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Meloriastacus ctenidis gen. et sp. nov.: a primitive interstitial copepod (Harpacticoida, Leptastacidae) from Tuscany

RONY HUYS
Crustacea Research Group, Zoology Department,
The Natural History Museum,
Cromwell Road, London SW7 5BD (England)

M. ANTONIO TODARO
Centro Interuniversitario di Biologia Marina "G. Bacci",
p.le Mascagni 1, I-57127 Livorno (Italy)
and
Dipartimento di Biologia Animale, Università di Modena,
via Università 4, I-41100 Modena (Italy)

ABSTRACT

A new interstitial copepod, *Meloriastacus ctenidis* gen. et sp. nov. (Harpacticoida, Leptastacidae), is described from the shallow Meloria Shoals, Tuscany (Italy). It represents the most primitive leptastacid known to date, displaying several unique plesiomorphic character states previously unknown in the family. A sistergroup relationship with *Archileptastacus* Huys is suggested on the basis of the detailed structure of the caudal ramus, the fifth legs, the distal endopodal armature of P2-P4 and the presence of spinule rows on either side of the anal opening. The ancestral leptastacid condition for the P5 setation is re-assessed and the homology of the caudal ramus setae discussed. The structure of the mouthparts in Meloriastacus suggests that mucus-trap feeding was adopted only secondarily in the evolution of the family.

KEY WORDS: Harpacticoida - Leptastacidae - interstitial meiofauna - Tuscany - Italy - Mediterranean benthos - taxonomy - phylogeny

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INTRODUCTION

The Leptastacidae currently encompass 15 genera (Huys, 1992) all of which inhabit sandy beaches or shallow subtidal localities. Six genera have been recorded from the Mediterranean thus far: *Leptastacus* T. Scott (Chappuis, 1954a-b; Delamare Deboutteville, 1954a, 1960; Soyer, 1971; Bodiou & Soyer, 1973; Nodot, 1978; Cottarelli & Venanzetti, 1989; Huys, 1992; Todaro, unpubl.), *Paraleptastacus* C.B. Wilson (Chappuis, 1954a; Delamare Deboutteville, 1954a; Božić, 1965), *Psammastacus* Nicholls (Chappuis, 1954a; Delamare Deboutteville, 1954b), *Minervella* Cottarelli & Venanzetti (Cottarelli & Venanzetti, 1989), *Psamathea* Cottarelli & Venanzetti (Cottarelli & Venanzetti, 1989; Huys *et al.*, 1996) and *Archileptastacus* Huys (Chappuis, 1954a; Delamare Deboutteville, 1954a-b; Kunz, 1975; Huys, unpubl.). *Leptastacus operculatus* Masry, described from the Israeli Mediterranean coast (Masry, 1970) and currently placed *species inquirenda* in the genus *Cerconeotes* Huys (Huys, 1992) is to be placed in a separate genus (Huys, inprep.).

The genus *Archileptastacus* is of considerable phylogenetic interest since it represents the most primitive lineage in the family, displaying several unique plesiomorphic character states in the antenna, P1 endopod and P2 setation (Huys, 1992). At present the genus accommodates two geographically widely separated species: the type species *A. dichatoensis* (Mielke) recorded from two exposed sandy beaches in Chile (Mielke, 1985, 1987), and *A. aberrans* (Chappuis) described from two beaches in Algeria (Chappuis, 1954a) and subsequently recorded from Cannes (Kunz, 1975) and the Bassin d Arcachon (Renaud-Debyser, 1963). Coull's (1971) record of the latter from the North Carolina continental shelf requires confirmation. Examination of a number of samples collected from the Meloria Shoals, Tuscany, resulted in the discovery of numerous females and males of a primitive leptastacid which is reminiscent of *A. aberrans* in various aspects but exhibits plesiomorphic characters that were previously unknown in the family (Todaro & Huys, 1997). Its description and placement in a new genus below has prompted us to re-assess the homology of the armature elements on the fifth legs and caudal rami in *Archileptastacus*.

METHODS

Sediment samples were collected on 15 April 1996 at a site located 300 m NW of the lighthouse of the Meloria Shoals, Livorno, Italy (43° 32' N; 10° 12' E). Samples were obtained by SCUBA diver hand coring 15 cm into the sediment with a plexiglas corer, 3.56 cm internal diameter. On board the research vessel meiofauna was first narcotized using a 7% $MgCl_2$ solution and subsequently fixed with 5% formalin pre-stained with Rose Bengal. At the time of the sampling, temperature at the sediment-water interface was 13° C and interstitial water salinity was 38‰. The sediment was a coarse sand with median grain size 1.4 mm and total organic content 2.16%.

Specimens were dissected in lactic acid and the dissected parts

were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). All drawings have been prepared using a camera lucida on a Zeiss Axioskop microscope equipped with differential interference contrast.

Females and males of *Meloriastacus ctenidis* gen. et sp. nov. were examined with a Hitachi S-800 scanning electron microscope. Specimens were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter-coated with palladium.

The descriptive terminology applied to segmentation and setation of body appendages is adopted from Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1 - P6, first to sixth thoracopods; exp, exopod; enp, endopod; exp(enp)-I(-2, -3), to denote the proximal (middle, distal) segment of a ramus.

Type material is deposited in the collection of the Zoology Department, The Natural History Museum, London.

TAXONOMIC ACCOUNT

Family LEPTASTACIDAE Lang, 1948

Genus *Meloriastacus* gen. nov.

Diagnosis

Leptastacidae. Integument pitted. Hyaline frill of urosomites well developed, plain. Anal opening flanked by conspicuous raised spinular combs. Caudal ramus long, with distal outer corner acutely produced posteriorly; seta I very long, flanked by 2 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; 7-segmented in ♀, with aesthetasc on segment 4 and as part of apical acrothek on segment 7; haplocer and 9-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 1 lateral and 2 distal setae. Labrum with few long spinules medially; without frontal spinous process; not distinctly trilobate. Mandibular palp 2-segmented; basis with 1 seta, endopod with 1 lateral and 4 apical setae. Maxillule with endopod and exopod represented by 3 and 2 setae, respectively; arthrite only slightly rotated relative to coxa and basis. Maxilla with 2 well developed cylindrical endites on syncoxa; endopod short. Maxilliped with seta on syncoxa; accessory seta of endopod strongly reduced.

P1 basis with both outer and inner seta. P1 exopod 3-segmented; exp-3 with 4 setae/spines. P1 endopod 3-segmented; enp-2 without seta; enp-3 with 1 vestigial and 2 geniculate setae; not prehensile. P2-P4 bases with outer seta; endopods 2-segmented; outer distal element of enp-2 fused to segment; inner seta of P1 enp-3 and P2 enp-2 vestigial. Armature formula of swimming legs:

	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	0.120

P5 uniramous and triangular in both sexes; produced distally into spinous process derived from fused spine; in ♀ with 8 setae; in ♂ with 6. Sixth pair of legs asymmetrical in ♂, with 3 setae each; represented by opercula closing off gonopores in ♀, with 3 setae each.

Type and only species: Meloriastacus ctenidis gen. et sp. nov.

Etymology: The generic name alludes to the Meloria Shoals, the type locality of its type species. Gender: masculine. The specific name is derived from the Greek *kteis*, meaning comb, and refers to the conspicuous spinular combs flanking the anal opening.

Meloriastacus ctenidis gen. et sp. nov.

Material examined: Holotype ♀ dissected on 12 slides (reg. no. 1997.85); paratypes are 1 ♂ dissected on 8 slides and 8 ♀♀, 6 ♂♂ and 2 cop V ♀♀ preserved in alcohol (reg. nos 1997.86-102).

Type locality: a bottom pit at 7.3 m depth, filled with organogenic coarse sand, located 300 m NW of the lighthouse of the Meloria Shoals, Livorno, Italy (43° 32' N; 10° 12' E).

Description

Female

Total body length 950-1075 µm (n = 8; $\bar{X}$ 1025 µm), measured from anterior margin of rostrum to posterior margin of caudal rami. Largest width (290 µm) measured at posterior margin of cephalothorax.

Body (Figs 1A, 2A) slender, cylindrical, without clear demarcation between prosome and urosome. Integument of rostral area, cephalic shield and body somites pitted, moderately chitinized. Body surface with sensillar pattern as figured. Hyaline frills smooth and plain on cephalothorax and body somites. Cephalic shield subrectangular with anterior corners rounded. Pleural areas of thoracic somites weakly developed. Intersomitic membranes distinct. Genital double-somite longer than wide; without distinct traces marking original segmentation (Fig. 2A-B). Penultimate somite with ventral transverse row of minute spinules anteriorly. Anal somite with paired spinular rows ventrally near anterior margin and two groups of 2 spinules posteriorly (Fig. 2B-C), anal operculum weakly

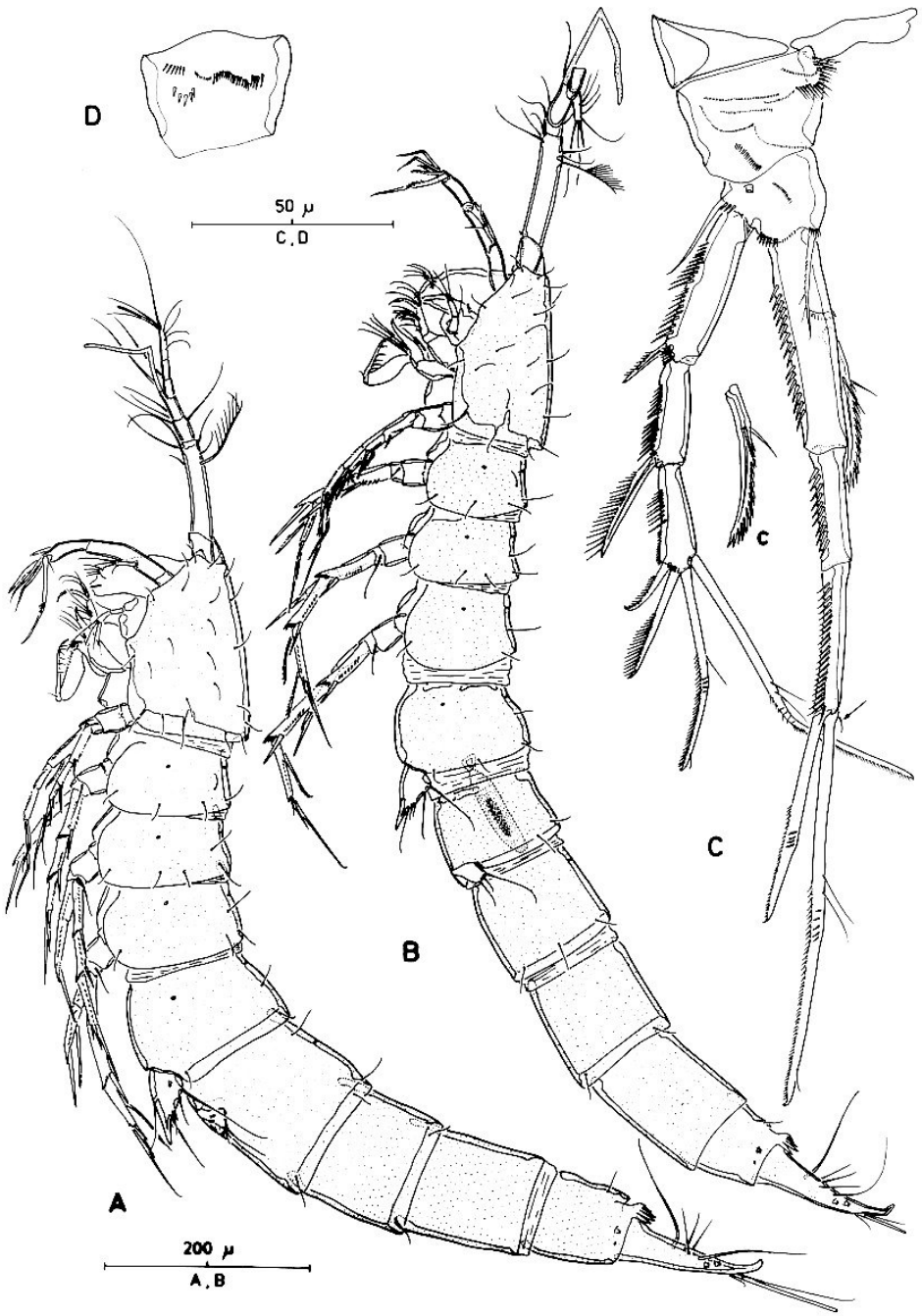

Fig. 1 - *Meloriastacus ctenidis* gen. et sp. nov. A, habitus ♀, lateral; B, habitus ♂, lateral; C, P1, anterior [inset c: inner seta of enp-1]; D, P1 coxa, posterior.

developed, rounded (Fig. 2E); anal opening flanked by conspicuous raised and backwardly directed spinular combs (Figs 2 D-E, 9C).

Caudal rami (Figs 2C-E, 9D) long, about 4.3 times as long as proximal width, distinctly tapering posteriorly; outer distal corner produced into backwardly directed, dorsally recurved spinous process; with 7 setae. Seta I very well developed, flanked by dorsal and ventral flattened elongate spinule (arrowed in Fig. 9D); setae II and IV slender and bare; seta III minuscule, displaced onto

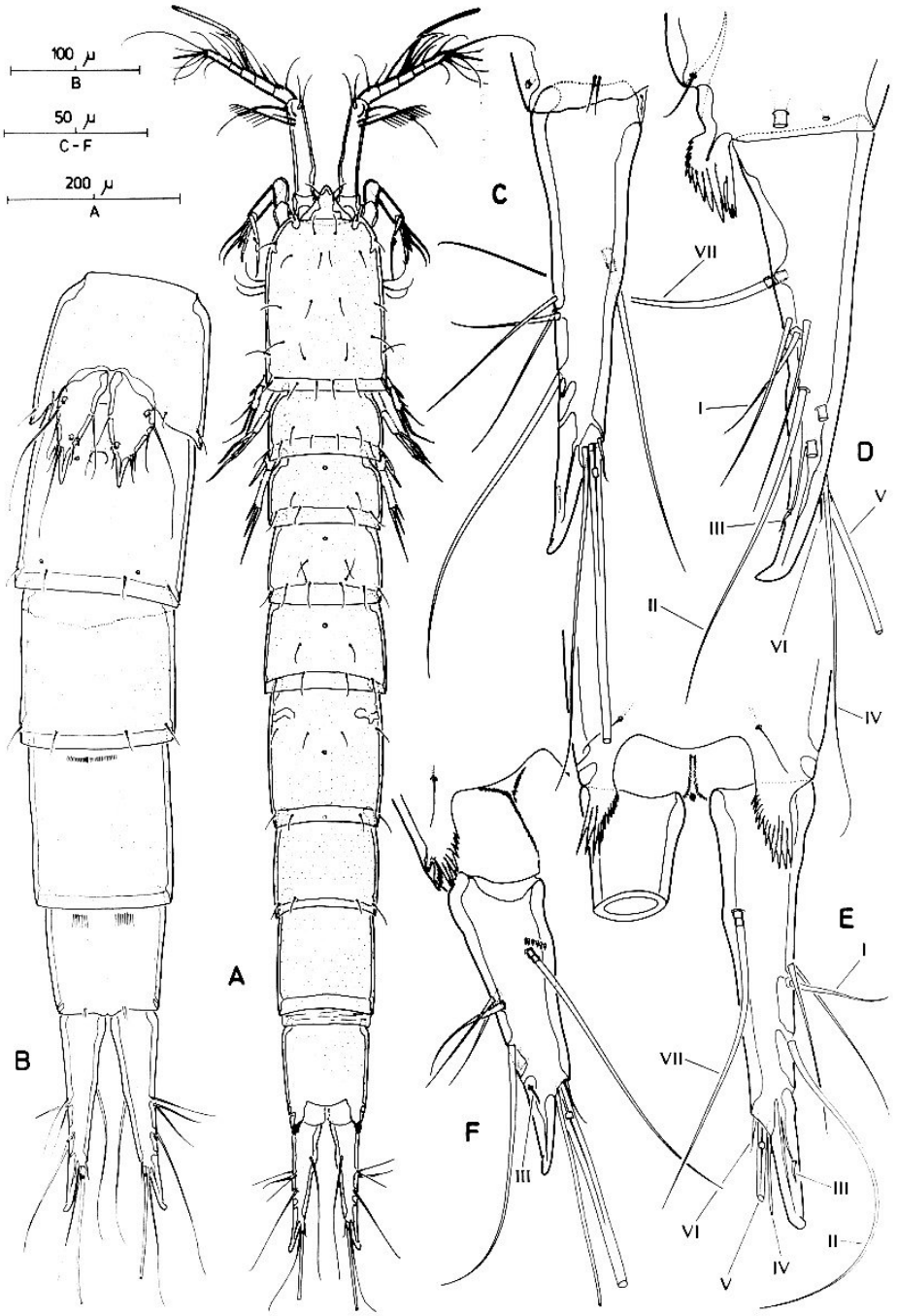

Fig. 2 - *Meloriastacus ctenidis*. A, habitus ♀, dorsal; B, urosome ♀, ventral; C, right caudal ramus, ventral; D, right caudal ramus and posterior margin of anal somite, lateral; E, right caudal ramus and posterior part of anal somite, dorsal; F, left caudal ramus of copepodid V.

posterior process; seta V long, with distinct fracture plane; seta VI vestigial; seta VII triarticulate at base and slender. Outer margin with 2 tubular secretory pores (Fig. 2D).

Rostrum (Fig. 3A) triangular, defined at base, slightly longer than basal width; recurved ventrally in lateral aspect (Fig. 10A); with middorsal integumental pore subapically and pair of sensilla laterally.

Antennule (Fig. 3A) 7-segmented, slender; small sclerite discernible at base (arrowed in Fig. 10A), well

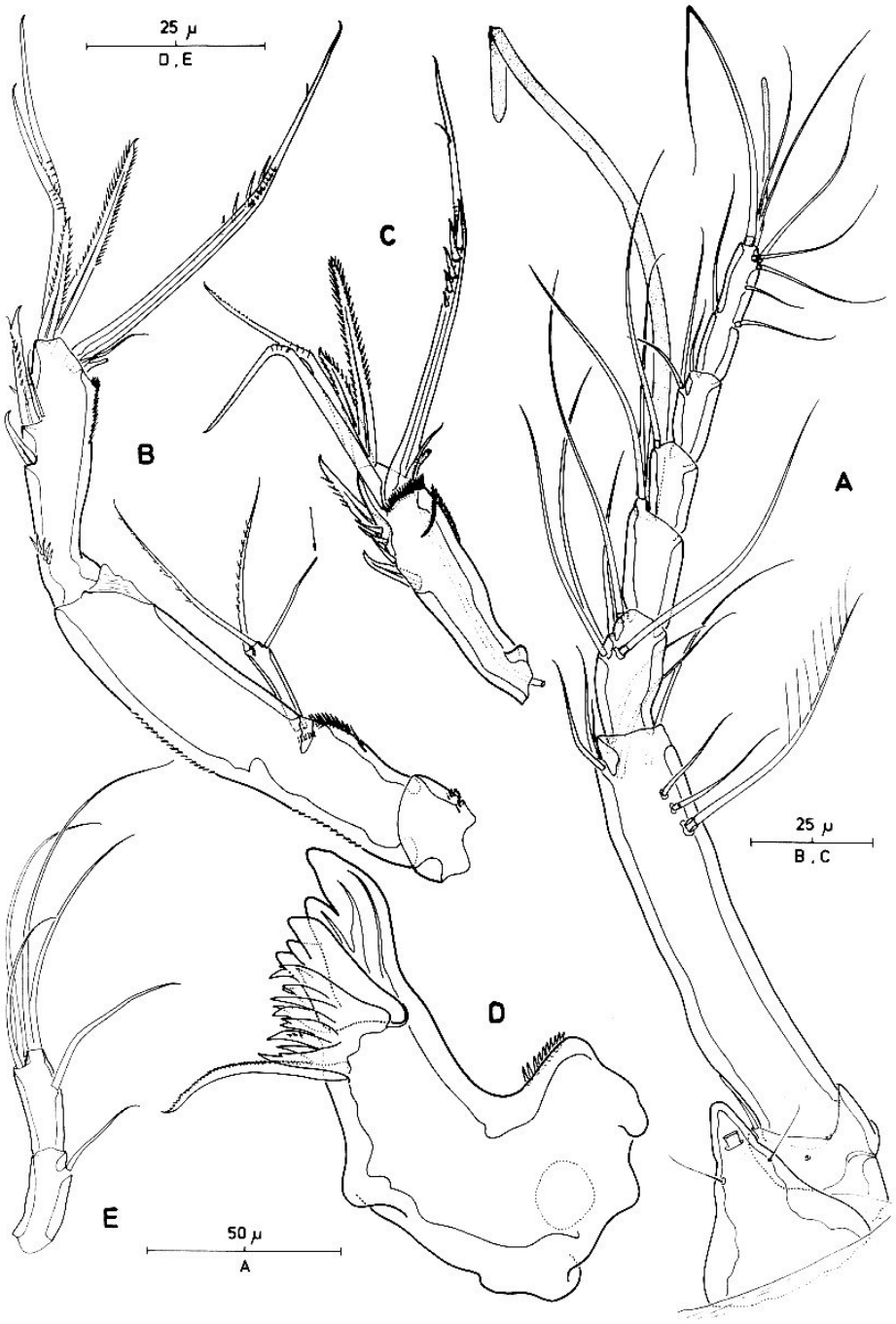

Fig. 3 - *Meloriastacus ctenidis*. A, rostrum and antennule ♀, dorsal; B, antenna [subapical tube seta on exopod arrowed]; C, antennary free endopod, other view; D, mandibular syncoxa; E, mandibular palp.

developed intersegmental membranes present between cephalic shield and segment 1. Segment 1 very short, with small tube pore on dorsal surface; segment 2 4.3 times as long as wide. Segment 4 with long aesthetasc (160 µm) fused basally to slender seta. All setae bare and slender except for long plumose seta on segment 2. Armature formula: 1-[1], 2-[8 + 1 plumose], 3-[5], 4-[(1 + ae) + 1], 5-[1], 6-[3],7-[7 + acrothek]. Acrothek consisting of aesthetasc (42.5 µm) fused basally to 2 slender setae.

Antenna (Figs 3B-C; 10 C). Coxa small, with spinule

row. Basis completely fused to proximal endopod segment forming elongate allobasis; original segmentation marked by small membranous insert at level of exopod; with 2 rows of tiny spinules along abexopodal margin. Exopod 1-segmented; surrounded by serrate frill at base (Fig. 10C); with 2 apical pinnate seta and 1 subapical tubular seta (arrowed in Fig. 3B). Endopod with spinule row in proximal third and 2 surface frills in distal third; lateral armature consisting of 2 spines and 1 vestigial seta; distal armature consisting of 2 bipinnate spines and 3 geniculate setae (longest one fused basally to vestigial seta and bearing spinules around geniculation); outer distal corner with tube pore leading to internal duct which extends into the allobasis (Fig. 3C).

Labrum (Figs 4A, 7D, 8). Large; slightly incised medially forming weakly developed lateral lobes; anterior surface with few long spinules subdistally and secretory pore with long duct medially; posterior surface with overlapping rows of spinules medially and spinular patches laterally.

Mandible (Fig. 3D-E). Coxa robust, gnathobase with 1 uniserrate spine at dorsal corner and several multicuspidate teeth around distal margin. Palp uniramous, comprising basis and 1-segmented endopod. Basis with 1 seta; endopod with 1 lateral, 2 subapical and 2 basally fused apical setae.

Paragnaths paired, not fused medially (Figs 4B, 7C-D); represented by well developed lobes with spinule rows along outer margin and series of overlapping spinules around distal inner margin (distalmost one distinctly larger and arrowed in Fig. 7C).

Maxillule (Fig. 4C-E). Praecoxa with several spinule rows as figured; arthrite strongly developed, marked at base by surface suture, with 2 tube-setae on anterior surface and 10 elements around distal margin; distalmost elements large and claw-like. Coxal endite small, cylindrical with 1 claw and 1 slender seta. Basis elongate, with closely set endites; with apical spine and 5 accessory setae. Rami completely incorporated into basis; exopod and endopod represented by 2 and 3 setae respectively. Praecoxal arthrite partly concealing coxa and basis but not markedly rotated as in other leptastacid genera.

Maxilla (Figs 4F, 7A, 8). Syncoxa with 2 spinule rows and 2 cylindrical endites closely adpressed to allobasis; proximal endite with conspicuous bipinnate spine and 2 spines with tubular extensions; distal endite with long curved spine and 2 spines with tubular extensions. Allobasis drawn out into strong pinnate claw with posterior tube pore; accessory armature comprising 2 naked setae. Endopod 1-segmented bearing 4 setae.

Midventral surface between maxillules and maxillae with conspicuous triangular swelling formed by 3 ridges bearing inwardly directed spinules (Figs 7B, 8).

Maxilliped (Fig. 4G). Subchelate, well developed, elongate. Syncoxa with spinular pattern as figured, with 1 seta. Basis with 1 spinule row on palmar margin near articulation with syncoxa. Endopod represented by short segment bearing bipinnate sigmoid claw with vestigial seta at base.

Midventral surface between syncoxae of maxillipeds and intercoxal sclerite of P1 forming backwardly directed, subrectangular outgrowth with truncate distal portion and provided with spinules around apical margin (arrowed in Fig. 9A-B).

Swimming legs (Figs 1C-D, 5A-D) with 3-segmented exopods and 3- (P1) or 2-segmented endopods (P2-P4). Intercoxal sclerite wide in P1, small in P2-P4; bare. Praecoxae represented by well developed U-shaped sclerites bearing spinules in P2-P4. Coxae with distinctive pattern of minute spinules on anterior (P1-P4) and posterior (P1-P3) surfaces; with anterior secretory pore in P3-P4. Bases with outer pinnate spine (P2) or bare seta (P1, P3-P4); anterior surface with secretory pore.

P1 (Fig. 1C-D) with endopod distinctly longer than exopod. Basis with inner pinnate seta. Exp-3 with 2 pinnate spines and 2 geniculate setae. Endopod not prehensile; enp-1 with serrate inner spine bearing 2 proximal spinules (see inset c in Fig. 1C); enp-2 shortest, without armature; enp-3 with 2 geniculate setae and 1 vestigial seta (arrowed in Fig. 1C).

P2-P4 (Figs 5A-D). Successive legs increasing in length. Exopods with proximal pore on anterior surface of exp-2 and exp-3, largely concealed under hyaline frill; all inner setae serrate; exp- 3 with 1 outer spine. Enp-2 with outer distal spine fused to segment forming pinnate spinous process; with secretory pore on posterior surface; P2 enp-2 with supplementary vestigial seta (arrowed in Fig. 5A). Spine- and seta formulae as for genus.

Fifth pair of legs (Figs 2B, 5E) not fused medially; exopod and baseoendopod fused forming triangular, distally produced plate. Outer margin with 2 long (proximal one being homologue of outer basal seta) and 4 short setae; inner margin with 1 long and 1 short seta plus a secretory pore; apex forming pointed spinous process derived from incorporated spine. Anterior surface with 2 secretory pores.

Genital field positioned in anterior third of genital double-somite (Fig. 2B). Gonopores paired (Fig. 5F-G); closed off by opercula derived from vestigial P6, each bearing outer long, sparsely plumose and 2 short naked setae; 2 rows of spinules present on anterior surface of sixth legs. Copulatory pore of moderate size; located in semicircular, shallow depression (arrowed in Figs 5F-G; 10D); leading via wide copulatory duct to paired seminal receptacles; flanked by 2 large secretory tube pores.

Male

Total body length 900-1075 μm (n = 6; $\bar{X}$ = 950 μm), measured from anterior margin of rostrum to posterior margin of caudal rami. Body more slender than in ♀. Sexual dimorphism in antennule, P5, P6, abdominal spinulation and genital segmentation.

Abdominal somites without ventral transverse rows of spinules except for few minute spinules at posterior margin of anal somite (Fig. 6C).

Antennule (Figs. 6A-B, 10B) 9-segmented, slender;

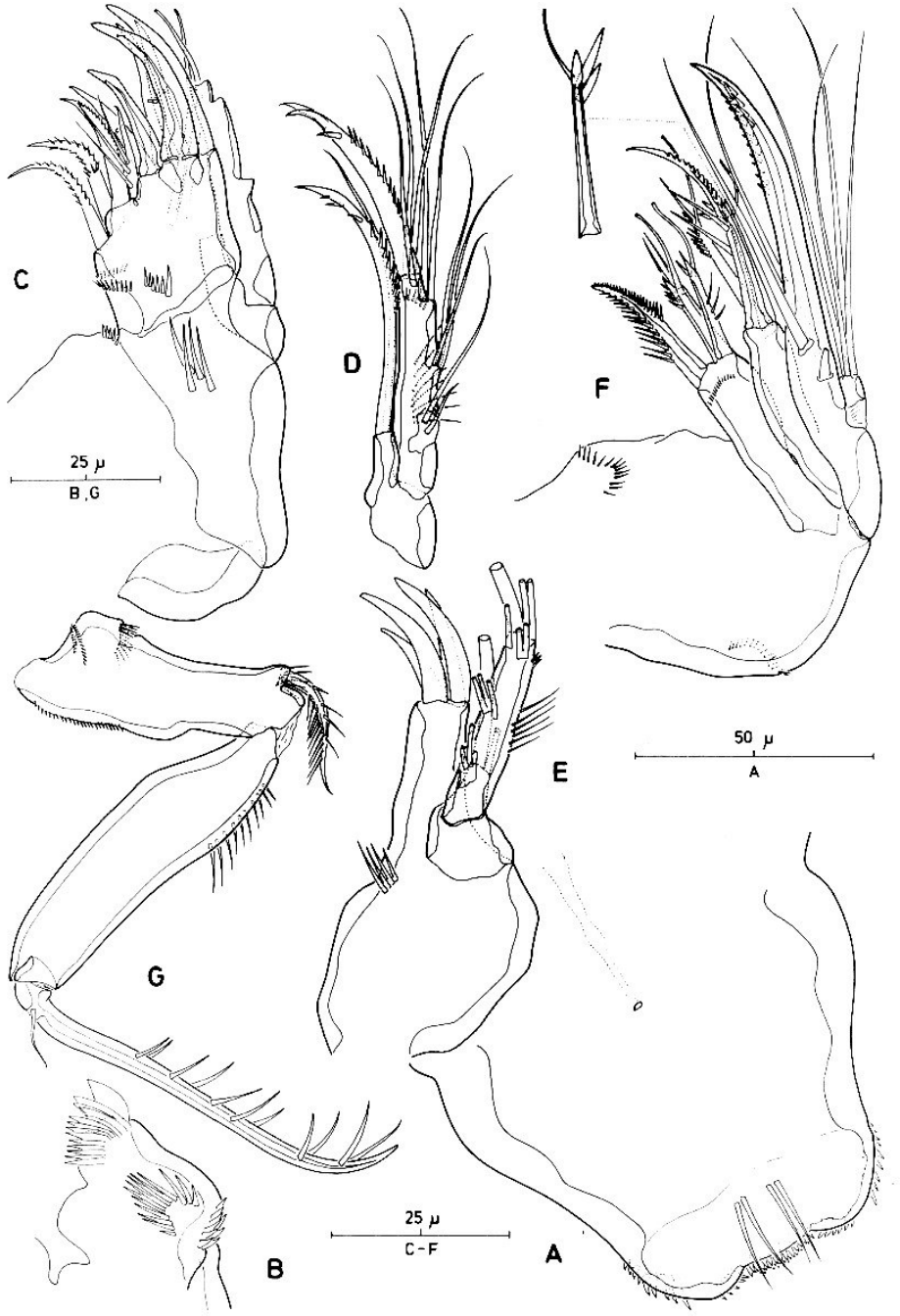

Fig. 4 - *Meloriastacus ctenidis*. A, labrum, anterior; B, paragnath; C, maxillule, posterior [armature of coxa and palp omitted]; D, coxa and palp of maxillule; E, maxillule, lateral, showing relative position of praecoxa, coxa and palp [not all elements of arthrite drawn]; F, maxilla [inset showing modified spine of distal syncoxal endite]; G, maxilliped.

haplocer with geniculation between segments 7 and 8; small sclerite discernible at base. Segment 1 short; anterior margin with ventral rows of minute spinules. Segment 2 very long. Segment 4 represented by incomplete ring (see inset of Fig. 6B). Aesthetasc present on segment 5 (145 μm) and as part of acrothek on segment 9 (25 μm). 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 + 3modified], 8-[1 + 1 modified + 2 tubular elements], 9-[7 + acrothek]. Acrothek consisting

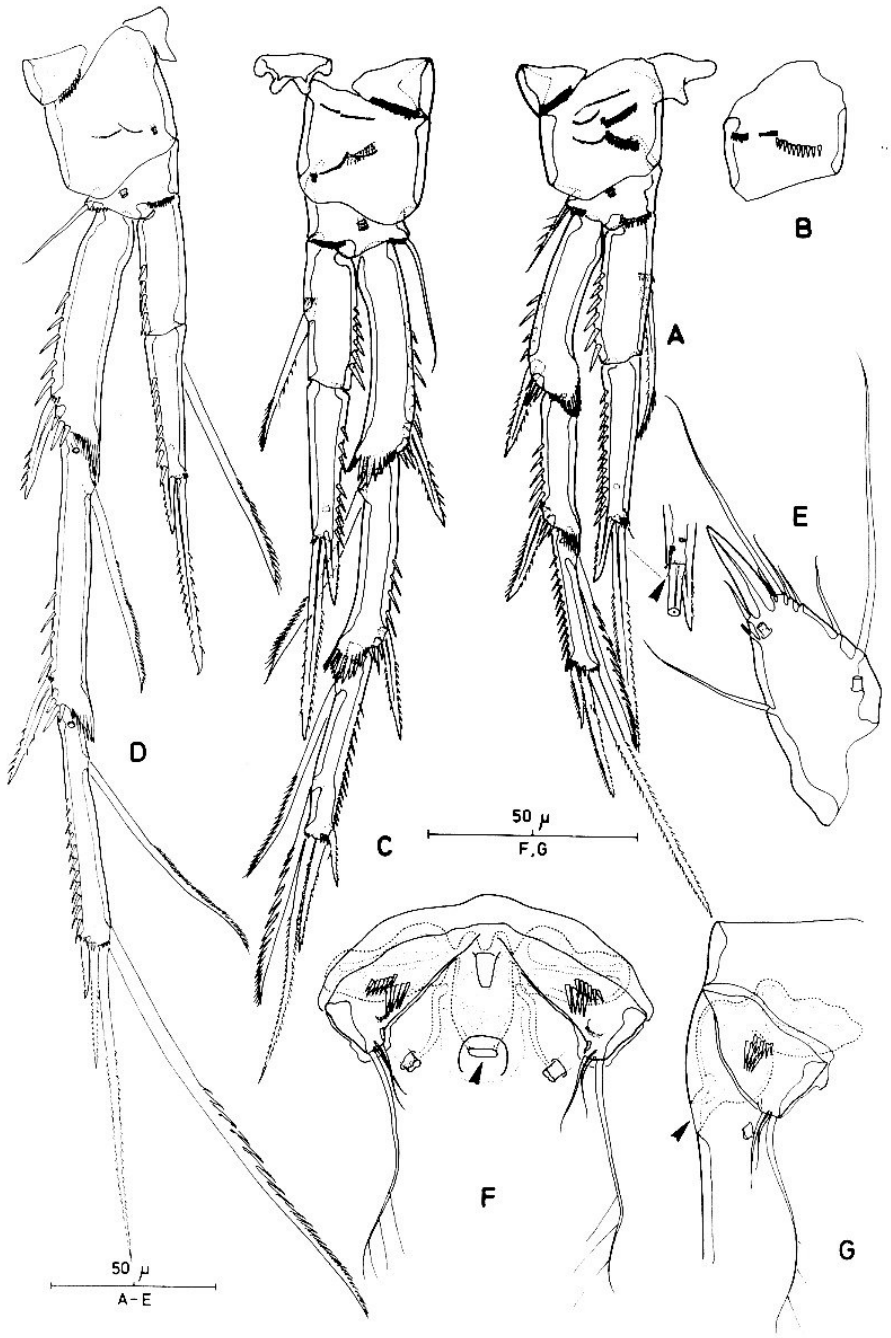

Fig. 5 - *Meloriastacus ctenidis*. A, P2, anterior [inset showing posterior view of tip of endopod; vestigial seta arrowed]; B, P2 coxa, posterior; C, P3, anterior; D, P4, anterior; E, P5 ♀, anterior; F, genital field ♀, ventral; G, genital field ♀, lateral[copulatory pore arrowed in F-G].

of aesthetasc fused basally to 2 slender setae. Segment 8 with 2 tubular elements (arrowed in Fig. 10B) arising from anterior concavity.

Fifth pair of legs (Figs 6C-D) separate; with exopod and baseoendopod fused forming triangular distally produced plate. Outer margin with 3 long (proximal one homologue of outer basal seta) and 3 short setae; inner margin without setae but with secretory tube pore; apex drawn out into spinous process derived from incorporated element. Anterior surface with 2 secretory pores.

Sixth pair of legs (Fig. 6C-D) asymmetrical, defined at base; each P6 with long outer and 2 short setae; largest

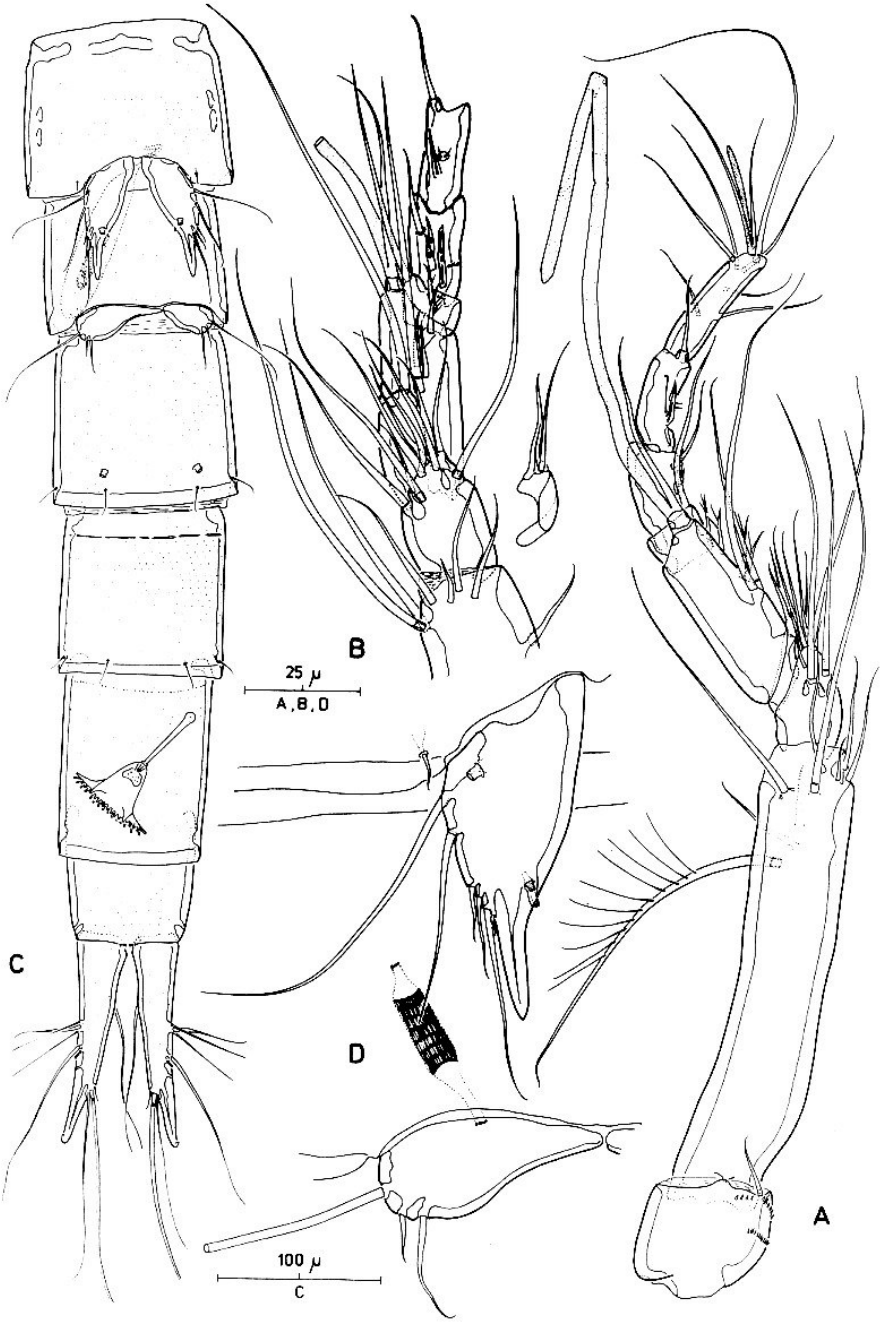

Fig. 6 - *Meloriastacus ctenidis*. A, antennule ♂, ventral; B, antennulary segments 2-7 ♂ [inset showing reduced segment 4]; C, urosome ♂, ventral [epizoic ciliate attached to third abdominal somite]; D, P5 and P6 ♂.

P6 functional one (operated by muscle shown in Fig. 6D). Spermatophore 117 μm.

Most specimens were infested by one or more ciliate Protozoa which predominantly occurred on the abdominal somites and caudal rami (Fig. 6C).

DISCUSSION

Meloriastacus gen. nov. and *Archileptastacus* occupy an ancestral and isolated position within the Leptastacidae by virtue of their 3-segmented P1 endopod,

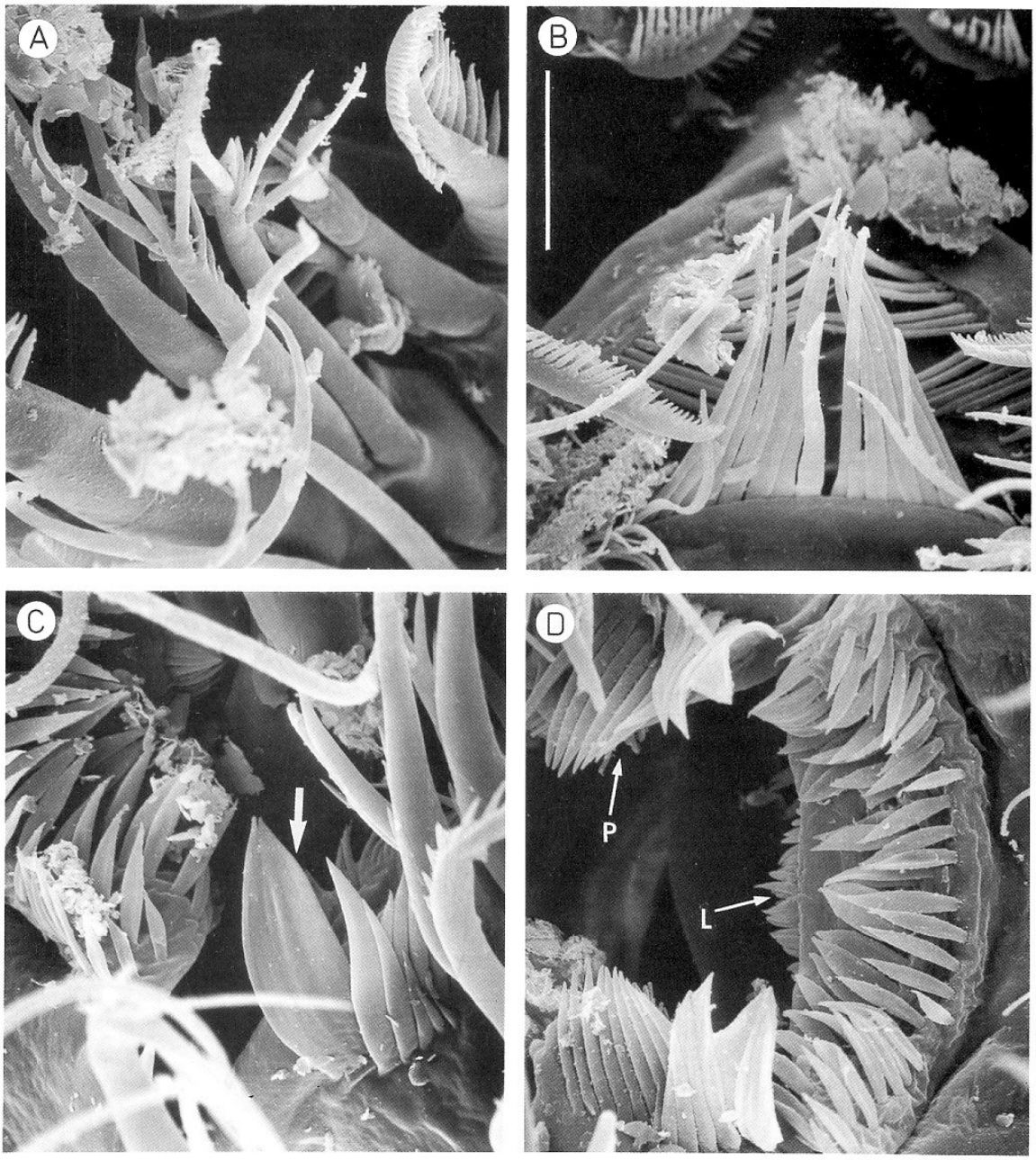

Fig. 7 - *Meloriastacus ctenidis*. SEM micrographs: A, endites of maxillary syncoxa; B, postoral triangular process; C, paragnath [largest spinule arrowed]; D, oral area showing paragnath (P) and labrum (L). Scale bars (indicated in B only): 6 µm (A, C), 7.5 µm (B, D).

trisetose antennary exopod and the presence of an inner seta on the distal exopod segment of P2. All other genera share the apomorphic states (or a further derived state) of these characters: 2-segmented P1 endopod (through fusion of en2 and -3), bisetose antennary exopod (loss of lateral seta) and no inner seta on P2 exp-3.

Meloriastacus ctenidis cannot be accommodated in *Archileptastacus* without grossly extending its generic boundaries. This is primarily due to the large number of plesiomorphies displayed by the Italian species. *M. ctenidis* is unique in the presence of a third element on the distal endopod segment of both P1 (arrowed in Fig. 1C) and P2 (arrowed in Fig. 5A). These additional elements are minute and might well have been overlooked in

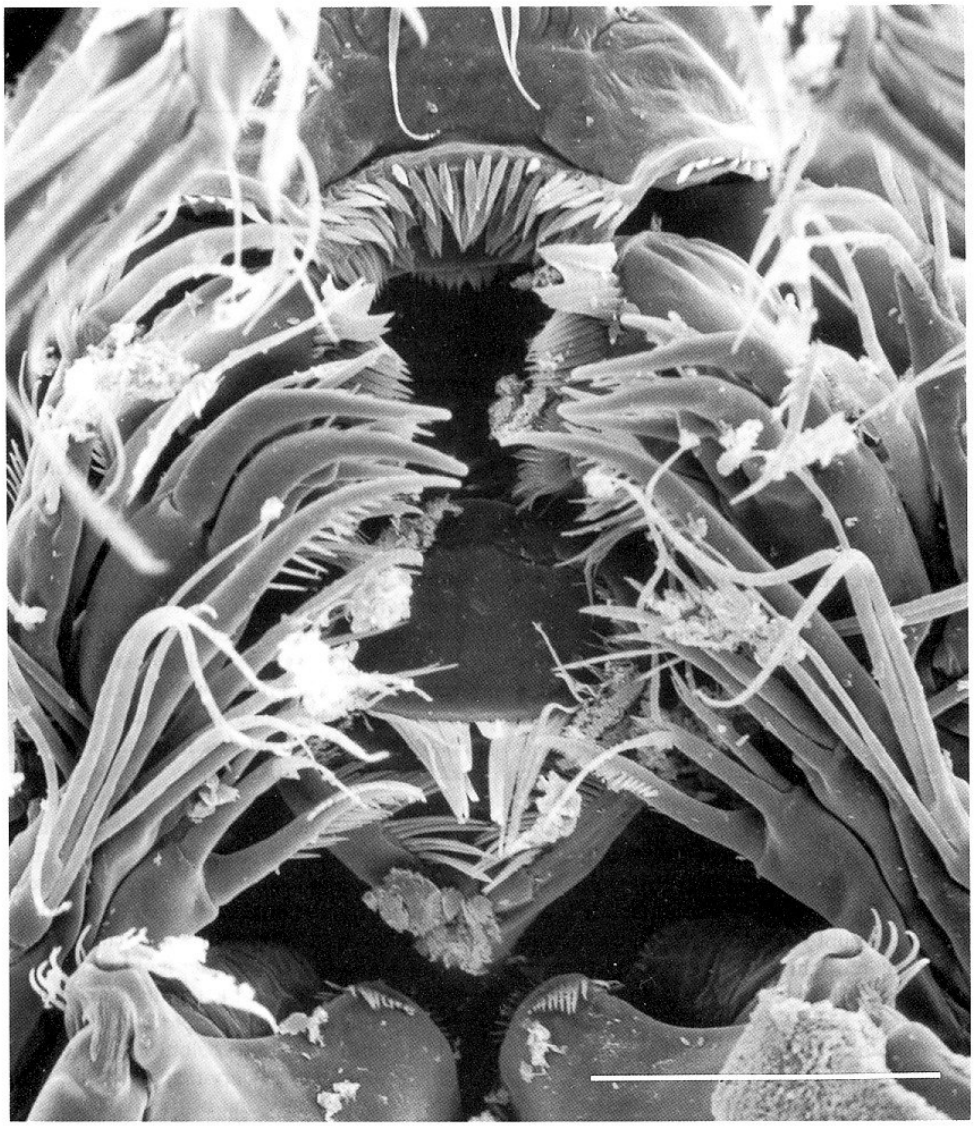

Fig. 8 - *Meloriastacus ctenidis*. SEM micrograph: ventral view of cephalic appendages showing relative position of labrum, paragnaths, postoral triangular process and syncoxae of maxillipeds. Scale bar: 25 µm.

earlier descriptions, however, re-examination of material of *A. aberrans* from Canet-Plage (France) and several *Paraleptastacus* species from NW Europe and Canada confirmed their absence in these genera. *M. ctenidis* is also the only leptastacid that has retained an inner seta on P3 exp-2 and P4 enp-2 and displays 2 inner setae on P3 exp-3 (the distal one being the additional element). Apart from the presence of 2 outer spines on the distal exopod segment of P2-P4, which is a character retained in *Paraleptastacus* only, the swimming leg armature formula of *M. ctenidis* represents the most primitive found in the family and the formula of the leptastacid hypothetical ancestor as reconstructed by Huys (1992) should be modified accordingly (Table I). An additional unique plesiomorphy of *Meloriastacus* is the presence of the inner basal seta on P1 which has been lost in all other genera.

The female fifth legs in *Meloriastacus* are of significant phylogenetic interest. The exopod and baseoendopod are fused into a triangular plate which is reminiscent of the P5 found in *Leptastacus* and related genera. Comparison (Fig. 11A-C) with the closely related *Archileptastacus* (particularly with *A. aberrans*) reveals that the spinous process is derived from an incorporated setal element. In *Leptastacus* and allied genera the spinous process is an outgrowth from the exopodal margin (Fig.

TABLE I - *Comparison of P2-P4 armature formula of a number of leptastacid genera (formula listed for* Paraleptastacus *and* Leptastacus *is the most primitive one found in each genus).*

	P2	P3	P4
Ancestor	0.0.122 1.120	0.1.222 1.020	0.1.222 0.120
Meloriastacus	0.0.121 1.120	0.1.221 1.020	0.1.221 0.120
Archileptastacus	0.0.121 0.010	0.0.121 0.010	0.0.121 0.010
Paraleptastacus	0.0.022 1.020	0.0.122 1.020	0.1.222 0.020
Leptastacus	0.0.021 1.010	0.0.121 1.010	0.1.221 0.020

11E; Huys, 1992). In an attempt to homologize the setal elements of the fifth legs in the various genera Huys (1992) labelled the seven setae of the generalized ancestral P5 alphabetically. The ancestral condition (Fig. 11D) thought to have persisted only in *Paraleptastacus* and *Arenocaris* consists of a biramous leg with a tetrasetose exopod (setae *c-f*) and a baseoendopod with a bisetose endopodal lobe (setae *a-b*) and an outer basal seta (*g*). Since only six setae are expressed in *Archileptastacus* (Fig. 11B-C), Huys (1992; Fig. 24C) suspected that it was seta *a* which had been lost or perhaps been replaced by a vestigial setule and that the spinous process corresponds with the exopodal seta *c*. With the discovery of *M. ctenidis*, which possesses a total of 9 elements (8 free and 1 incorporated), both suppositions are no longer tenable. Vertical tracking of the setation elements throughout ontogeny using copepodids of *A. aberrans* (Huys, unpubl.) revealed that the innermost spine is endopodal in origin and corresponds to seta *a* in Huys (1992) scheme. This element is free in *A. aberrans* (Fig. 11B) but basally fused and forming a distal spinous process in *A. dichatoensis* (Fig. 11C) and *M. ctenidis* (Fig. 11A). By using the process as a reference point it is apparent that the inner seta *z* in *Archileptastacus* [labelled *b* in Huys (1992)] has no homologue in *Paraleptastacus* and is therefore assumed to have been lost in all other leptastacid genera except for *Meloriastacus*. It also implies that *Archileptastacus* has not retained the full complement of exopodal setae, however with the exception of the long seta *c* it is impossible to decide which two setae have been lost. *Meloriastacus* differs from *Archileptastacus* in that all four exopodal setae are expressed and in that the innermargin carries two setae. By using the lateral pore as a reference point (Fig. 11C) it can be deduced that seta *z* in *Archileptastacus* represents the positional homologue of the proximal inner seta in *M. ctenidis* (Fig. 11A). The distal seta y is therefore unique to *Meloriastacus* and is lost in all other leptastacid genera. Although both rami are fused in this genus it can be inferred from its setation pattern that the biramous fifth leg of the lepastacid ancestor possessed at least four exopodal and four endopodal setae.

The primitive position of *Meloriastacus* is also demonstrated by the morphology of the mouthparts. Huys (1992) pointed out the peculiar arrangement and modifications of the mouthparts in the Leptastacidae which can be viewed collectively as the morphological impact of the adoption of mucus-trap feeding as a feeding strategy. Significant modifications involve the transformation of the syncoxal elements on the maxillary endites, the forward rotation of the maxillulary arthrite and maxillary endites and the formation of a large trilobate labrum. In *Meloriastacus* the maxillary endites are well developed cylindrical lobes, bearing three long setae each which do not resemble the stubby modified elements of other leptastacids. The arthrite and coxal endite of the maxillule, the maxilla and the maxilliped of *M. ctenidis* are not anteriorly rotated towards the preoral chamber but are medially directed. Finally, the labrum is only slightly trilobate and its ornamentation is weak in comparison to that of other leptastacids. From these differences it is conceivable that in the Leptastacidae mucus trap-feeding was only adopted secondarily allowing the smaller-sized species to colonize sediments with a higher silt content. In this context it is noteworthy that *M. ctenidis* represents one of the very few species that attains 1 mm in body length.

The posteriorly produced caudal rami display some important apomorphies supporting the sistergroup relationship between *Meloriastacus* and *Archileptastacus*. Huys (1992) identified the backwardly directed process in the latter as an outgrowth of the outerdistal corner of the ramus. The process found in *Meloriastacus* clearly has a similar origin. This is supported by reference to the relative position of setae III and IV (Fig. 2E). The minuscule seta III is located halfway on the dorsal surface of the spinous process, however comparison with the copepodid V (Fig. 2F) shows that this position is secondary as a result of posterior migration at the final moult. The presence of seta III in *M. ctenidis* unequivocally defines the homology of the spinous process and of the 2 long setae present along the outer margin of both *Archileptastacus* and *Meloriastacus*. The long distal seta is identified as seta II, the shorter proximal seta is the

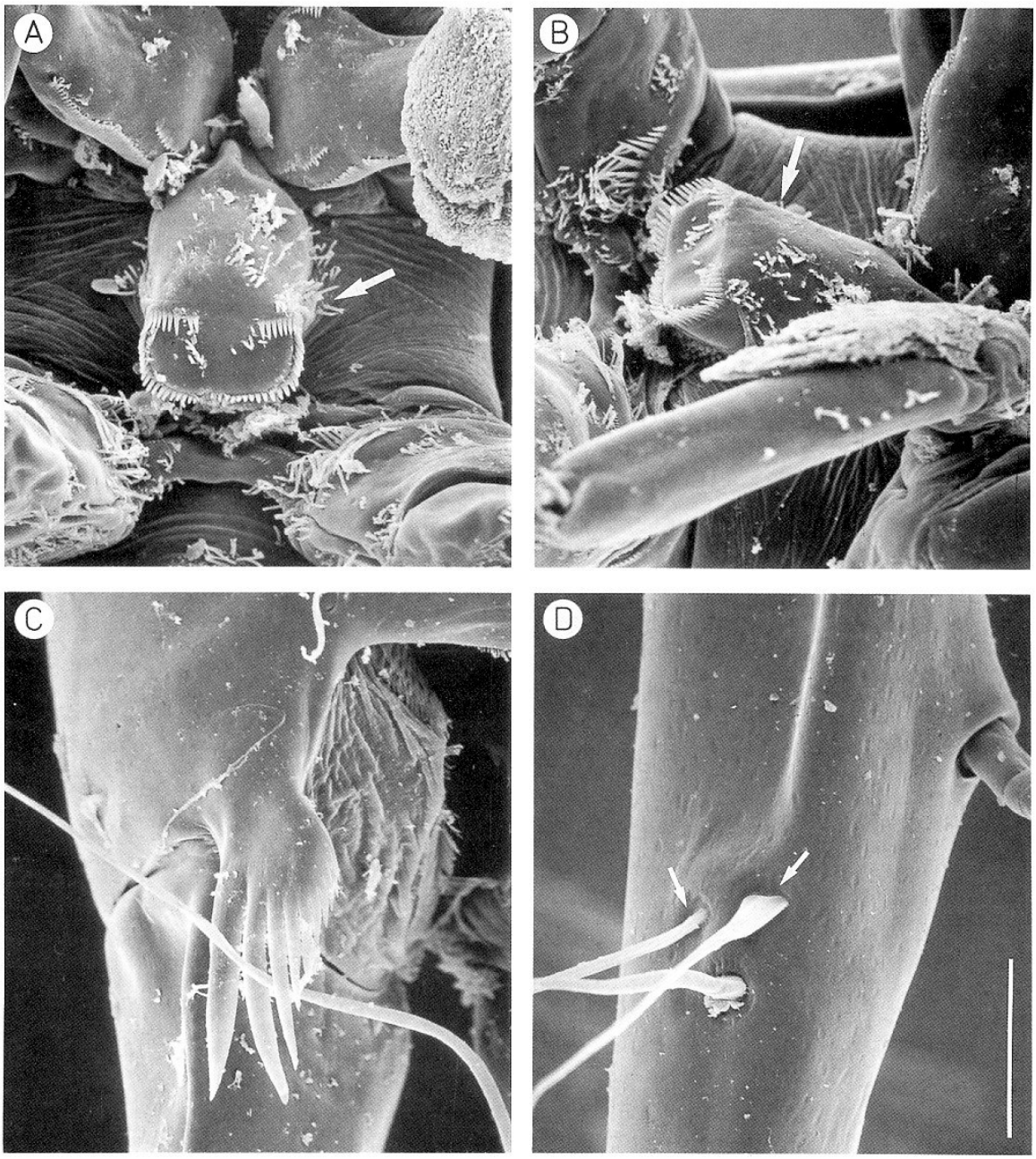

Fig. 9 - *Meloriastacus ctenidis*. SEM micrographs: A, truncate semi-cylindrical process (arrowed) between maxillipeds and first pair of legs, ventral; B, same, lateral; C, spinular comb at posterior corner of anal opening, dorsal; D, lateral view of caudal ramus showing seta I flanked by elongate spinules (arrowed). Scale bars (indicated in D only): 20 µm (A, B), 15 µm (C), 10 µm (D).

unusually well developed seta I which is typically flanked by 2 long seta-like spinules (1 dorsal, 1 ventral). The extreme development of seta I and the presence of the accessory spinules is a double synapomorphy linking both genera. In Archileptastacus seta III is absent (confirmed in *A. aberrans*) and is presumably entirely incorporated in the spinous process. The interruption of the outer cuticle illustrated by Mielke (1975) for *A. dichatoensis* does not mark the original position of seta III, yet merely corresponds to the lateral secretory pore located posterior to seta II.

Archileptastacus and *Meloriastacus* can be considered

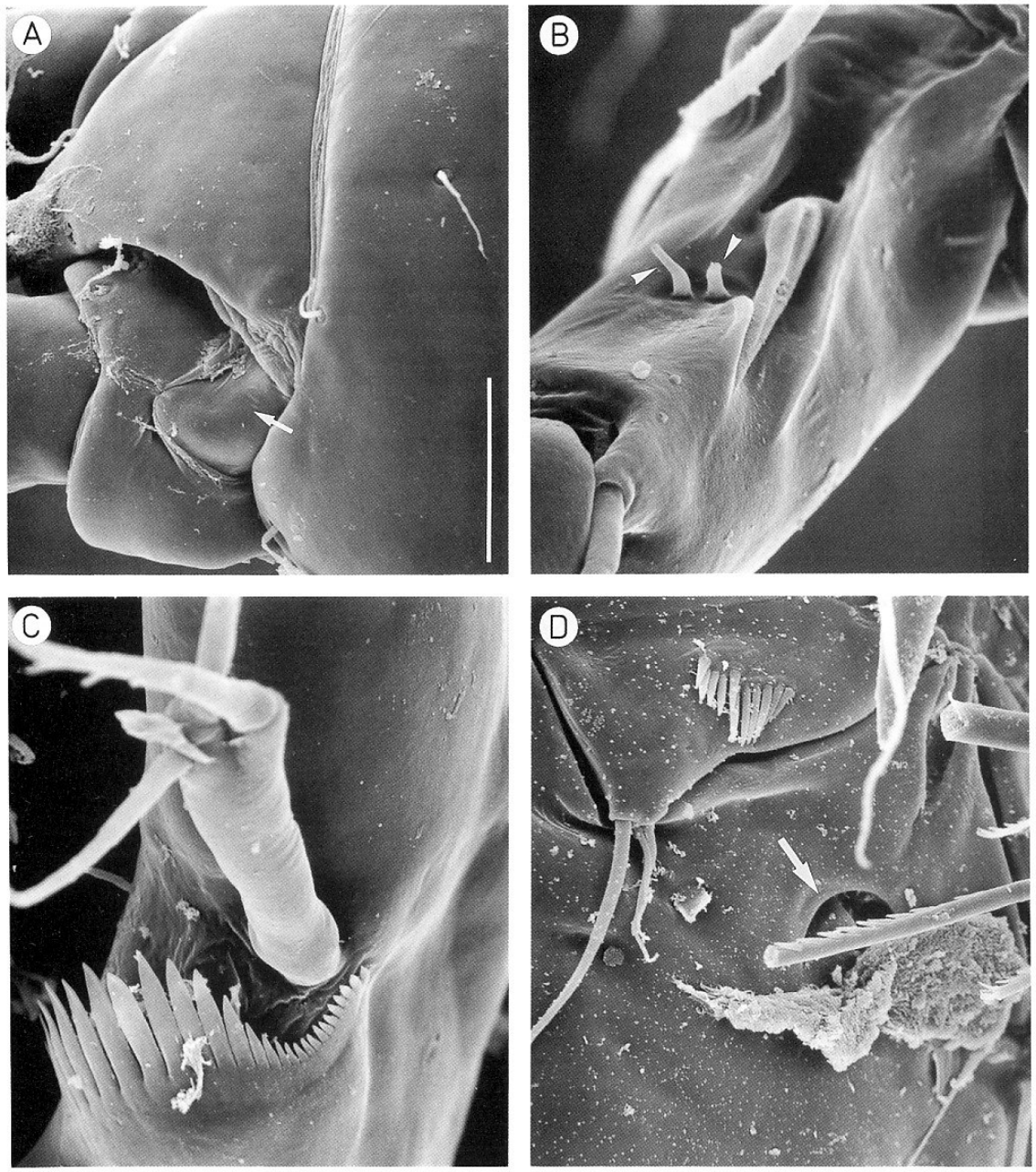

Fig. 10 - *Meloriastacus ctenidis*. SEM micrographs: A, rostrum and base of left antennule, lateral (antennulary sclerite arrowed); B, antennulary segment 8 of ♂, anterior (rudimentary tubular structure arrowed); C, antennary exopod; D, genital field ♀ (copulatory pore arrowed). Scale bars (indicated in A only): 15 µm (A, D), 6 µm (C), 4.3 µm (B).

sister taxa on the basis of the following suite of synapomorphies: (1) caudal ramus with strongly developed seta I flanked by 2 elongate spinules; (2) caudal ramus forming backwardly directed spinous process derived from integumental outgrowth; (3) caudal ramus seta III vestigial (entirely lost in *Archileptastacus*); (4) P5 exopod and baseoendopod fused forming triangular plate in both sexes; (5) outer distal spine of P2-P4 enp-2 fused to segment (completely incorporated and lost in *Archileptastacus*); (6) P2-P4 exp-3 with 1 outer spine; (7) anal opening flanked by spinular rows around posterior margin (forming spinular combs in *Meloriastacus*). The

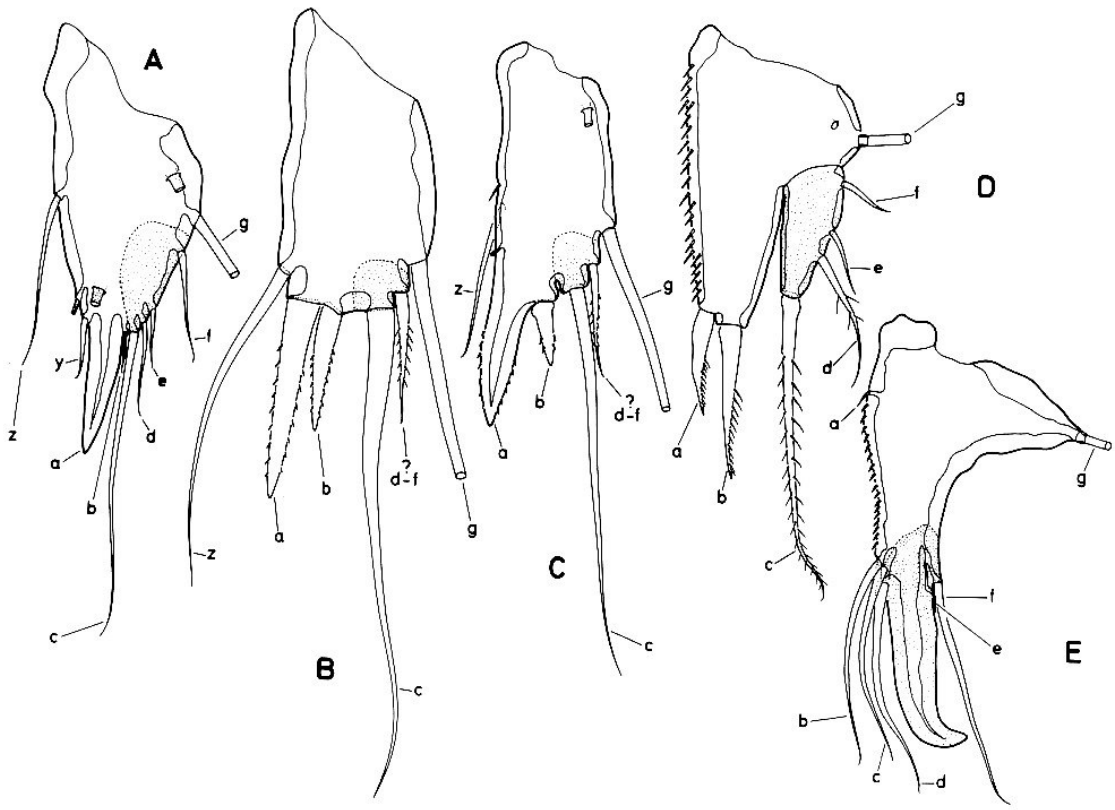

Fig. 11 - Homology of setal elements in female P5 of *Meloriastacus* (A), *Archileptastacus aberrans* (B), *A. dichatoensis* (C), *Paraleptastacus* (D) and *Leptastacus* (E), [Stippled area in A-C, E representing leg portion omologous to incorporated exopod - compare D].

Meloriastacus-Archileptastacus clade represents the first offshoot in the evolution of the Leptastacidae, the remainder of the genera being grouped in a monophyletic lineage in which *Paraleptastacus* represents the most primitive taxon (Huys, 1992). Autapomorphies for *Meloriastacus* include: (1) elongation of antennulary segment 2 in both sexes; (2) reduction of the accessory seta on the maxillipedal endopod; (3) conspicuous spinular combs on anal somite.

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