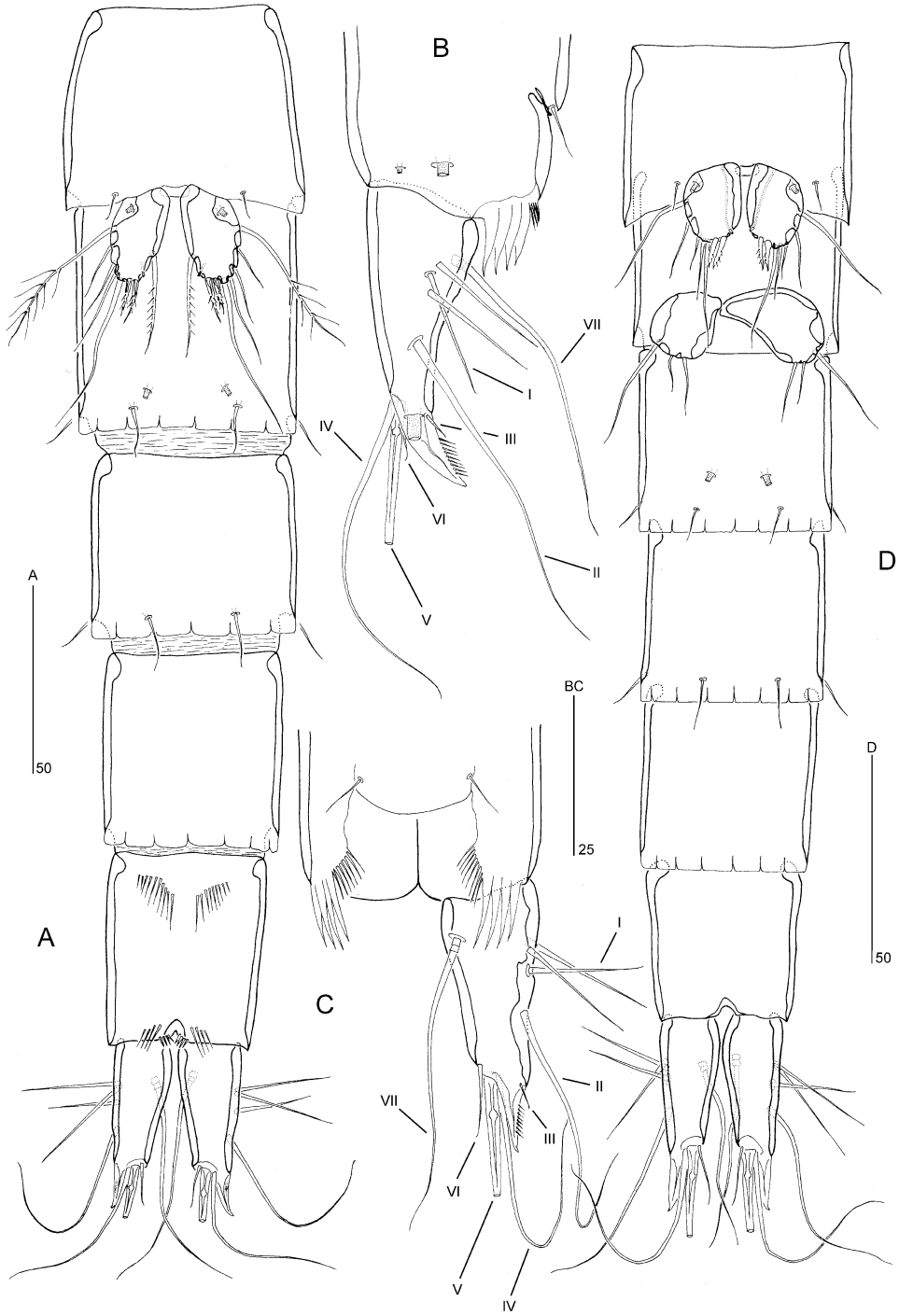


Figure 2. *Ciplakastacus mersinensis* gen. nov. sp. nov.: (A) urosome ♀, ventral, (B) anal somite and caudal ramus ♀, lateral, (C) anal somite and caudal ramus ♀, dorsal, (D) urosome ♂, ventral [(A)–(C) holotype ♀, NHM reg. no 2008.620; (D) paratype ♂, NHM reg. no 2008.621].

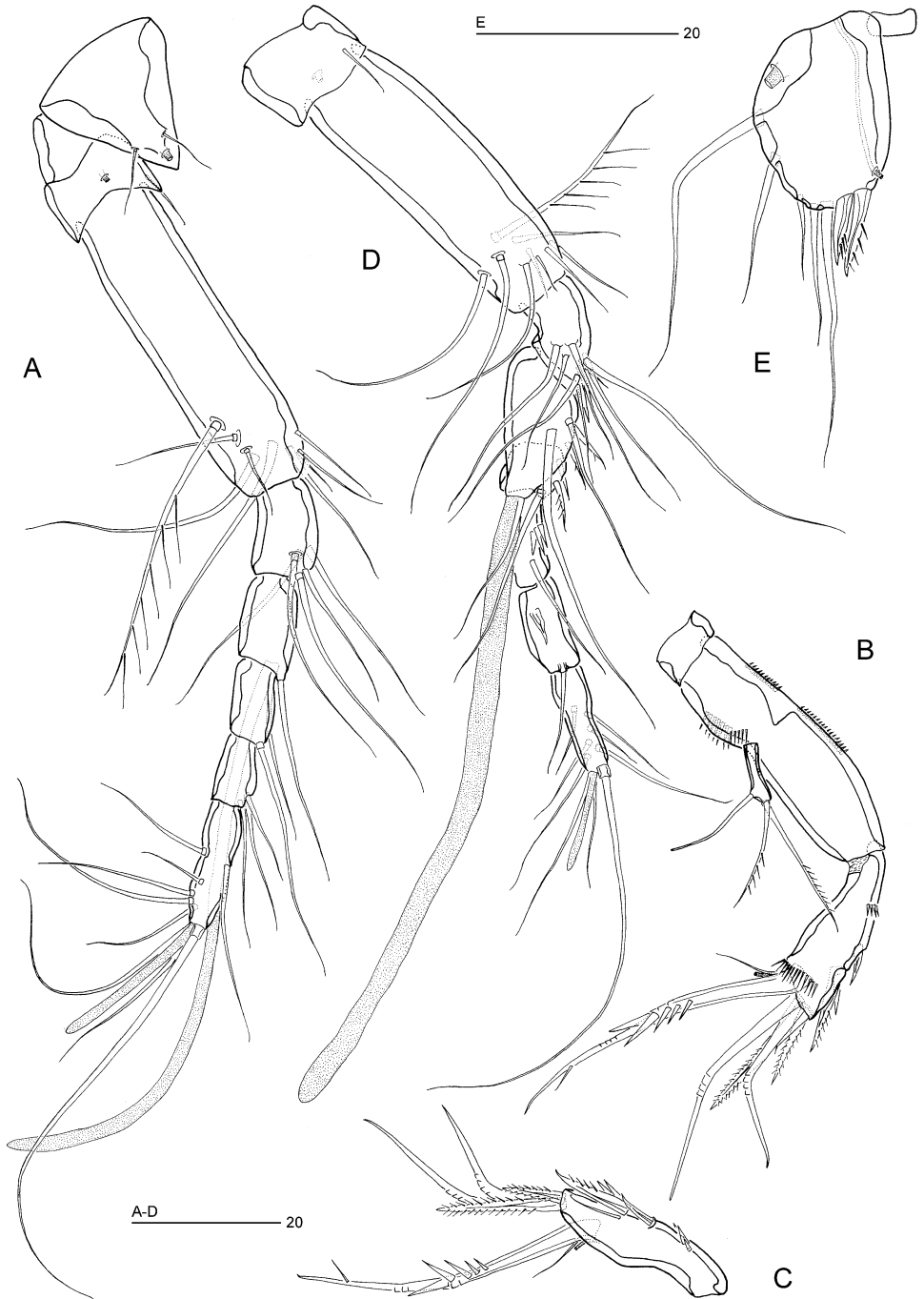


Figure 3. *Ciplakastacus mersinensis* gen. nov. sp. nov.: (A) rostrum and antennule ♀, dorsal, (B) antenna ♀, (C) antennary free endopod ♀, (D) antennule, ventral ♂, (E) P5 ♂, anterior [(A)–(C) holotype ♀, NHM reg. no 2008.620; (D), (E) paratype ♂, NHM reg. no 2008.621].

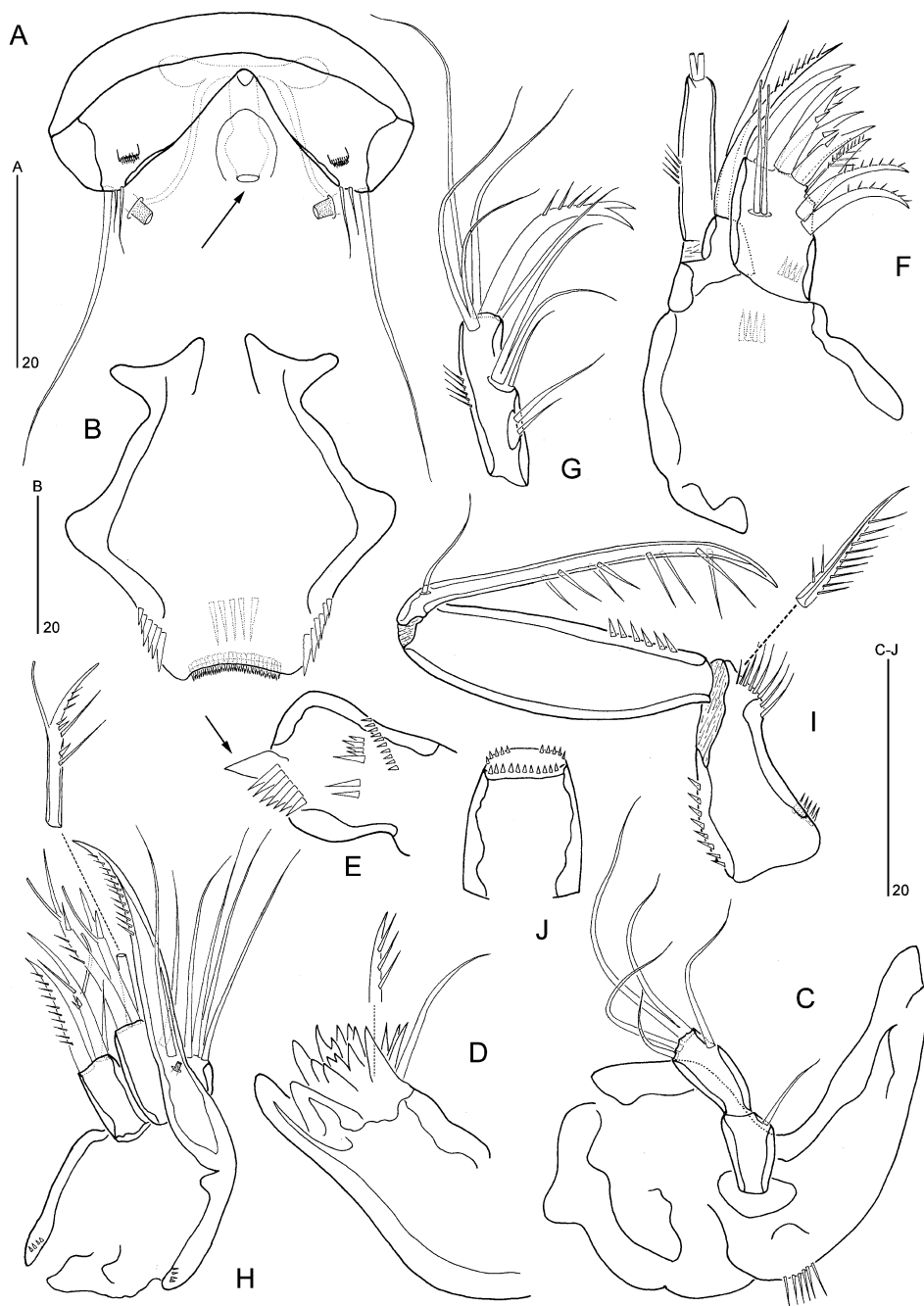


Figure 4. *Ciplakastacus mersinensis* gen. nov. sp. nov. (holotype ♀; NHM reg. no 2008.620): (A) genital field, ventral (arrow indicates copulatory pore), (B) labrum, posterior, (C) mandible, (D) mandibular gnathobase, (E) right paragnath, anterior (arrow indicates distalmost spinule), (F) maxillule, anterior, (G) maxillulary palp, (H) maxilla, anterior, (I) maxilliped, (J) truncate midventral subcylindrical process between maxillipeds and first pair of swimming legs.

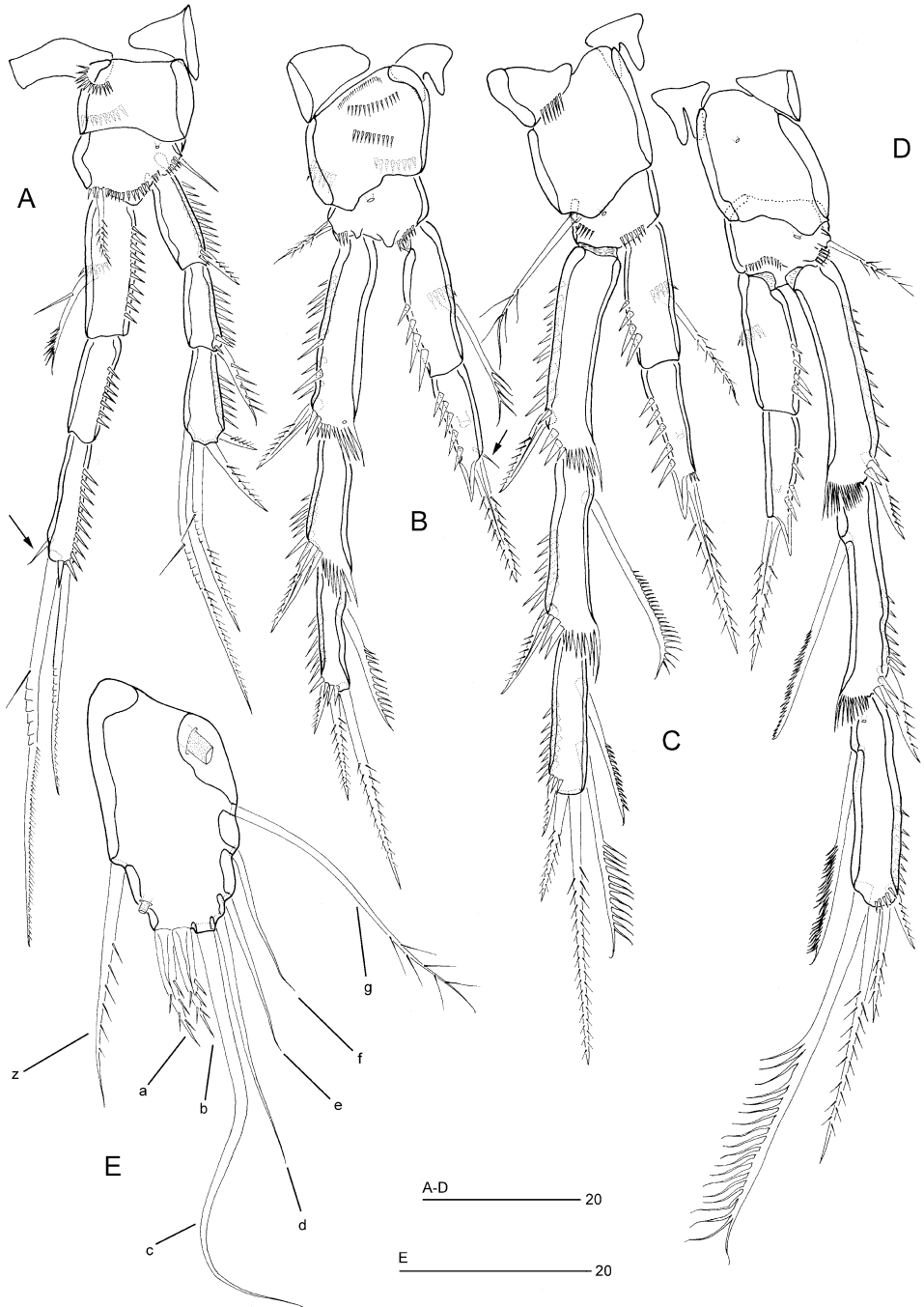


Figure 5. *Ciplakastacus mersinensis* gen. nov. sp. nov. (holotype ♀; NHM reg. no 2008.620): (A) P1, anterior (arrow indicates inner distal seta on enp-3), (B) P2, anterior (arrow indicates inner distal seta on enp-2), (C) P3, anterior, (D) P4, anterior, (E) P5, anterior.

Largest width measured at posterior margin of P5-bearing somite. Body slender, cylindrical, without clear demarcation between prosome and urosome. Integument of rostral area, cephalic shield and body somites smooth, moderately chitinized. Body surface with sensillar pattern as figured. Hyaline frills smooth and plain on cephalothorax and thoracic somites; those of genital double-somite and free abdominal somites incised, forming rectangular lappets. Cephalic shield subrectangular with anterior corners rounded. Pleural areas of cephalothorax and thoracic somites weakly developed. Intersomitic membranes distinct. Genital double-somite longer than wide; without traces marking original segmentation; with paired dorsolateral chitinous reinforcements (muscle attachments). Anal somite (Figure 2A) about 1.2 times longer than wide; with spinular rows either side of ventral midline in anterior third and near posterior margin; anal operculum weakly developed, rounded (Figure 2C); anal opening flanked by conspicuous, backwardly directed, serrate extensions (Figure 2B, C).

Caudal rami (Figure 2B, C). Elongate, about 2.9 times longer than wide, tapering posteriorly, outer distal corner produced into backwardly directed, dorsally recurved spinous process; with seven setae (indicated by Roman numerals I–VII in Figure 2B, C). Seta I well developed, flanked by dorsal and ventral elongate spinule; setae II and IV slender and bare; seta III vestigial, displaced onto posterior spinous process; seta V long with fracture plane; seta VI small; seta VII slender, located dorsally, tri-articulate at base. Outer margin of spinous process with a pore.

Antennule (Figure 3A). Seven-segmented; long and slender; sclerite small, visible at base. Segment 1 very short, with small tube-pore on dorsal surface. Segment 2 longest, about 3.7 times longer than wide. Segment 4 with long aesthetasc (length=82 µm) fused basally to a slender seta. All setae naked and slender except for long plumose seta on segment 2. Apical acrothek consisting of an aesthetasc (length=23 µm) and two slender setae. Armature formula 1-[1], 2-[8+1 plumose], 3-[5], 4-[1+(1+ae)], 5-[1], 6-[3], 7-[7+acrothek].

Antenna (Figure 3B, C). Coxa small. Basis completely fused to proximal endopod segment forming elongate allobasis with two rows of tiny spinules along abexopodal margin and with two spinule rows near base of exopod. Exopod one-segmented; with two apical pinnate setae and a subapical tubular seta. Endopod with a tiny spinular row in proximal third and with surface frill distally; lateral armature consisting of two spines and a minute seta; distal armature consisting of two bipinnate spines and three geniculate setae (longest one fused basally to vestigial seta and bearing strong spinules around geniculation); outer distal corner with tube pore.

Labrum (Figure 4B). Large; free margin slightly concave, with spinules subdistally on anterior surface, posterior surface with overlapping rows of spinules medially and spinular rows laterally.

Mandible (Figure 4C, D). Coxa robust, gnathobase with naked seta at dorsal corner and several multicuspidate teeth around distal margin. Palp uniramous, comprising

basis and one-segmented endopod. Basis with one seta; endopod with one lateral, two subapical and two basally fused apical setae.

Paragnaths (Figure 4E). Paired, not fused medially; represented by well-developed lobes with spinule rows along outer margin and series of overlapping spinules around distal inner margin (distalmost one distinctly larger; arrowed in Figure 4E).

Maxillule (Figure 4F, G). Praecoxa with a spinule row on posterior surface; arthrite with two tubular setae on anterior surface, a spinule row on posterior surface and 10 elements around distal margin. Coxal endite small, cylindrical with one unipinnate spine and one naked seta. Basis elongate (Figure 4G), with closely set endites; with apical unipinnate spine and five setae (two of which fused at base) around distal margin. Rami completely incorporated into basis; exopod and endopod represented by two and three setae, respectively. Praecoxal arthrite partly concealing coxa but not markedly rotated as in most other leptastacid genera.

Maxilla (Figure 4H). Syncoxa with two minute spinular rows and two closely-set, cylindrical endites; proximal endite with one large unipinnate spine, one bare seta and one spine with tubular extension; distal endite with three spines with tubular extensions. Allobasis drawn out into strong pinnate claw with posterior tube pore and two accessory naked setae. Endopod one-segmented with four naked long setae.

Maxilliped (Figure 4I). Subchelate, well developed, elongate. Syncoxa with spinular pattern as figured and with one pinnate seta. Basis with a spinular row on palmar margin near articulation with syncoxa. Endopod represented by short segment bearing bipinnate sigmoid claw with a short seta at base. Midventral surface between syncoxae of maxillipeds and intercoxal sclerite of P1 forming backwardly directed, subcylindrical outgrowth with truncate distal portion and provided with spinules around apical margin (Figure 4J); relative position similar as in *Meloriastacus* (see Huys and Todaro 1997: Figures 9A–B).

Swimming legs (Figure 5A–D). With three-segmented exopods and three-segmented (P1) or two-segmented (P2–P4) endopods. Intercoxal sclerite bare, wide in P1 and small in P2–P4. Praecoxae represented by well-developed U-shaped sclerites bearing spinules in P3 only. Coxae with distinctive pattern of minute spinules on anterior and posterior surfaces of P1–P2; with anterior secretory pore in P4. Bases with outer bare seta (P1), pinnate spine (P2), or plumose seta (P3–P4); anterior surface with secretory pore.

P1 (Figure 5A). Coxa with spinular row near inner margin as figured. Basis smaller than coxa; with spinules along distal margin, with inner bipinnate seta and outer bare seta. Exopodal segments with spinules along outer margin; exp-3 with two unipinnate spines and two geniculate pinnate setae. Endopod distinctly longer than exopod, not prehensile; segments with spinules along outer margin; enp-1 with serrate inner seta bearing one large proximal spinule; enp-2 without armature; enp-3 with two geniculate setae and one inner vestigial seta (arrowed in Figure 5A).

P2–P4 (Figure 5B–D). Bases with spinular rows near the bases of the rami. Outer margins of exopodal segments with spinular rows; outer spine of exp-3 relatively small. Endopodal segments with spinules along outer margin. Outer distal spine of enp-2 fused to segment forming naked spinous process; P2 enp-2 with vestigial seta (arrowed in Figure 5B). Armature formula of swimming legs as for genus.

Fifth pair of legs (Figure 5E). Not fused medially; exopod and baseopod fused forming elongate-oval plate. Outer margin with plumose (basal) seta (*g*) and three naked setae (*d–f*); apex with two bipinnate spines (*a, b*) and one long naked seta (*c*); inner margin with one unipinnate seta (*z*) and a secretory pore. Anterior surface with a secretory pore near proximal outer margin.

Genital field (Figure 4A). Positioned in anterior third of genital double-somite. Gonopores paired; closed off by opercula derived from vestigial P6, each bearing outer long and two short naked setae; two raised row of spinules present on anterior surface of sixth legs. Copulatory pore of moderate size; located in semicircular, shallow depression (arrowed in Figure 4A); leading via wide copulatory duct to paired seminal receptacles; flanked by two large secretory tube pores.

Description of male

Total body length from tip of rostrum to posterior margin of caudal rami 460 μm (paratype NHM reg. no. 2008.621) (448–463 μm ; mean 459 μm ; $n=8$). Body slender and cylindrical (Figure 1C); ornamentation generally as in female. Hyaline frills of abdominal somites incised, forming rectangular lappets. Sexual dimorphism in antennule, P5, P6, abdominal spinulation, and genital segmentation. Spermatophore length 78 μm . Anal somite without spinular ornamentation on ventral surface (Figure 2D).

Antennule (Figure 3D). Nine-segmented, slender, haplocer with geniculation between segments 7 and 8. Segment 1 short, with small tube-pore on dorsal surface. Segment 2 longest, about 3.2 times longer than wide. Segment 4 small, represented by incomplete sclerite. Segment 5 with long aesthetasc (length=90 μm) fused basally to a slender seta. Armature formula: 1-[1], 2-[8+1 plumose], 3-[8], 4-[1+1 fused spine], 5-[2+3 spines+(1+ae)], 6-[1+1 spine], 7-[1+3 modified], 8-[1+1 modified], 9-[7+acrothek]. Acrothek consisting of an aesthetasc (length=14 μm) fused basally to two slender setae.

Fifth pair of legs (Figures 2D; 3E). Not fused medially; exopod and baseopod fused forming subcircular plate; outer basal seta naked. Outer margin with two naked setae; distal margin with two slender naked setae and two unipinnate spines; inner margin without setae/spines but with a small secretory tube pore. Anterior surface with a secretory pore near proximal outer margin.

Sixth pair of legs (Figure 2D). Asymmetrical, defined at base; each P6 with long outer and two short setae; largest P6 functional one.

Etymology

The new species is named after the Mersin Province where the type locality is situated.

Discussion

The new genus *Ciplakastacus* is reminiscent of *Archileptastacus* Huys, 1992 and *Meloriastacus* in the three-segmented condition of the P1 endopod, the trisetose antennary exopod and the presence of an inner seta on the distal exopod segment of P2. These plesiomorphic character states effectively exclude *C. mersinensis* from the crown group Leptastacidae, which shares a two-segmented P1 endopod (failure to separate of enp-2 and -3), bisetose antennary exopod (loss of lateral seta) and no inner seta on P2 exp-3 (Huys 1992; Huys and Todaro 1997). Huys and Todaro (1997) considered *Archileptastacus* and *Meloriastacus* to be sister taxa on the basis of the following suite of synapomorphies: (1) caudal ramus with strongly developed seta I flanked by two elongate spinules (one ventral, one dorsal); (2) caudal ramus forming backwardly directed spinous process derived from integumental outgrowth of outer distal corner; (3) caudal ramus seta III vestigial; (4) P5 exopod and baseoendopod fused forming single plate in both sexes; (5) outer distal spine of P2–P4 enp-2 fused to segment (entirely lost in *Archileptastacus*); (6) P2–P4 exp-3 with one outer spine; (7) posterior margin of anal somite serrate either side of anal opening (forming serrate combs in *Meloriastacus*). All these derived states are also displayed by *Ciplakastacus*, supporting the common ancestry of these three genera (*ACM*-clade). Further evidence for such a basal dichotomy in the evolution of the Leptastacidae is provided by the rostrum shape, which is bell-shaped or triangular in the *ACM*-clade but distinctly elongate in the other genera. Although polarity in rostral morphology is difficult to assess in the absence of a designated outgroup (the sister group to the Leptastacidae is as yet unknown), we postulate that the bell-shaped/triangular shape is the apomorphic state. Another synapomorphy supporting the monophyly of the *ACM*-clade is the sexually dimorphic ornamentation on the anal somite. Females invariably possess paired spinule rows on the ventral surface while males consistently lack them [confirmed in *Archileptastacus aberrans* (Chappuis, 1954) by RH].

The *ACM*-clade is primarily Mediterranean in distribution. The monotypic genera *Meloriastacus* and *Ciplakastacus* are restricted to the Meloria Shoals in Livorno (Huys and Todaro 1997; Todaro and Huys 1998) and Mersin Province in Turkey, respectively. The type species of *Archileptastacus* was originally described from three beaches in Algeria (Chappuis 1954a) and subsequently recorded from Cannes (Kunz 1975) and Canet-Plage (R. Huys unpublished results) along the Mediterranean coast of France and from the Bassin d'Arcachon along the Atlantic coast by Renaud-Debyser (1963). The record of Cape Fear by Coull (1971) on the North Carolina continental shelf is considered doubtful. The only confirmed outlier in the *ACM*-clade is *Archileptastacus dichatoensis* (Mielke, 1985) which is known from two exposed sandy beaches in Chile (Mielke 1985, 1987). Thistle (1980) and Reidenauer and Thistle (1981) reported *Leptastacus* cf. *aberrans* from St. George Sound in Florida. This species was subsequently referred to as *Leptastacus* cf. *rostratus* Nicholls, 1939 by Foy and Thistle (1991) but proved upon

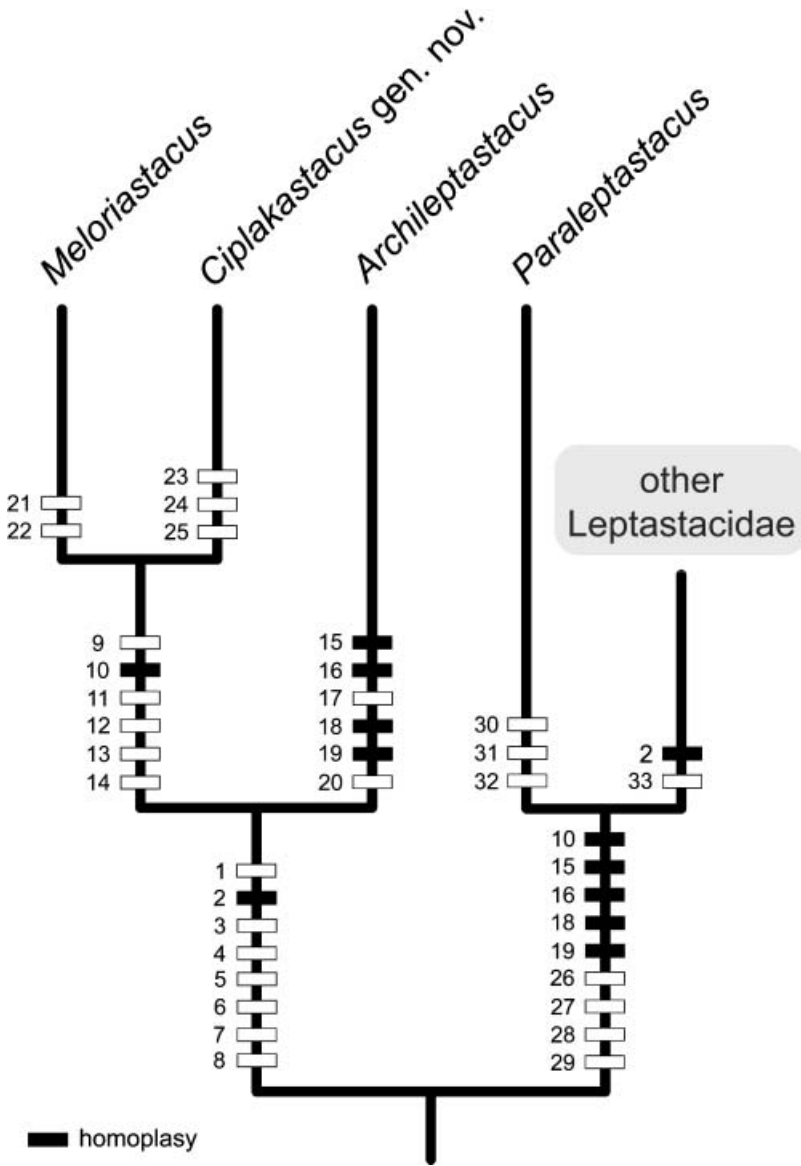


Figure 6. Hypothetical relationships between basal taxa of Leptastacidae. Numbers refer to apomorphic character states: (1) rostrum bell-shaped or triangular; (2) P2–P4 exp-3 with one outer spine; (3) P5 exopod and baseoendopod fused forming single plate in both sexes; (4) ventral ornamentation on anal somite sexually dimorphic; (5) anal somite with serrate posterior margin either side of anal somite; (6) caudal ramus forming backwardly directed spinous process derived from integumental outgrowth (homologous to outer distal corner of ramus); (7) caudal ramus with strongly developed seta I flanked by two elongate spinules (one ventral, one dorsal); (8) caudal ramus seta III vestigial; (9) second segment of antennule extremely elongated in both sexes; (10) antenna with allobasis; (11) accessory seta on maxillipedal endopod reduced; (12) sternal area between maxillipeds and first pair of swimming legs forming subcylindrical truncate process; (13) outer distal spine of P2–P4 enp-2

re-examination to be an amalgam of three different species, none of which belongs to *Archileptastacus*.

Within the ACM-clade *Ciplakastacus* appears most closely related to *Meloriastacus*. In both genera the second segment of the antennule is extremely elongated in females and males, the basis and proximal endopod segment of the antenna are fused forming an allobasis, the long accessory seta on the maxillipedal endopod is strongly reduced, the sternal area between the maxillipeds and the first pair of swimming legs is produced into a raised, subcylindrical truncate process, and the posterior margin of the anal somite possesses paired laterodorsal, backwardly directed, serrate extensions. The principal difference between both genera is the morphology of the P5 in both sexes. In *Meloriastacus* the fifth leg bears an apical spinous process, which represents a derivative of seta *a* (see Huys and Todaro 1997 for P5 setal homologies) and seta *b* is reduced to a small setule. Conversely, in *Ciplakastacus* all setal elements are defined at the base, both elements *a* and *b* are well-developed bipinnate spines, and seta *y* is absent. The inner seta on P4 enp-2 remains a unique plesiomorphy for *Meloriastacus*, being absent in all other leptastacid genera, including *Ciplakastacus*. The presence of well-developed incised hyaline frills that form rectangular lappets on all abdominal somites is another character that serves to distinguish the latter genus from *Meloriastacus*. Similar abdominal frills have evolved convergently in a number of other leptastacid genera, including *Paraleptastacus*, *Arenocaris* Nicholls, 1935, *Neopsammastacus* Cottarelli and Venanzetti, 1989 and *Minervella* Cottarelli and Venanzetti, 1989 (in the latter also on the genital somite in the male).

The structure of the mouthparts and labrum in *Ciplakastacus* conform well to those of *Meloriastacus*. The absence of a distinctly trilobate labrum further corroborates the suggestion by Huys and Todaro (1997) that mucus-trap feeding was only secondarily adopted in the evolution of the Leptastacidae and did not represent an ancestral attribute of the family as originally postulated by Huys (1992). The hypothetical phylogenetic relationships between the basal taxa of the Leptastacidae and corresponding synapomorphies for the major branching events are depicted in Figure 6.

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fused to segment; (14) posterior margin of anal somite forming laterodorsal, backwardly directed, serrate extensions; (15) inner basal spine P1 absent; (16) P1 enp-3 inner vestigial seta absent; (17) outer distal spine of P2–P4 enp-2 absent; (18) inner vestigial seta of P2 enp-2 absent; (19) P3 exp-2 inner seta absent; (20) P3 exp-3 with one inner seta; (21) P5 with apical spinous process in both sexes (derived from element *a*); (22) seta *b* of P5 vestigial in both sexes; (23) hyaline frills of abdominal somites with rectangular lappets; (24) P4 enp-2 without inner seta; (25) seta *y* of female P5 absent; (26) antennary exopod bisetose; (27) labrum trilobate; (28) P1 endopod two-segmented; (29) P2 exp-3 without inner seta; (30) P3 exp-3 with sexually dimorphic tube-pore (in males); (31) caudal ramus with posteriorly directed process (homologous to inner distal corner of ramus); (32) hyaline frills of urosomites with rectangular lappets; (33) outer distal spine of P2 enp-2 absent.

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