

# REDESCRIPTION OF *ENHYDROSOMA LACUNAE* JAKUBISIYAK, 1933 (COPEPODA, HARPACTICOIDA); WITH COMMENTS ON THE *ENHYDROSOMA* SPECIES REPORTED FROM WEST ATLANTIC LOCALITIES, AND A DISCUSSION OF CLETODID DEVELOPMENT

FRANK FIERS

## SARSIA



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Thus far, 16 species of the cletodid genus *Enhydrosoma* have been reported from localities in the West Atlantic. Reexamination of these records revealed the following: (1) *Cletodes stylicaudatus* WILLEY, 1929 should be assigned to the genus *Stylicletodes* and quoted as *Stylicletodes stylicaudatus* (WILLEY, 1929); (2) the Patagonian specimens identified as *Enhydrosoma propinquum* by PALLARES (1975) represent an unknown species, named hereafter *Enhydrosoma rosae* sp. n.; (3) *E. propinquum* reported from North Inlet Estuary (South Carolina) turned out to be a different and unknown species and should be referred to as *Enhydrosoma* spec.; (4) additional comments on the male juvenile features of *E. nicobaricum* SEWELL are given. Following these amendments, *E. lacunae* JAKUBISIYAK is redescribed based on material from Celestún Lagoon (Yucatan, Mexico). *E. woodini* THISTLE is considered a junior synonym of *E. lacunae*. There seem to be sufficient reasons to consider the Brazilian species, *E. mangroviae* JAKOBI and *E. gerlachi* JAKOBI as junior synonyms of *E. lacunae*. Finally, the copepodid development of *E. lacunae* is described. The segment additions in the ramal development are compared with *Cletodes*. The heterochronic development resulting in the unique segmentation of the exopodal rami of *Enhydrosomella* is discussed and the homology of the male P3 dimorphic apophysis in Cletodidae is reconsidered.

Frank Fiers, Royal Belgian Institute for Natural Sciences, Invertebrate Section, Vautierstraat 29, B-1000 Brussels, Belgium.

KEYWORDS: Harpacticoida; Cletodidae; developmental constraints.

## INTRODUCTION

The first record of a representative of the genus *Enhydrosoma* from a West Atlantic locality is from WILLEY (1929) who reported on *Cletodes* (= *Enhydrosoma*) *buchholtzi* BOECK, 1872 from Fundy Bay in New Brunswick (Canada). The rather brief description deals nearly exclusively with the previously unknown male. Up to now, WILLEY'S (1929) description is still the only available reference to the male morphology of this species. Recently, GEE (1994) provided strong arguments indicating that *E. buchholtzi*, as a representative of a species-group consisting of five closely related species, is more closely related to some species of the genus *Cletodes* than to those presently assigned to *Enhydrosoma*.

JAKUBISIYAK (1933) provided a rather brief description of a new *Enhydrosoma* species, *E. lacunae*, from a lagoon near Matanzas on the north coast of Cuba. This species is reported here for the second time. Several specimens,

including all copepodid stages, were found in Celestún Lagoon, a small estuary on the north-west corner of the Yucatan Peninsula.

In 1935, WILLEY reporting on the copepod fauna of Bermuda, defined *Cletodes stylicaudatus* based on a single male specimen. Soon afterwards, LANG (1936) allocated the species from its original genus to *Enhydrosoma* where it remained until today although it displays very distinctive features regarding the morphology of the legs and, most particularly, the shape of the sexual dimorphic third leg.

Curiously, LANG (1948:1261-1262, 1273) became puzzled with the orientation of the male endopodite of the third leg, which exhibits a long straight outer apophysis on the median segment. In his monograph, he even omitted WILLEY'S (1935) illustration of the P3 in the belief that the appendage was reversed during dissection. However he failed to see the close similarity of the appendages of *C. stylicaudatus* with those of the two species allocated by him to the genus *Stylicletodes*. Personal observations on

males from a *Stylicletodes* species from California confirmed that the male endopodite of the third leg in this genus is three-segmented with a long, straight and sharp apophysis arising from the outer distal edge of the median segment. Pace LANG (1936, 1948), *Cletodes stylicaudatus* cannot be referred to the genus *Enhydrosoma*, but has to be assigned to the genus *Stylicletodes* and quoted as *Stylicletodes stylicaudatus* (WILLEY, 1935).

COULL (1975) described *E. baruchi* from North Inlet Estuary (Georgetown) in South Carolina, and provided an updated key of the genus. The co-existence of *E. baruchi* and *E. propinquum* in this South Carolina estuary, provided the impetus for detailed statistical and morphological analyses of both species (IVESTER & COULL 1977, also referred to in COULL & VERNBERG 1970, 1975; COULL 1977; MONTAGNA & al. 1983; COULL & DUDLEY 1985; ELLIS & COULL 1989; and probably CHANDLER 1990). However, as there are serious doubts about the identity of these animals and because of the striking resemblance between *E. propinquum* from South Carolina and *E. lacunae* as redescribed here, topotypic specimens kindly placed at my disposal by B. Coull were re-examined. This revealed that the South Carolina specimens represent an unknown species. The description of this species, which until then should be referred to as *Enhydrosoma* sp. (IVESTER & COULL 1977), will form part of a future paper dealing with the specific status of the specimens reported from West Atlantic localities and thus far identified as *E. propinquum*.

PALLARES (1975) contributed an excellent description of an *Enhydrosoma* species from Patagonia and identified her specimens as *E. propinquum* (BRADY, 1880). Despite the resemblance of the caudal rami and fifth legs with those of *E. propinquum*, the Patagonian specimens represent a different species clearly defined by the presence of only two terminal setae on the endopodites of P3 and P4. In this respect, the Patagonian specimens resemble more *Enhydrosoma baruchi* COULL, 1975 than to any other species presently assigned to the genus *Enhydrosoma*. The species is named here *Enhydrosoma rosae* sp. n. in honour of Dr. Rosa E. Pallares for her outstanding work on Patagonian marine copepods.

THISTLE (1980) added two more species to the genus: *Enhydrosoma franklini* found subtidally in Florida and *E. woodini* from a *Spartina* estuarine marsh in North Carolina. FIERS (1987) questioned the generic assignment of *E. franklini* because of the particular segmentation of the exopodal rami of the natatorial legs and transferred the species to the genus *Enhydrosomella*. His view was recently confirmed by GEE (1994). Specimens of *Enhydrosomella franklini* collected between the reefs at Cozumel (Mexico, unpublished) will be included in the ongoing work on the marine copepods from the Yucatan continental shelf.

The second species, *E. woodini* could easily be distinguished from the other *Enhydrosoma* species because of the unique setal combination on the female P5 with only two elements on the exopodal ramus and three on the vestigial endopodite. In respect to the noticeable variability of caudal rami and positions of endopodal elements on the female fifth leg as observed in the specimens from Celestún Lagoon, the specific status of *E. woodini* is discussed in detail below; this taxon is considered a junior synonym of *E. lacunae*.

RAVENEL & THISTLE (1981), studying the effects of sediment characteristics on the distribution of sublittoral copepods, found *E. littorale* WELLS, 1967 in samples recovered from the east coast of Florida. *E. littorale*, originally described from Inhaca Island (Mozambique), is rather easily distinguished from the other *Enhydrosoma* species because of the remarkable long spiniform outer sub-distal spine on the endopodite of the fourth leg. This species would be the first representative of the genus with clear Indo-Pacific affinity.

The latest addition of an *Enhydrosoma* species to the fauna of the West Atlantic is *E. herrerae* BELL & KERN, 1982, from shallow sublittoral stations in Tampa Bay, Florida. Apart from its type locality, this harpacticoid is found frequently but in low densities in the Bay of Campeche (western continental shelf of the Yucatan Peninsula) to depths of 50 m (pers. obs.).

Only a few other species of *Enhydrosoma* were listed in papers dealing with regional fauna analyses or with meiobenthic ecology. *Enhydrosoma propinquum* (BRADY) and *E. (= Stylicletodes) stylicaudatum* WILLEY were found in samples from Bermuda (COULL 1970b; COULL & HERMAN 1970). The former constitutes up to 10 % of the harpacticoid copepod community in the deeper parts of Castel Harbour, but was only occasionally present in the other stations. Most regrettably, *E. (= Stylicletodes) stylicaudatum* was not described, although 10 specimens were encountered in the same samples with *E. propinquum*.

*Enhydrosoma buchholtzi* (BOECK), *E. curvirostre* (T. SCOTT), and *E. propinquum* (BRADY) were reported from the North Carolina continental shelf (COULL 1971). The former two were found in samples recovered from depths of 340 and 465 m, while *E. propinquum* (BRADY) was found in 6 out of 18 samples recovered from depths ranging between 340 and 450 m.

COULL (1977) referred to BRICKMAN (1972) who identified *E. longifurcatum* SARS, 1909 contained in samples from New Jersey salt marshes, and to *E. propinquum* (BRADY) from mud flats in Lynn Harbour (Massachusetts), while FLEEGER (1980) reported on *E. propinquum* from a Louisiana salt marsh. More recently, DECHO & FLEEGER (1988) reported *E. woodini* (= *E. lacunae*) from Cocodrie (Louisiana) in their experiments on micro-scale dispersion.

The six *Enhydrosoma* species from Sao Paulo in the Brazilian state Paraná (JAKOBI 1955) are consistently omitted from the literature and keys since LANG (1965) advised they be ignored because of the inaccurate original descriptions. Indeed, the contradictions between the brief descriptions, the composite plates and the listed setal formulae make identification of these species hazardous. However, when focusing on the illustrations only, some information can be obtained which certainly will be helpful in future identification of these animals. In the present work, two of the Brazilian species, namely *E. mangroviae* and *E. gerlachi* are thought to be possible junior synonyms of *E. lacunae*. However, it is evident that only reexamination of the type-specimens and/or study of newly obtained materials from Sao Paulo can provide a decisive answer about the identity/validity of these harpacticoid species.

#### MATERIAL AND METHODS

*Enhydrosoma lacunae* JAKUBISIAK, 1933 was recovered from a sample taken along the shore of Celestún Lagoon (sometimes indicated as Estuario Celestún, Yucatan, Mexico), at the right side of the bridge spanning the estuary in the direction of Celestún Village (estimated coordinates. 20°49'59" N, 90°21'50" W; Leg. F. Fiers, 15 March 1993, MEX 93-95). The sample consisted of the 'aufwuchs' covering the submerged pneumatophores of mangrove trees. At collection the sample was fixed in 4 % buffered formalin; whereas the animals sorted out were transferred to 75 % denaturated ethyl alcohol for long-term storage. Observations and dissections were made in glycerin with coverglasses sealed for permanent slides. Observations and drawings were made at 1250 X on a Leitz Diaplan light microscope, equipped with a drawing tube. The physico-chemical characteristics of the locality can be found in VALDÉS & al. (1988) and HERRERA-SILVEIRA (1994).

The harpacticoid fauna found in the sample has been listed elsewhere (FIERS 1995) and several of the taxa will be dealt with in future papers. The collection of *Enhydrosoma lacunae* is stored at the Royal Belgian Institute for Natural Sciences.

#### TAXONOMICAL ACCOUNT

##### *Enhydrosoma lacunae* JAKUBISIAK, 1933

*Enhydrosoma woodini* THISTLE, 1980, ? *Enhydrosoma gerlachi* JAKOBI, 1955, ? *Enhydrosoma mangroviae* JAKOBI, 1955.

**Type-locality.** Cuba, Lagoon near Matanzas (North coast of Cuba; JAKUBISIAK 1933).

**Material examined.** Dissected, 3 females (labelled COP 3940A-B, 3943A-B, 3944A-B), 2 males (labelled COP 3941A-B, 3942A-B), 1 CI (COP 3945), 1 CII (COP 3946), 1 CIII (COP 3947), 3 CIV (COP 3948, 3949, 3950), 2 CV (COP 3951, 3952); ethanol preserved: 12 ♀♀ (3 ovigerous), 12 ♂♂, 3 CI, 2 CII, 2 CIII and 2 CV(♂), labelled COP 3971.

#### Description of the adults

(Figs 1 - 6)

**Female.** - Habitus (Fig. 1A, B). Body tapering gradually from posterior margin of cephalothorax towards anal segment. Aspect of body curved in lateral view. Length (from tip of rostrum to proximal margin of caudal rami, in dorsal view): 462-478 µm, with largest width near posterior margin of cephalothorax (± 120 µm). Proportional lengths: cephalothorax 1/4 of body-length; urosome (including caudal rami) half as long as body.

Cephalothorax with strongly folded lateral sides, and a dorsal pair of longitudinal ridges; pedigerous somites with rounded pleurites, and medio-lateral sclerotized longitudinal ridges (one on either side); abdominal somites with posteriorly directed triangular lateral edges, and a more dorsally situated curved sclerotized ridge; posterior margin of cephalothorax with 8 sensillae arising from small but distinct cones; second to fifth thoracic somite with 10, 12, 12, and 8 posterior cones, respectively; first genital somite with 6 cones, and second genital somite with 8 dorsal cones and one sensilla on either side along postero-ventral margin; second abdominal somite with six dorsal and two ventral cones; penultimate somite without sensillae, but with 1 pair of dorsal tube pores and one pore on each lateralmost edge. Integument of all somites finely striated (not illustrated in Fig. 1); genital double somite and subsequent somite with a median short row of slender spinules along posterior ventral margin, accompanied with fragile hairs along entire margin in third abdominal somite, while entire postero-ventral margin of preanal somite is ornamented with spinules, arranged in discrete groups (Fig. 2A).

Anal somite with rounded lateral margins, a crescentic spinulose operculum, and 1 pair of cones. Caudal rami with variable shape ranging from long ovate to cylindrical, with L/W ratios of 2.93 (long ovate form, Fig. 2A), over 5 (intermediate form, Figs 2B, 6A), and 7.88 (cylindrical form, Fig. 2C). Lateral setae and biarticulate dorsal seta arising in proximal half (2 in proximal fourth, dorsal and third lateral near middle). Outer principal seta fused at base with inner one and as long as medial seta. Inner principal seta broken off in all specimens.

Rostrum (Fig. 3G) fused with cephalothorax, strongly bent ventrally; lateral margins tapering, giving rostrum triangular aspect; apex with slightly produced rounded tip, furnished with long hairs on ventral side; one pair of sensorial setae, pores not observed; dorsal integument striated.

Antennule (Fig. 3D) 5-segmented with following armature (Arabic numerals) on segments (Roman numerals): I(1) - II(6) - III(8+aesth) - IV(1) - V(11+aesth); setae ornamented with minute spinules (segment II), strongly spinulose (on segments I and V), or smooth (segment III and V); segment

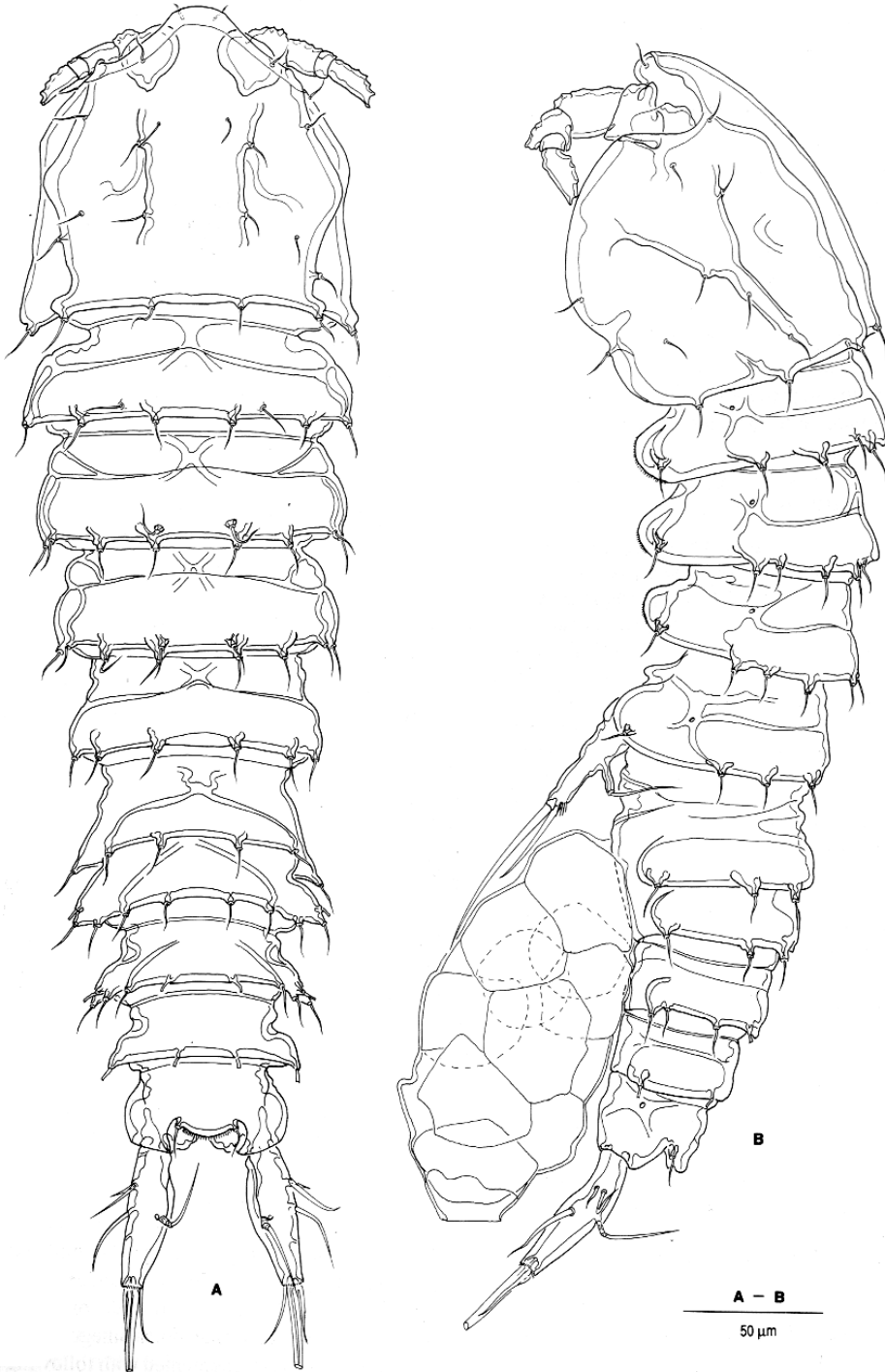


Fig. 1. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A. Female habitus, dorsal. B. Female habitus, lateral.

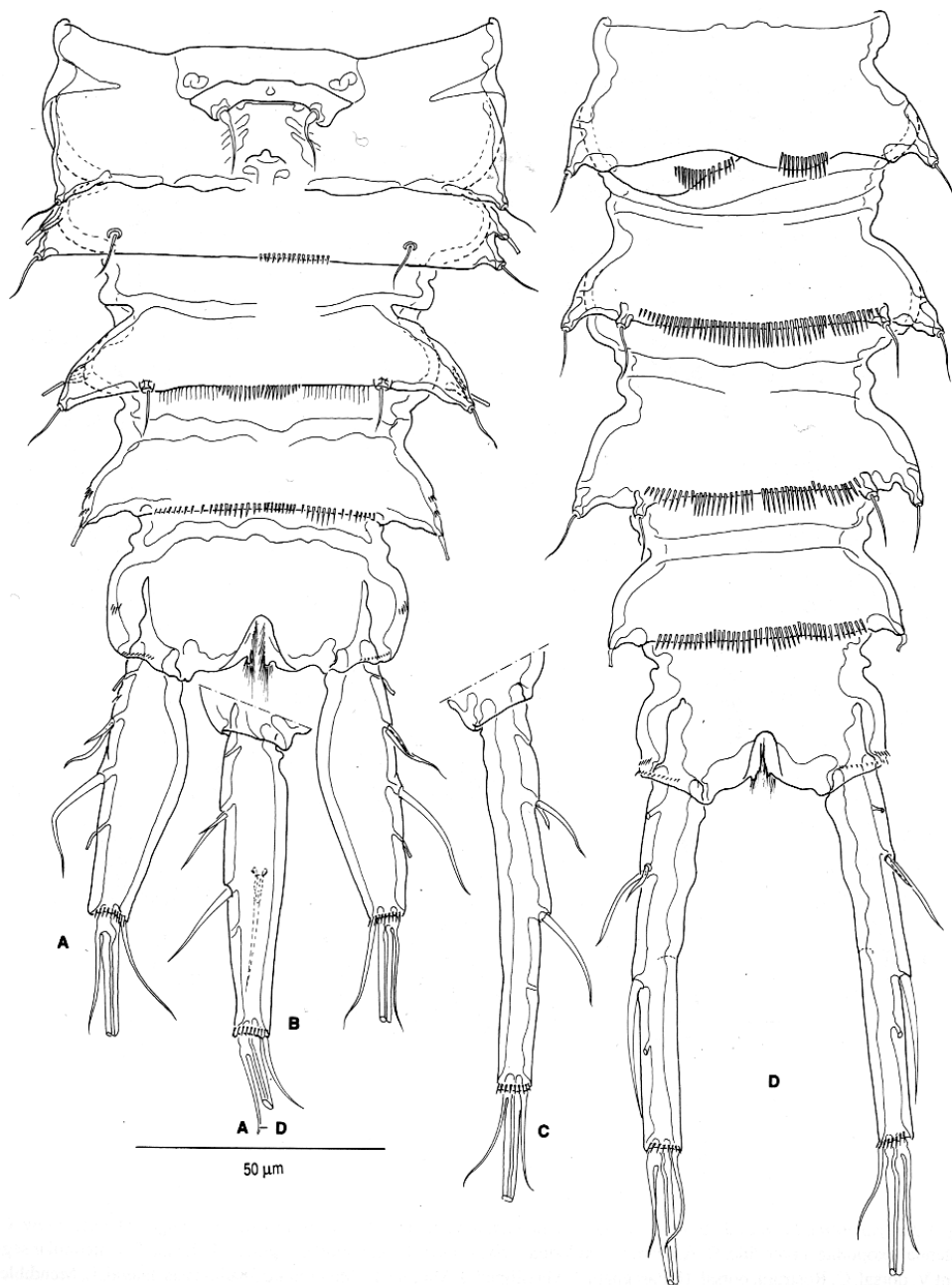


Fig. 2. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A. Female abdomen, ventral. B. Caudal ramus of female specimen illustrated in Fig. 6B, ventral. C. Caudal ramus of another female specimen, ventral. D. Male abdomen, ventral.



Fig. 3. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A. Antenna, medial view. B. Distalmost antennal segment, outer view. C. Antennal exopodite, outer side. D. Antennule, exploded view, ventral. E. Antennular segment II, dorsal. F. Antennular segment V, dorsal. G. Rostrum, dorsal. H. Paragnath. I. Maxilliped. J. Maxilla. K. Mandibular gnathobasis, lateral. L. Mandible. M. Maxillule.



Fig. 4. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A. Male antennule. B. Inner margin of antennular segment IV. C. P1, posterior. D. P2, anterior. E. P4, anterior. F. Female P5, posterior. G. Baseoendopodal region of another female specimen. H. Male P5, anterior.



Fig. 5. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A. Female P3, anterior. B. Male P3, anterior. C. Endopodite P3 of male copepodid IV. D. Endopodite P3 of female copepodid V. E. Endopodite P3 of male copepodid V. F. Endopodite P3, adult male, posterior. G. Endopodite P3 of *Stylicletodes* spec. (in G: right side is external; in A-F setal ornamentation not illustrated).



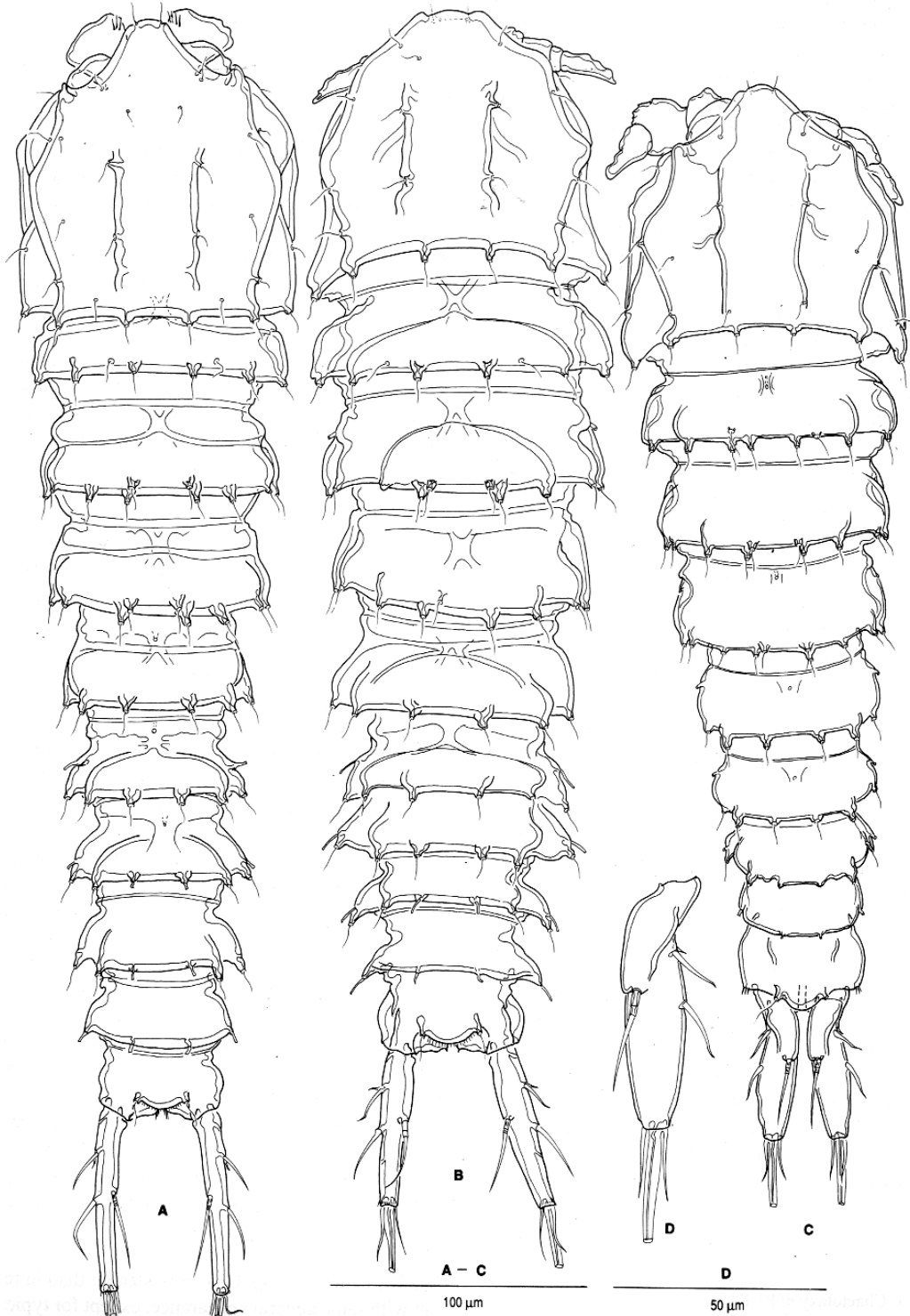


Fig. 6. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A. Male habitus, dorsal. B. Habitus of female with cylindrical caudal rami, dorsal. C, D. Copepodid V. C. Habitus of male, dorsal. D. Caudal ramus of male, dorsal.

II with a dorsal slender and smooth seta, arising from a well marked circular structure (Fig. 3E); dorsal surface partially marked with fine striae on segment II, and with minute spinules in segments II and V (Fig. 3E, F); ventral surface of segment I with 4 crescentic rows of long spinules, of all other segments smooth.

Antenna (Fig. 3A) with allobasis and well-developed one-segmented exopodite. Allobasis without abexopodal seta; surface of coxa and allobasis ornamented with some rows of slender spinules. Endopodal segment with seven elements: 2 lateral spines, 3 apical spines and 2 apical geniculate setae; the outermost flagellated spine without trace of fused seta; integument of endopodal segment with long spinules along abexopodal margin, and slender spinules along opposite side (Fig. 3B). Exopodite with a median lateral and an apical spinulose seta; surface furnished with a proximal and a distal row of spinules (Fig. 3C).

Mandible (Fig. 3K, L) with very slender medial part of gnathobasis; biting edge with 6 sharp, non-articulating spines and a single spinule at inner edge; palp short with 3 pinnate setae.

Maxillule (Fig. 3M). Coxa, basis and rami fused together; arthrite with 4 terminal curved spines, 3 lateral short setae, and 1 seta on surface; coxa-basis furnished with two pairs of apical setae, and endopodite represented by one seta only.

Maxilla (Fig. 3J). Syncoxa with a single endite (proximal one), having two slender elements and a spinulose one; distal endite furnished with a spinulose and a smooth seta; a transversal line (articulation or fold ?) between syncoxa and basis; claw of basis unarmed; endopodite vestigial, represented by 2 setae, fused at base; inner and outer margin of syncoxa, and margin of basis near implantation of endopodal setae set with spinules.

Maxilliped (Fig. 3I) prehensile, with short (twice as long as wide) syncoxa, lacking armature, but furnished with some slender spinules in proximal half; basis ovate, ornamented with a single row of long spinules parallel to inner margin of palm; claw strongly curved distally, unarmed, without accessory setae.

P1 (Fig. 4C). Triangular praecoxa, devoid of ornamentation; coxa tapering medially, furnished with two rows of spinules on anterior surface; basis strongly sclerotized, with few spinules near implantation of outer seta, and a long row of spinules in front of articulation with endopodite; inner

seta spinulose, reaching halfway second endopodal segment. Exopodite 3-segmented, endopodite 2-segmented; the latter reaching just beyond second exopodal segment; outer margins of exopodal segments and outer margin of second endopodal segment ornamented with long spinules; inner margins of second exopodal and endopodal segments set with slender hairs. Chaetotaxy as in Table 1.

P2 (Fig. 4D), P3 (Fig. 5A), and P4 (Fig. 4E). Praecoxae minute, square in anterior view, triangular in posterior view, and ornamented with a row of minute spinules in P2; coxae tapering medially, furnished with a row of spinules parallel to outer margin and a transverse row close to the medial edge; bases ornamented on anterior surface with some spinules near implantation of outer element, a long row of long spinules in front of articulation with endopodite, and a few spinules close to medial margin, the latter covering a small pore orifice; posterior surfaces of coxae and bases smooth. Exopodites 3-segmented, endopodites 2-segmented; the latter reaching to distal half of third exopodal segments. Distal exopodal segment of P4 rather broad, about 1.5 times as long as wide. Setae with long setules, widely spaced; spines armed with small but distinct spinules. Ornaments of segments as in P1, and chaetotaxy as listed in Table 1.

P5 (Fig. 4F, G). Baseoendopodite sub-squarish, with a long cylindrical outer extension, bearing outer seta, but without a produced endopodal lobe; endopodal vestige represented by three strong spines. Outermost endopodal spine, about 3/4 as long as exopodal segment, and situated beside (Fig. 4F) or in front (Fig. 4G) of median spine. Median and innermost endopodal spines longer than exopodal segment. Exopodal segment 2.5 times as long as wide with slightly undulating margins, armed with a long inner apical rigid spine and a spinulose outer sub-distal curved seta. Articulation of exopodite with baseoendopodite presented as a fine suture along frontal side, frontal and caudal side, or entirely absent. Surface of P5 ornamented with long spinules near basis of baseoendopodal extension, and with small spinules near implantation of endopodal elements.

P6 (Fig. 2A). Median curved smooth plate in anterior half of first somite of genital complex. Each vestigial leg represented as a single smooth seta, thickened near implantation. Copulatory pore in posterior half of same somite, giving access to a broad, laterally extended inner complex, without visible differentiation of ducts or seminal receptacula. Ovipigerous females carrying single egg-sac reaching almost to end of caudal rami, containing  $\pm$  12 eggs.

Male. - Habitus (Fig. 6A) more slender than in female but with same general appearance, except for typical dimorphism in antennulae, separated genital somites, and caudal rami. Length: 464-474  $\mu$ m, with largest width near posterior edge of cephalothorax.

Table 1. Chaetotaxy of P1-P4.

	P1	P2	P3	P4
Exopodite	0-0-022	0-0-022	0-0-122	0-0-122
Endopodite	0-011	0-020	0-021	0-021

Integumental organs and structures as in female, except for postero-ventral margins of urosomal somites being ornamented with longer spinules, lined up along entire width (Fig. 2D).

Caudal rami (Figs. 2D, 6A) cylindrical, up to 7.3 times as long as wide, with same setal armature as in female.

Antennule (Fig. 4A) 6-segmented, sub-chirocer, with same ornamentation and armament of segment I as in female; setal armament of other segments: II(8) - III(7) - IV(9+serrate spine+aesth) - V(2 spines) - VI(8+aesth). Segment IV globulous, ornamented with a longitudinal row of long spinules on dorsal surface, and equipped with a compact modified tri-serrate spine on proximal edge of palm (Fig. 4B). Segment VI claw-shaped.

No dimorphic features observed in P1, P2, and P4. P3 exopodite with robust outer spines; second endopodite segment with a broad short, unornamented outer distal process with hyaline aspect (Fig. 5B). P5 (Fig. 4H) resembling the female P5 closely, somewhat more slender (L/W ratio: 1/2.7), and bearing only two strong and armed endopodal spines; suture between baseoendopodite and exopodite hardly visible, even absent on posterior side.

P6 vestige not differentiated on left side; but position indicated by a crescentic row of spinules; right P6 vestige represented as an ovate plate furnished with a medial row of spinules (Fig. 2D).

### *Description of the copepodid stages*

#### Copepodid I

(Figs 7A-F; 8A-C, M-N)

Habitus (Fig. 7A, B). Body with 5 tagmata; length 257-263  $\mu\text{m}$  (n = 4). Cephalothorax with folded integument and a pair of sclerotized dorsal ridges; thoracic somites well defined, having marked pleural regions; anal somite slender anteriorly, much wider with folded lateral margins posteriorly; anal operculum crescentic, and smooth. Integument of all somites devoid of ornamentation, except for 2 pairs of rows of spinules on ventral surface of anal somite (Fig. 7C).

Caudal rami (Fig. 7D-F) as long as anal somite, with a distinct proximal curvature of inner margin, and slowly tapering distally; L/W ratio: 2.5/1; tri-articulate dorsal seta arising from a small but distinct elevation of dorsal surface (Fig. 7E); 2 proximal lateral setae situated proximally from

biarticulate dorsal seta; 1 median lateral seta and 1 outer distal one; principal caudal setae fused together, with outer one as long as ramus and setulose; no inner distal seta present.

Rostrum broad at basis, having a rounded aspect, and furnished with a pair of sensillae; rostral tip not acute.

Antennule (Fig. 8N) 3-segmented with following armature: I(2) - II(2+aesth) - III(11+aesth); pinnate spines present on segments I and III; segment I with 2 rows of spinules.

Antenna (Fig. 8M) with allobasis, 1-segmented exopodite and endopodite; endopodal segment with 2 lateral and 4 elements; exopodite rather large, bearing 3 elements: a lateral and a distal long finely pinnate seta and a short smooth distal element; abexopodal seta not present; spinules along abexopodal margins of allobasis and endopodite, and near implantation of setae on exopodite and endopodite. Mouthparts not observed.

P1 (Fig. 8A) with spinulose protopodal components and spinulose one-segmented rami; outer seta on basis present, inner one absent; chaetotaxy in Table 2. P2 (Fig. 8B) resembling P1, but differs in number of elements on exopodite and in length of outer distal seta of endopodite; chaetotaxy in Table 2. P3 (Figs 7C, 8C) present as a distinct bud, bearing apically three smooth setae: outer one slightly thickened proximally, median and inner ones slender.

#### Copepodid II

(Figs 7G-L; 8D-G, O)

Habitus (Fig. 7H, I). Body with 6 tagmata; length 292-295  $\mu\text{m}$  (n = 3); differs from Cop I in the more strongly folded lateral margins of cephalothorax, the more ventrally bent rostrum, the more rounded lateral margins of the last somites, and in the number of sensorial setae on head, pedigerous somites 2 and 3.

Caudal rami (Fig. 7J-L) resembling rami of Cop I closely, but outer distal seta absent, and inner distal seta now present; outer principal seta smooth, only as long as inner distal one, and shorter than half length of ramus.

Antennule (Fig. 8O) 3-segmented with following armature: I(1)-II(7+aesth)-III(11+aesth); with a hardly visible transversal ridge on dorsal surface, indicating future suture between segm. II and III; pinnate setae/spines on segments I and III; segment I ornamented with 3 rows of spinules.

Fig. 7. (next page) *Enhydrosoma lacunae* JAKUBISIAK, 1933. A-F Copepodid I. A. Habitus, dorsal. B. Habitus, lateral. C. Third free somite to anal somite, ventral. D. Caudal ramus, dorsal. E. Idem, lateral. F. Idem, ventral. G-L Copepodid II. G. Fourth free somite to anal somite, ventral. H. Habitus, dorsal. I. Habitus, lateral. J. Caudal ramus, dorsal. K. Idem, lateral. L. Idem, ventral.

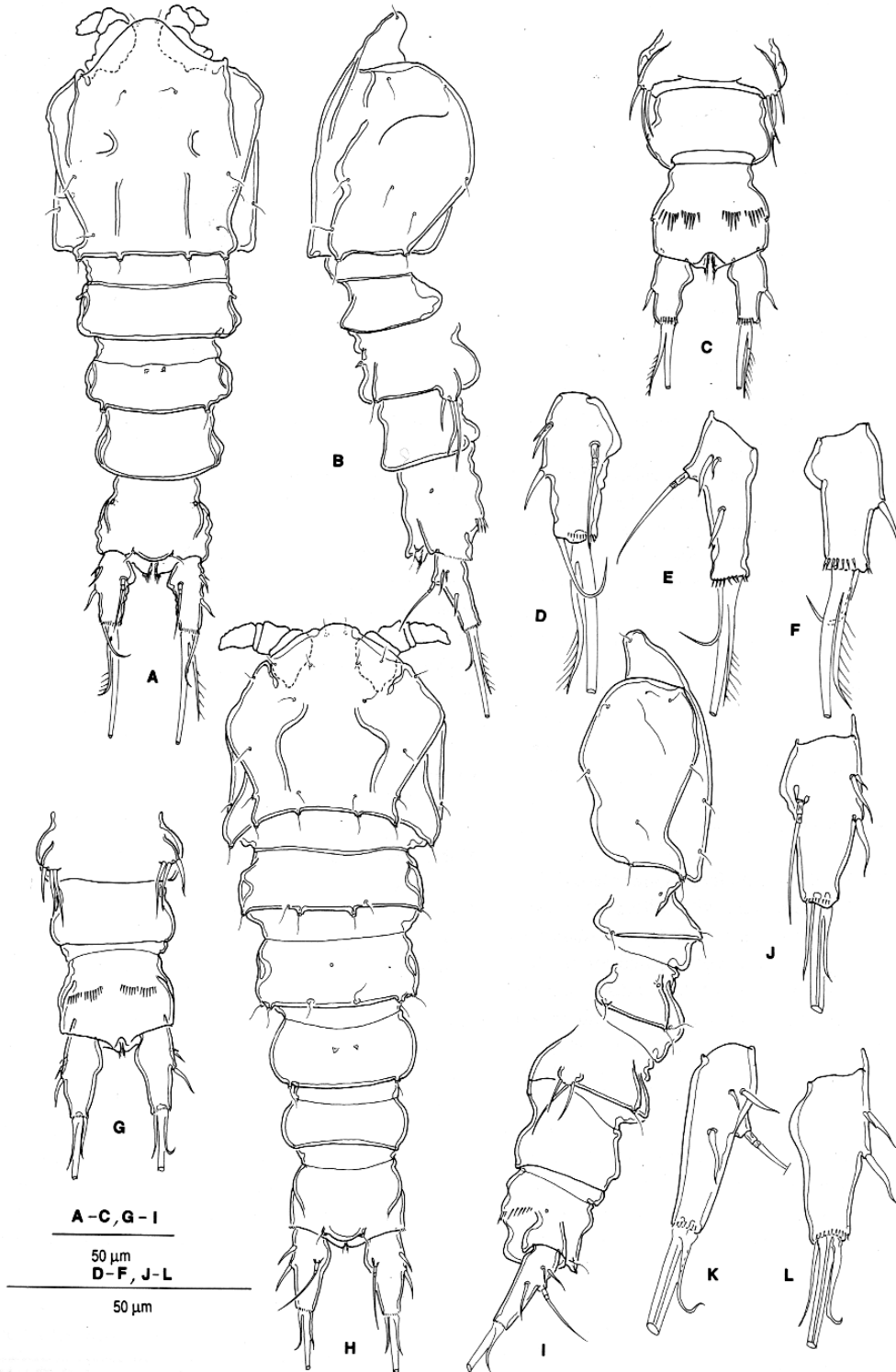


Fig. 7. (see previous page)

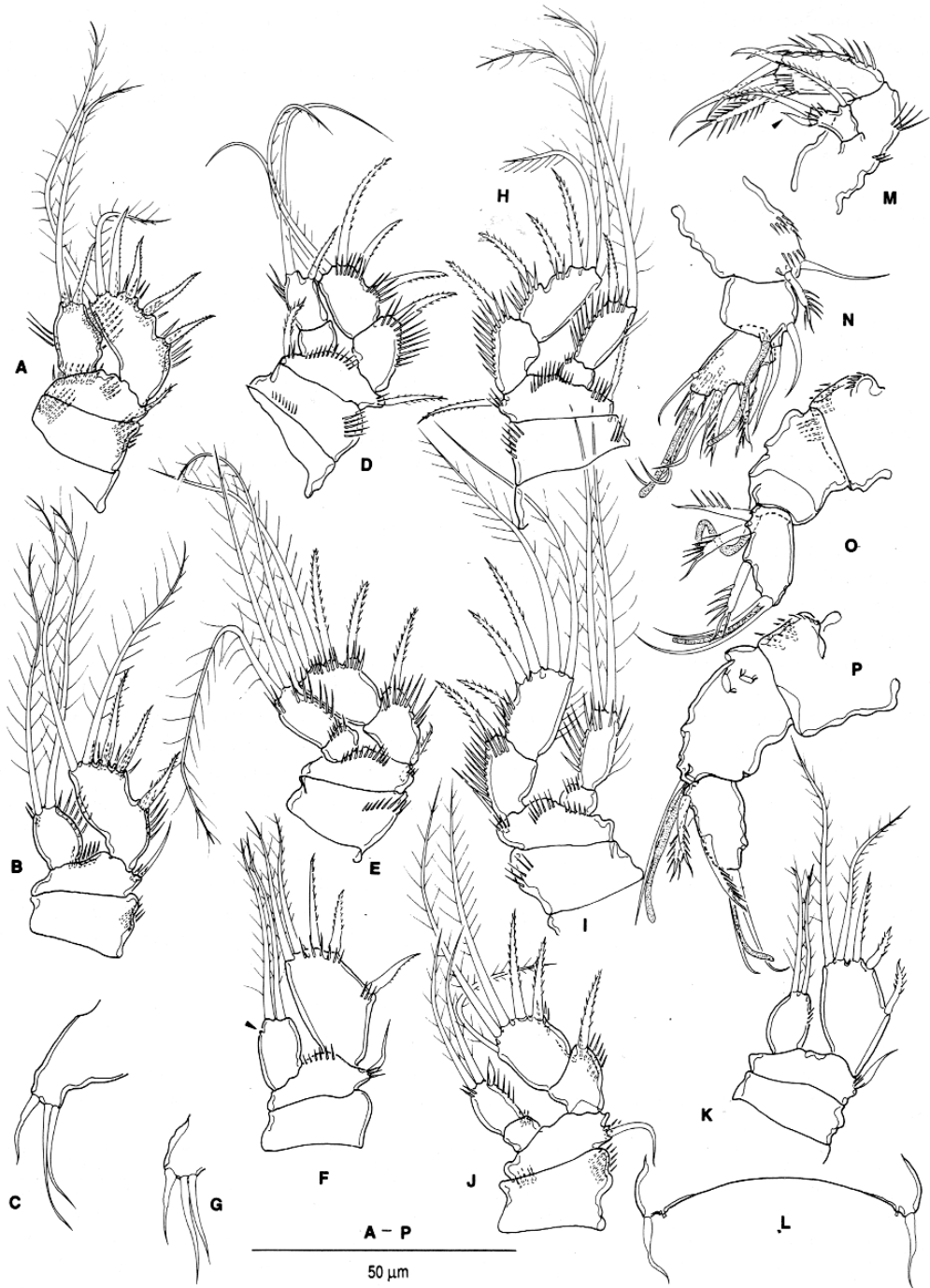


Fig. 8. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A-C Copepod I. A. P1, posterior. B. P2, posterior. C. P3. D-G Copepod II. D. P1, anterior. E. P2, anterior. F. P3, anterior (arrow indicating pore orifice). G. P4. H-L Copepod III. H. P1, anterior. I. P2, anterior. J. P3, posterior. K. P4, anterior. L. P5. M-N Copepod I. M. Antenna (arrow indicating additional seta on exopodite). N. Antennule. O. Antennule, copepod II. P. Antennule, copepod III.

Antenna as in adult with 2 setae on exopodite and 7 elements on endopodal segment.

P1 (Fig. 8D) and P2 (Fig. 8E) with same chaetotaxy as in Cop I, but with two-segmented rami; P1 with inner spine on basis present. P3 (Fig. 8F) with few spinules on protopodal components, and with one-segmented rami; endopodal segment with a small hyaline tubular pore orifice on inner margin.

P4 (Figs 7G, 8G) represented as a small bud, having an outer thickened smooth seta and two inner slender and smooth setae.

### Copepodid III

(Figs 8H-L, P; 9A-B)

Habitus (Fig. 9A) as in Cop II, but with an additional somite; length: 300-307 (n=3); second pedigerous somite with short medio-lateral ridges and 8 cones; third to penultimate somites still unornamented, respectively with 4, 4, 2 and 0 pairs of cones; penultimate somite furnished with slender spinules over entire posterodorsal margin, smooth along ventral margin; penultimate somite markedly shorter ventrally than dorsally (Fig. 9B).

Caudal rami 3 times as long as wide, with a less pronounced inner protuberance, having a more elongated aspect than in former stages; positions of setae as in adult.

Antennule (Fig. 8P) three-segmented, slightly longer than in Cop II, and ornamented as follows: I(1)-II(8+aesth)-III(1)-IV(11+aesth). Antenna and mouthparts as in adult.

P1 (Fig. 8H) and P2 (Fig. 8I) as in previous stage, except for an additional spine on second exopodal segment of P2, and for longer shape of individual segments of rami. P3 (Fig. 8J) with well developed and spinulose protopodal components, and 2-segmented rami; outer sub-distal spine on second endopodal segment short, with hyaline appear-

ance. P4 (Fig. 8K) with nearly smooth protopodal components and 1-segmented rami, resembling closely P3 in previous stage. Chaetotaxy of legs in Table 2.

P5 (Figs 8L, 9B) represented as a pair of little differentiated protuberances, bearing a single slightly thickened seta, and furnished with a minute hyaline tubular pore orifice.

### Copepodid IV, male

(Figs 5C; 9C-D; 10A-D, J; 11B)

Habitus (Fig. 9D). Body with 8 tagmata, resembling Cop III closely, except for further development of number of cones on pedigerous somites: 6, 8, 10 and 12; length: 360-368  $\mu$ m (n = 3); pedigerous somite 6 ornamented along posterodorsal margin with spinules, and with same length in dorsal and ventral view; penultimate somite with strongly folded and protruded posterodorsal margin, forming a transversal ridge ornamented with a cluster of spinules on each corner; somite distinctly shorter ventrally, surface with double row of spinules; anal somite with distinctly more convex lateral margins, but with rami similar to those in previous stage.

Antennule (Fig. 11B) of male copepodid 4-segmented with following armature: I(1)-II(7)-III(6+aesth)-IV(12+aesth); with a rounded extension of distal frontal corner of segment III (arrow in Fig. 11B); ornamentation as in preceding stages. Buccal appendages as in adult.

P1-P3 (Fig. 10A-C) nearly identical to those of adults, except for two-segmented rami; outer distal spine on endopodites P3 and P4 with a hyaline appearance; P4 (Fig. 10D) as P3 in previous stage: few spinules on segments, and 2-segmented rami.

P5 (Fig. 10J) with cylindrical outer extension, bearing outer seta of basis; exopodal lobe differentiated, not articulating, and bearing two apical smooth setae; endopodal

Table 2. Development of the chaetotaxy in *Enhydrosoma lacunae* (notation according to HUMES & HO 1969). NP: not present in this developmental stage; Data above line = adult characters, below line = preadult characters. \* armature of female/male P5, respectively.

Leg/stage	CI	CII	CIII	CIV	CV	ADULT
P1 exo	0.11.IV	0.1 - 0.11.III	0.1 - 0.11.III	0.1 - 0.11.III	0.1 - 0.11.III	0.1 - 0.1 - 0.11.II
end	0.1.1	0.0 - 0.1.1	0.0 - 0.1.1	0.0 - 0.1.1	0.0 - 0.1.1	0.0 - 0.1.1
P2 exo	0.11.III	0.1 - 0.11.II	0.1 - 0.11.III	0.1 - 0.11.III	0.1 - 0.11.III	0.1 - 0.1 - 0.11.II
end	0.2.0	0.0 - 0.2.0	0.0 - 0.2.0	0.0 - 0.2.0	0.0 - 0.2.0	0.0 - 0.2.0
P3 exo	3	0.11.III	0.1 - 1.11.II	0.1 - 1.11.III	0.1 - 1.11.III	0.1 - 0.1 - 1.11.II
end		0.2.0	0.0 - 0.2.1	0.0 - 0.2.1	0.0 - 0.2.1	0.0 - 0.2.1
P4 exo	NP	3	0.11.III	0.1 - 1.11.III	0.1 - 1.11.III	0.1 - 0.1 - 1.11.II
end			0.2.0	0.0 - 0.2.1	0.0 - 0.2.1	0.0 - 0.2.1
P5*exo	NP	NP	1	?/2	2/2	2/2
bas				?/2	3/2	3/2
P6	NP	NP	NP	NP	NP	1/0

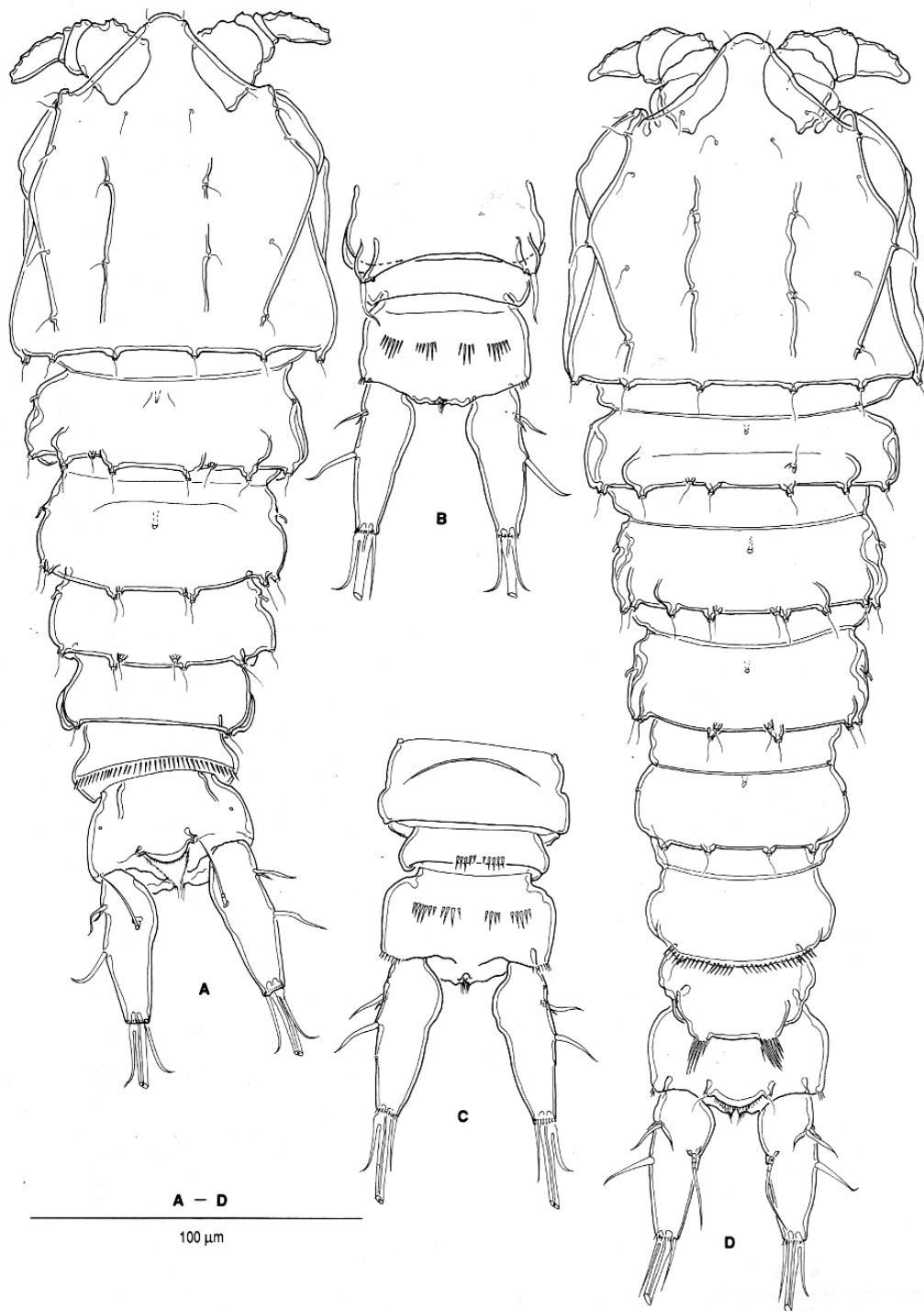


Fig. 9. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A, B Copepodid III. A. Habitus, dorsal. B. Fifth free somite to anal somite, ventral. C, D Copepodid IV. C. Sixth free somite to anal somite, ventral. D. Habitus, dorsal.

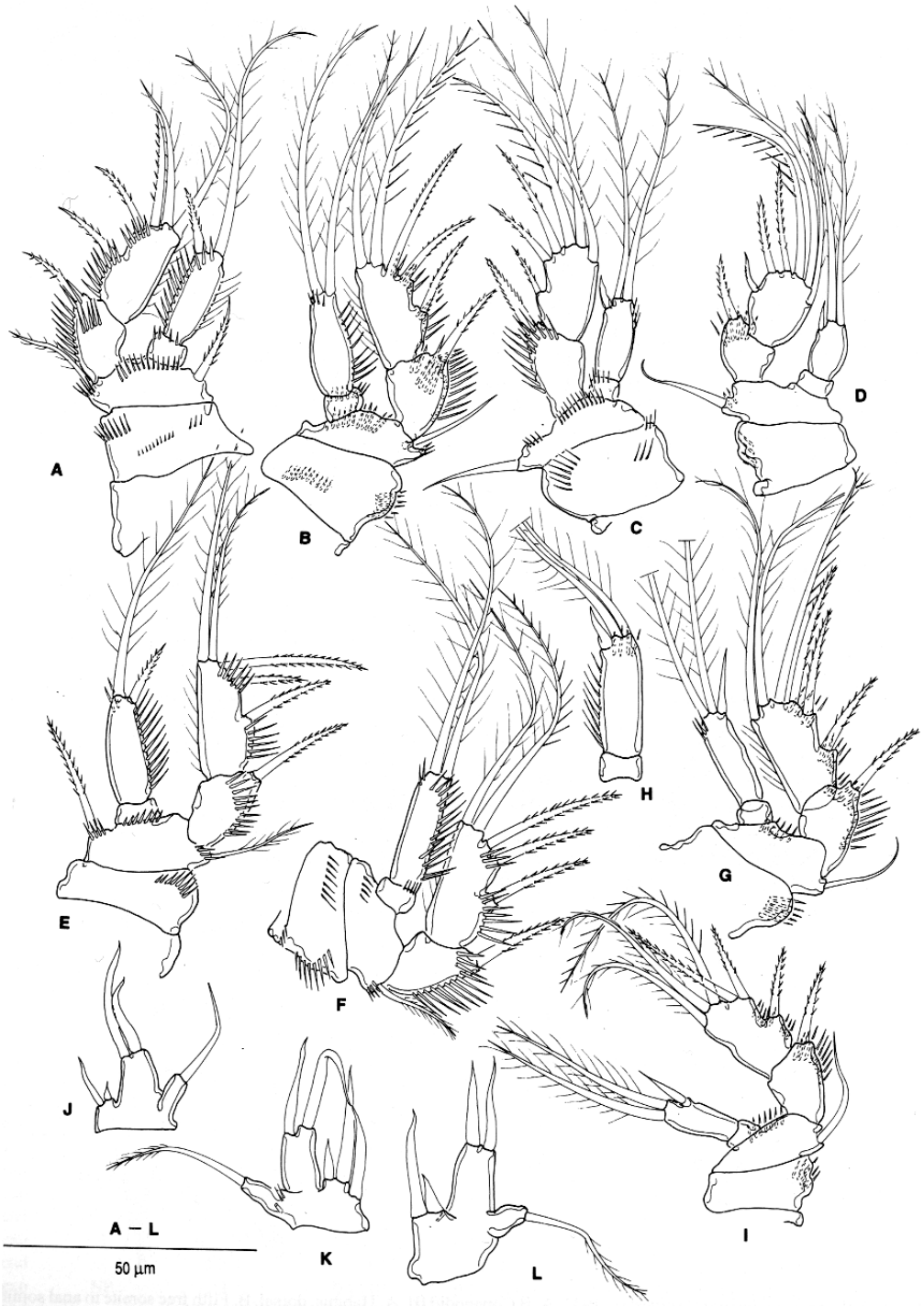


Fig. 10. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A-D Copepodid IV. A. P1, Anterior. B. P2, posterior. C. P3, anterior. D. P4, posterior. E-I Copepodid V. E. P1, anterior. F. P2, anterior. G. P3, posterior (female). H. Endopodite P3, anterior (male). I. P4, posterior. J. P5, copepodid IV. K, L Copepodid V. K. Female P5. L. Male P5.



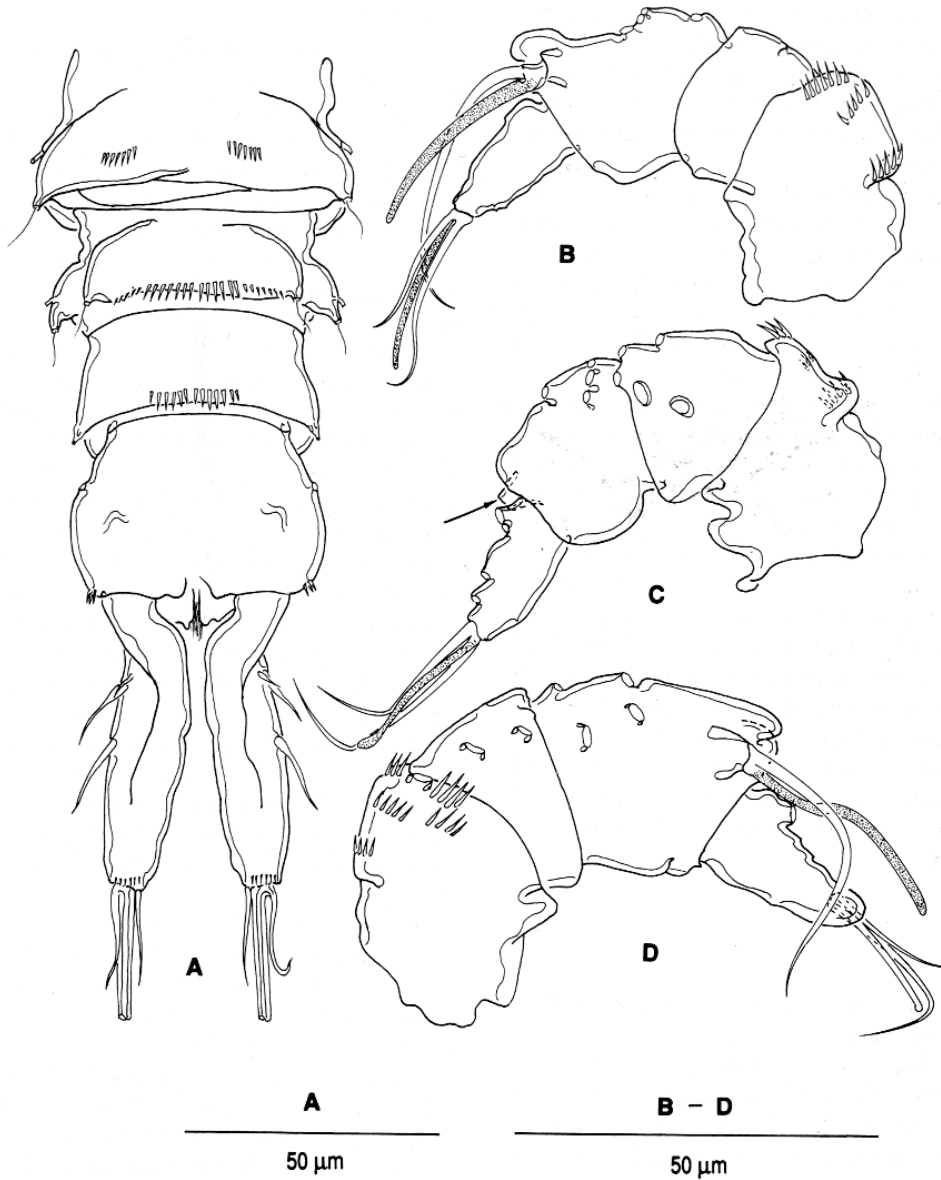


Fig. 11. *Enhydrosoma lacunae* JAKUBISIAK, 1933. A. Male abdomen, copepodid V, ventral. B. Male antennule, copepodid IV, ventral. C, D Copepodid V. C. Female antennule, dorsal (arrow indicates implantation of aesthetasc). D. Male antennule, ventral.

area, not produced, bearing an outer short and an inner long smooth seta. P5 of female and male copepodids are probably identical.

P6 not differentiated; ventral surface of somite smooth, only showing a fine crescentic integumental ridge in anterior half (Fig. 9C).

Copepodid V (female and male)  
(Figs 5D-E; 6C-D; 10E-I, K-L; 11A, C-D)

Habitus (Fig. 6C) with head and first pedigerous somite resembling adult; succeeding somites with less ornamentation and strongly tapering towards anal somite; number of sensorial hairs and pores along posterior margins as in

adult; length 412-423  $\mu\text{m}$  ( $n = 4$ ); nine tagmata. Ventral surface of P6-bearing somite with a pair of spinule rows; first and second abdominal somites ornamented with spinules along the posteroventral margin.

Caudal rami (Fig. 6D) long ovate, with distinct invagination in proximal half of outer margin; L/W-ratio: 4/1, with adult setal position; integument smooth; shape similar in both sexes.

Female antennule (Fig. 11C) 4-segmented with following armature: I(1)-II(7)-III(9+aesth)-IV(12+aesth); general appearance as Cop IV antennule of male, but lacking frontal extensions. Male antennule (Fig. 11D) more robust than female antennule with following armature: I(1)-II(8)-III(13+aesth)-IV(12+aesth), and with 2 blunt extensions on distal frontal corner of segm. III.

P1-P4 (Figs 10E-I) as in previous stage, except for longer distal segments of rami, and the more spinulose aspect of P4; endopodite P3 of male copepodid (Fig. 10H) resembling closely that of female, except for the slightly shorter and more curved outer distal spine on second segment, which has a hyaline appearance (Fig. 5E); chaetotaxy as in adult, see Table 2.

Female P5 (Fig. 10K) bearing three thick setae on endopodal vestige, and two on distal margin of exopodal lobe; the latter not differentiated from baseoendopodite, and at the most twice as long as wide. Male P5 (Fig. 10L) as in female but with only two setae on endopodal vestige.

P6 vestiges in female not differentiated; in male (Fig. 11A) represented as a long ovate impression along right side of posterior margin of somite; without additional ornamentation.

#### Citations

*Enhydrosoma lacunae* nov. spec. - JAKUBISIAK 1933:93-94, pl. XIX: figs 1-8.

*Enhydrosoma lacunae*: LANG 1936:469; LANG 1948:1271, fig. 506(2); JAKOBI 1955:91; LANG 1965:431 (key); WELLS 1976:165 (key); THISTLE 1980:392, 395 (key), table 1; WELLS & al. 1982:173; BELL & KERN 1983:902 (key); GEE 1994:84.

*Enhydrosoma woodini* n. sp. - THISTLE 1980:388-392, figs 3-4; BELL & KERN 1983:902 (key); WELLS 1983:5 (key); DECHO & FLEGER 1988:234; BODIN 1988:171; GEE 1994:100.

? *Enhydrosoma gerlachi* JAKOBI 1955:91, fig. 3.

? *Enhydrosoma mangroviae* JAKOBI 1955:90, fig. 2.

#### DISCUSSION

##### Synonymies

Among the species assigned to the genus *Enhydrosoma* (see for a recent definition: GEE (1994) few possess in both sexes a P5 exopodal segment bearing only two apical spiniform setae. So far, only *E. lacunae* JAKUBISIAK, 1933, *E. woodini* THISTLE, 1980, *E. nicobaricum* SEWELL, 1940 and two species, *E. mangroviae* and *E. gerlachi* described by JAKOBI (1955), exhibit this diagnostic feature. *E. lacunae* and *E. woodini* are currently recognized and appear in several identification keys, whereas the two Brazilian species were omitted because of the inaccuracy of the original descriptions (LANG 1965; THISTLE 1980; BODIN 1988).

In concordance with GEE (1994), it should be noted that *E. nicobaricum* was established on a copepodid V, almost certainly a juvenile male, instead of an adult female as stated by SEWELL (1940:344). In recent identification keys the species is distinguished from *E. lacunae* on the basis of the segmentation of the antennulae (LANG 1965) or the chaetotaxy of the female fifth leg (COULL 1975; THISTLE 1980; BELL & KERN 1982). The diagnostic features of this species, namely the 4-segmented antennulae and the 2 elements on the vestigial endopodite and exopodite are typical juvenile features encountered in male copepodids (see below, copepodids of *E. lacunae*). The antennal complement and the presence of 3-segmented exopodites in the natatorial legs are topics discussed in detail in the section dealing with the copepodid development of *E. lacunae*. Until a redescription of this species, based on adult material, is available, the species should be considered as a *species inquirenda*.

At first sight, the specimens found among the 'aufwuchs' in Celestún Lagoon and here identified with *E. lacunae*, resemble most *E. woodini* described from an intertidal *Spartina* marsh in North Carolina (THISTLE 1980). Indeed, the setal armature of the fifth legs in both sexes, and most importantly the vase-shaped appearance of the female caudal rami are obviously similar. However, the distinct articulation between exopodite and baseoendopodite as illustrated for *E. woodini* differs significantly from the subtle suture, or even the absence of an articulation, between both P5 components in the specimens from Celestún.

The original description of *Enhydrosoma lacunae* is rather brief, dealing mainly with the gross morphology of the natatorial legs and caudal rami. Of the cephalic appendages, only brief descriptions of the antennule and antennal exopodite were provided while the other buccal appendages were regarded as resembling those of the type. Notwithstanding the concise original description, *E. lacunae* has been considered as a well defined species, clearly differentiated from the other species of the genus because of the particular chaetotaxy of the fifth leg, which

has only 2 spines on both rami in male as well as in female. Unfortunately, since the original description (JAKUBISIAK 1933), the species has never been reported again.

Some confusion arose about the nature of the inner distal small element on the exopodite of the fifth leg mentioned by JAKUBISIAK (1933). As stated by WELLS & al. (1982), the exopodal segment has been considered several times as having 3 distal setae. Obviously such a statement strongly affects the accuracy of the recent identification keys (LANG 1965; THISTLE 1980; BELL & KERN 1983). In concurrence with WELLS & al. (1982), the small inner distal element on the female fifth leg exopodite is considered here as the lateralmost spinule of a short posterior bristle row.

The Celestún specimens display a remarkable variability in the position of one of the endopodal setae in the female P5. As illustrated (Fig. 4F), the outermost spine is seen at the side of the median one, but can also be found hidden away behind the median spine (Fig. 4G). Because both the outer and median spine are equally sclerotized, and the outer one is distinctly shorter than the median spine, the former is hardly visible when they arise in apposition. In Jakubisiak's description of the female fifth leg of *E. lacunae* only two long endopodal spines were illustrated, but it seems reasonable that the outermost spine was not found as it was hidden by the median one, and that in fact *E. lacunae* possesses three endopodal spinulose setae on the endopodal vestiges of the female fifth leg.

Apart from the P5 chaetotaxy and the presence or absence of articulation of the exopodite, *E. woodini* and *E. lacunae* are still well recognizable on the basis of the shape of the female caudal rami: vase-shaped in the former, elongated and nearly cylindrical in the latter. Again, the Celestún specimens show a noticeable variability of this appendage. Among the 15 female specimens in collection, 6 females have caudal rami resembling Figs. 1A, B (L/W:  $\pm 3/1$ ), 5 possessing rami more or less like those illustrated in Figs. 2B, 6B (L/W: between 4-6/1), and 4 females have rami as in Fig. 2C (L/W: between 7-8/1). In this respect females with nearly cylindrical caudal rami closely resemble the males, but differ from the latter in the more expanded somites, genital double somite and antennulae. Although JAKUBISIAK (1933) does not indicate the sex of the specimen used for his illustration of the caudal rami, it seems not impossible (cf. the expanded last urosomal somites) that the rami were drawn from a female specimen with rami of the intermediate type.

Thus, it is obvious that the shape and L/W ratio of the caudal rami of *E. woodini* fall within the range displayed in the Celestún specimens. This, in combination with the above remarks concerning the observed variability of chaetotaxy and articulation of the rami of the female fifth leg, and the striking resemblance of the males of both species (as noted by THISTLE (1980:395) in his key), show

that it is impossible to distinguish *E. woodini* from *E. lacunae*. The former should therefore be considered as a junior synonym of the latter.

The variable shape of the caudal rami observed here is of particular interest as the form of the rami has often been used as an important species-diagnostic characteristic in the genus *Enhydrosoma*. In their comparison of *E. variabile* with the other *Enhydrosoma* species with long cylindrical caudal rami, Wells & al. (1982) drew attention to the primordial importance of the position of the lateral setae along the outer margin of the rami. In the different shapes of the rami as displayed in the Mexican population of *E. lacunae*, the three lateral setae are found in the proximal half of the rami, with the distal lateral one arising a little more distally than, but close to, the median positioned dorsal seta. A similar position of the lateral setae is described for *E. variabile* WELLS & al., *E. caeni* RAIBAUT, *E. migoti* MONARD, *E. tunisense* MONARD, *E. ponticum* JAKUBISIAK, but also in *E. pericoense* MIELKE, which is distinctly characterized by its very short, nearly globulose rami. In contrast, other species such as *E. curticauda* BOECK (see GEE 1994), have two lateral setae in the proximal half and one seta in a position far more distally than the dorsal seta. Unfortunately, in many *Enhydrosoma* species the exact position of the lateral and/or dorsal caudal setae has not been accurately described.

As stated above, two other species, *E. mangroviae* JAKOBI, 1955 and *E. gerlachi* JAKOBI, 1955, have an identical armature on the female fifth leg as *E. lacunae*. But since LANG (1965) advised to simply ignore the 6 Brazilian species because of contradictions between illustrations, descriptions and setal listings, the species have been omitted in keys and comparisons (but see RAIBAUT 1965). However, as the illustrations of the P5 in both species show a square exopodite, bearing two apical setae, and an undifferentiated endopodal part armed with three spines, their possible status should be discussed within the context of the present paper. Apparently the fifth leg of both Brazilian species resembles closely the fifth pereopod of *E. lacunae*. JAKOBI (1955) himself noted the close resemblance between *E. gerlachi* and *E. lacunae*. Notwithstanding the contradictions between description, illustrations and table, it is my opinion that *E. gerlachi* is conspecific with *E. lacunae*.

The illustration of the female P5 of *E. mangroviae* shows a median endopodal seta on the P5 which is considerably shorter than the outer one. This could be an important diagnostic feature, were it not that the median and outer setae may be found in apposition, as discussed above. It is clear that Jakobi failed to remove the P5 from the urosome, and had to observe the appendage compacted between urosomal somites and coverglass. It is thus quite possible that the outer setae bent inwards, giving the impression of a median

position. The possible status of this species is less clear than that of *E. gerlachi*, but it does not seem impossible that *E. mangroviae* too is conspecific and that the differences in the chaetotaxy (end P3: 0-020; end P4: 0-121 in *E. mangroviae*) result from erroneous interpretation as the animals were, presumably, not properly dissected.

THISTLE (1980) stated that *E. woodini* (= *E. lacunae*) shared most characteristics with *E. longifurcatum* SARS, 1909, and distinguished the females of both species on the basis of the chaetotaxy of the fifth leg (with on exopodal lobe 2 pinnate setae in *E. lacunae*, 3 in *E. longifurcatum*). *E. lacunae* is also distinguishable from *E. longifurcatum* by the position of the distal lateral seta close to the dorsal one on the caudal rami. Males of both species are distinguishable by the relative position of the caudal rami armature and by the presence (*E. lacunae*) or absence (*E. longifurcatum*) of a sexual dimorphic P3 endopodite. Differences in armature of buccal appendages (e.g. presence of an element on the syncoxa of the maxilliped) have to be confirmed, as they are erroneously or inaccurately described (J.M. GEE pers. commn).

#### Developmental patterns

Reference was made earlier by GEE (1994) and confirmed herein (see above) to the fact that *E. nicobaricum* SEWELL was defined on a fifth copepodid stage instead of an adult. The P5 armature with only two endopodal and two exopodal setae indicates that the illustrated copepodid is a juvenile male and not a female as was supposed by SEWELL in the description (1940:344; but curiously captioned as male in his text-fig. 85). In comparison with the other species of *Enhydrosoma* (including the *buchholtzi* group), *E. nicobaricum* is a distinct outsider as it displays two setae on the abexopodal margin of the antenna and three setae on the exopodal segment. It is obvious that *E. nicobaricum* has to be excluded from the genus *Enhydrosoma*, and it may turn out that this species constitutes a separate genus together with an undescribed Californian species.

The following paragraphs focus on the phylogenetic significance of the developmental patterns and chaetotaxy of the antennal exopodite, the post-maxillipedal rami, and on the homology of the male sexually dimorphic P3 endopodite.

The antennal exopodite. Within the family Cletodidae *sensu* POR (1986) a one-segmented antennal exopodite bearing three exopodal setae is only known, so far, for the genera *Limnocletodes* BORUTZKY and *Scintis* POR, and most unexpectedly in *Enhydrosoma nicobaricum* SEWELL. The trait seems to be variable in *Acrenhydrosoma* LANG (see SARS 1920; LANG 1965; SCHIZAS & SHIRLEY 1994). In *A. perplexum* (T. SCOTT) an additional slender seta on

the lateral margin of the exopodite was described by SARS (1920), whereas in *A. karlingi* LANG and *A. maccalli* SCHIZAS & SHIRLEY a condition is found with only one lateral and one distal pinnate seta, thus resembling the antennal exopodite of the other *Enhydrosoma* species. However, the exact nature of the proximalmost lateral seta in *A. perplexum* is unsettled: it may turn out to be a long spinule, as the antennal exopodite generally is furnished with a (sometimes quite long) spiniform ornamentation in the same place.

The unique antennal exopodite as found in *E. nicobaricum*, with a lateral pinnate seta, in addition to one pinnate and one slender smooth seta on the distal margin provides more interesting clues for phylogenetic analyses. This type of antennal exopodite was not considered by GEE (1994:100) in his discussion of the taxonomical characteristics of the antenna. Although *E. nicobaricum* was established on a juvenile specimen, the presence of three elements on the exopodite of the antenna cannot be considered as a juvenile feature, as a closely related second species (yet undescribed) possesses an identical armature on this appendage.

We demonstrated herein that for *E. lacunae* the antenna of the first copepodid possesses a well developed exopodal segment equipped with three elements: a lateral pinnate seta and a distal pinnate seta accompanied by a smaller smooth element. During the moult from first to second copepodid stage, the second distal seta disappears, and the exopodite achieves its adult appearance with a single lateral and a single distal seta. This developmental scenario seems to be a general phenomenon in *Enhydrosoma* as it is found in the first copepodids of yet undescribed other species (pers. obs.).

FIERS (1991) showed that in the first copepodids of *Cletodes macrura* FIERS and *C. tuberculatus* FIERS the antennal exopodites possess two large pinnate setae instead of a single pinnate seta known for the adults. The number of setae decreases and the shape of the exopodal segment changes to a conical bud during the moult from first to second copepodid, after which stage there are no further changes up to the adult form. The exopodal segment in copepodid I of *Cletodes* is remarkably similar, though it is smaller, to the exopodal segment in the adults of *Enhydrosoma* (except for the *buchholtzi* species-group, see GEE 1994), *Enhydrosomella* MONARD, *Acrenhydrosoma* LANG (at least in two out of the three species), *Stylicletodes* LANG, and *Kollerua* GEE.

In concurrence with GEE (1994), the *Cletodes*-like antennal exopodite is considered as the apomorphic characterstate of this element. With the *Enhydrosoma*-like exopodite as an intermediate, the larger uni-segmented exopodite equipped with three pinnate setae is clearly the most plesiomorphic state of this appendage actually known within the family.

Among the specimens of *E. curticauda* examined by GEE (1994), a single female specimen was found with three setae on the exopodite of one of the antennae. Unfortunately, no illustration was given of this most interesting appendage. As discussed at length by CRISCI & STUESSY (1980), minor abnormalities in organogenesis are among the group of first level criteria in polarity determinations and indicate the plesiomorphic character state. The presence of such anomalous exopodal setation in *E. curticauda* provides a strong argument for the transformation series of the exopodite. Moreover, the argument is corroborated by the presence of an antennal exopodite with three setae in the earliest juvenile stage of *Enhydrosoma* (see Fig. 8M for Cop I of *E. lacunae*).

It should be noted here that re-examination of the antenna of *Enhydrosoma* sp. IVESTER & COULL demonstrated that this species possess an antennal exopodite with two elements as in the other *Enhydrosoma* species. The SEM illustration (fig. 5 in IVESTER & COULL 1977) either depicts an anomalous exopodite or shows a seta of a post-antennal appendage stuck to the exopodite during preparation of the animals.

**Ramal development.** The addition of ramal segments in the legs of the early copepodid stages of *E. lacunae* is essentially in accordance with the pattern known as the common development pattern as presented by FERRARI (1988) in his fig. 2. Legs appear as primary buds and are reorganized during the next moults into legs with 2-segmented rami. In contrast with the common scheme, the exopodal rami remain 2-segmented in the fifth stage instead of being reorganized into 3-segmented rami. The definitive morphology with 3-segmented rami appears only in the adult (see Table 2, Fig. 12).

A similar development of the post-maxillipedal legs was reported (FERRARI 1988, fig. 3A, after AMORES-SERRANO 1978) for the cyclopid genus *Mesocyclops*, which is a representative of a copepod group known for the conservative chaetotaxy of the natatorial legs in the majority of its genera. This similar development scheme in two totally unrelated taxa strengthens the hypothesis that ramal development and the way the setae are successively added during development, are two different character suites which have to be explored separately.

In contrast with the developmental pattern observed in *E. lacunae*, the leg development of *Cletodes* species (FIERS 1991, and amended development of *C. macrura* in Table 3, Fig 12: P2 development) follows the common development pattern as the exopodal rami of the legs appear three-segmented in the pre-adult stage and remain unchanged in the following moult. Thus the post-maxillipedal leg development in *Enhydrosoma* must be considered as neotenic, in comparison with the *Cletodes* scenario (see McNAMARA 1986). However, despite the paedomorphic leg development in *Enhydrosoma*, the resulting adult shape and chaetotaxy of the legs is similar in both genera.

At first sight, *E. nicobaricum* does not fit into this scheme as its fifth copepodid stage displays distinctly three-segmented rami. In addition to the morphology of the antenna, the presence of three-segmented exopodal rami in the copepodid V is another weighty reason to remove this species from *Enhydrosoma*. In Fig 12, the diagram of the P2 exopodite of *E. nicobaricum* (including the hypothetical adult shape) is placed between that of *Cletodes* and *Enhydrosoma*. It is assumed here that *E. nicobaricum* and its supposed congener (an undescribed Californian species) share a common ancestor with the branch leading to *Enhydrosoma* (the *buchholtzi* group excluded), *Enhydrosomella*, *Kollerua*, and probably *Stylicletodes*.

Table 3. Development of the chaetotaxy in *Cletodes macrura* (after FIERS 1991, amended). NP: not present in this developmental stage; Data above line = adult characters, below line = preadult characters. \* armature of female/male P5, respectively.

Legs/stage	CI	CII	CIII	CIV	CV	ADULT
P1 exo	0.11.IV	0.1 - 0.11.III	0.1 - 0.11.III	0.1 - 0.11.III	0.1 - 0.1 - 0.11.II0.1	0.1 - 0.11.II
end	1.1.1	0.0 - 1.1.1	0.0 - 1.1.1	0.0 - 1.1.1	0.0 - 1.1.1	0.0 - 1.1.1
P2 exo	0.11.III	0.1 - 0.11.II	0.1 - 1.11.III	0.1 - 1.11.III	0.1 - 1.1 - 0.11.II0.1	1.1 - 0.11.II
end	0.2.0	0.0 - 0.2.0	0.0 - 0.2.0	0.0 - 0.2.0	0.0 - 0.2.0	0.0 - 0.2.0
P3 exo	3	0.11.III	0.1 - 0.11.II	0.1 - 1.11.III	0.1 - 1.1 - 0.11.II0.1	1.1 - 0.11.II
end		0.2.0	0.0 - 0.2.1	0.0 - 1.2.1	0.0 - 1.2.1	0.0 - 1.2.1
P4 exo	NP	3	0.11.III	0.1 - 1.11.III	0.1 - 1.1 - 0.11.II0.1	1.1 - 0.11.II
end			0.2.0	0.0 - 1.2.1	0.0 - 1.2.1	0.0 - 1.2.1
P5*exo	NP	NP	3	5/?	5/4	5/4
bas				2/?	3/2	3/2
P6	NP	NP	NP	NP	NP	0/0

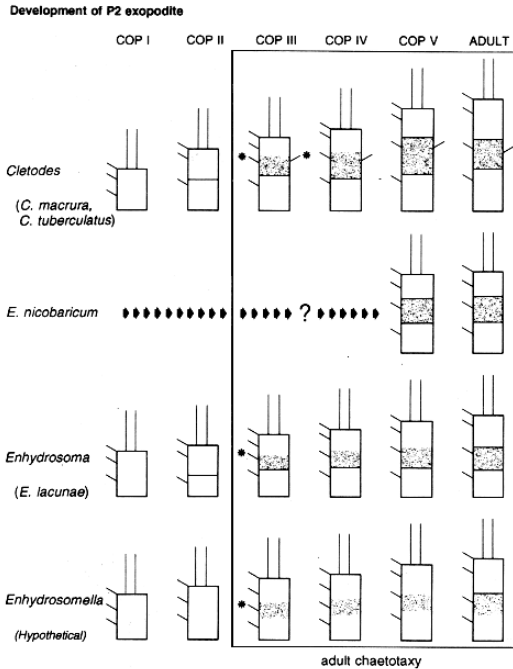


Fig. 12. Schematic representation of exopodite P2 development in *Cletodes*, *Enhydrosoma sens. lat.* and *Enhydrosomella*. \* indicates acquisition of new element; stippled areas represent position of median segment.

In this context, it is thought worthwhile to reflect on the unique morphology of the natatorial legs in *Enhydrosomella*. The main diagnostic characteristic of this genus is the presence of 2-segmented exopodites in P2-P4 possessing two outer spines on the proximal exopodal segments. Taking in consideration that the chaetotaxy (i.e. total number of setae and spines) of the exopodites in *Enhydrosomella* is identical with that of *Enhydrosoma*, the possible course of development (as yet conjectural) of the elements during copepodid development is illustrated for the P2 exopodite in Fig. 12. As in the other schematic representations of the P2 exopodite, the spine indicating the position of the median segment (stippled area) appears in the third copepodid, giving the leg its adult number of elements (Table 2 and 3, above the line). However, in contrast with the other developmental schemes presented in Fig. 12, the moult from first to second copepodid does not induce the differentiation of the proximal segment. During the succeeding development, the exopodite remains 1-segmented until the ultimate moult (Cop V to adult), where the distal exopodal segment becomes differentiated.

Of course, another way to achieve 2-segmented rami may be hypothesized. The addition of ramal segments in the legs might follow the same pattern as found in *Enhydrosoma*, resulting in 2-segmented rami in copepodid V. In the last moult, the leg would then be reorganized, with differentiation of the distal segment in addition to the suppression of the articulation between the proximal and median segment. In my opinion, however, such a developmental scenario is implausible, as such rearrangements would seem to require a very complex epigenetic mechanism. Moreover, the progressive retardation of the exopodal rami as observed in *Cletodes*, and the fifth copepodid of *E. nicobaricum* on the one hand versus *Enhydrosoma* in the other, favours the first scheme instead of the second one.

Development of chaetotaxy. In Tables 2 and 3, a line divides the chaetotaxies in the several copepodid stages in two groups: the group of setal formulae above the line is identical with the number of elements found in the adult legs, whereas all character states below the line still have fewer elements than in the adult stage. As a matter of fact, the adult chaetotaxy of the legs is acquired in the early copepodid stages in the genera *Enhydrosoma* and *Cletodes*, and the division line in the two tables is the same for both. The P1 displays the adult number of elements from the first copepodid stage on, whereas the P2 and P3 acquire the adult number of setae/spines in the 3rd and 4th copepodid stage, respectively (i.e. after three moults: Nauplius VI-Cop III). The P4, which appears for the first time as a small bud in the second copepodid, needs only two moults to develop the adult number of elements. Apart from the P5 and P6, all natatorial legs are equipped with a complete set of elements in the fourth copepodid stage.

Examination (unpublished) of several other harpacticoids, and more particularly of those species known to have a 'primitive' chaetotaxy (3 outer spines on last exopodal segments, inner setae on first endopodal segments: e.g. *Laophonte cornuta* PHILLIPI, 1840) revealed that the adult chaetotaxy emerges first in the fifth copepodid stage. The only known cletodid armed with a full setal complement on the distal exopodal segments (P2: 123, P3 and P4: 223) is *Scintis variifurca* POR, 1985. Unfortunately, the copepodid development of this species is unknown, but it does not seem impossible that the adult morphology of *Scintis* is the outcome of a developmental scenario comparable with that of species possessing a 'primitive' chaetotaxy. It seems natural therefore to assume that the adult chaetotaxy of *Cletodes* and *Enhydrosoma* is pedomorphic in origin. Because the chaetotaxy of the legs in the early stages is similar to the 'primitive' condition, and becomes altered during the successive moults, the adult pattern is considered neotenic according to the definition of McNAMARA (1986).

P3 sexual dimorphism. In his review of taxonomic characters within the Cletodidae, GEE (1994) defined three types of sexual dimorphism in the P3 endopodite. Within the genus *Enhydrosoma* (excluding the *buchholtzi*-group) two types occur: P3 endopodites which are identical in both sexes (type 1 = no sexual dimorphism), and male P3 endopodites with an outer apophysis/element (fused to or articulating with the segment), sometimes ornamented with a distinct pattern differing from the female spine ornamentation (type 2).

Among the species unified in the redefined genus *Enhydrosoma*, the adult overall morphology of those male P3 endopodites characterized as type 2 ranges from distinctly 3-segmented (examples: *E. herrerae* and *Enhydrosoma* sp. IVESTER & COULL, pers. obs.) over a two-segmented endopodal ramus still showing the position of the third segment (example: *E. pericoense*) to a 2-segmented endopodite closely resembling the female morphology, except for a fused and often ornamented outer sub-distal apophysis (examples: *E. curticauda* see GEE 1994: fig. 7B; *E. lacunae*: see Fig. 5B and F). Within this context it is important to note that the males in the genus *Kollerua* display a type 2 dimorphic P3 endopodite as in *E. curticauda* although females lack an outer subdistal element on the second endopodal segment.

On the basis of the adult appearance of the P3 endopodite in *Enhydrosoma* and observations on the developmental suite of the P3 of *Cletodes macrura*, GEE (1994) concluded that the outer subdistal process in type 2 dimorphism is homologous with the outer subdistal spine of the female P3 endopodite. Indeed, following the successive stages (CIII - Adult) of the outer subdistal element on the P3 endopodite of *E. lacunae* (Figs 5C-F; 8J; 10C, H, G), it seems evident to consider those elements in both sexes as homologous structures.

However, as the homology of the subdistal element seem to be evident for those *Enhydrosoma* species possessing a setal complement of the endopodite P3 as 0-021, the unexpected presence of a 3-segmented type 2 endopodite in the male of *E. baruchi* and a 2-segmented type 2 dimorphism in the genus *Kollerua* creates serious problems in this context. Indeed, whereas the males of the five species assigned to *Kollerua* and the unique *E. baruchi* display a P3 apophysis, female legs of these species are diagnosed with a two setae complement on the second endopodal segment of the legs. Thus, we encounter here the same problem as dealt with by GEE (1994:104) in his discussion on the homology of the male type 3 apophysis in *Cletodes*. Consequently, if the same reasoning is followed, we are compelled to assume that the outer subdistal process in the males of these species, and thus in all type 2 displaying enhydrosomids, is not a dimorphic homologue of the subdistal outer spine in the female P3, but a novel structure.

Arriving at this point, it is worth while to examine and relate the dimorphic structures in the genus *Cletodes* as this information certainly will turn out to be of primordial importance in the phylogenetic analyses of the Cletodidae.

HAMOND (1973, table 3A and B) provided a most elegant overview of the setal formula types and dimorphic features found in the genus *Cletodes*. In my opinion the formulae listed in table 3B for the P3 and P4 endopodite of the 'type B species' *C. pusillus* SARS, 1920 has to be 1.1.0 instead of 0.2.0, and for that of the 'type C species' *C. reyssi* SOYER, 1964, has to be read as 0.2.1 instead of 1.1.1. (codes h.i.j. of table 3A and B in HAMOND 1973). These corrections are concluded after re-examination of the descriptions, and deduced from the fact that in the males the apical endopodal segment bears 1 (*C. pusillus*) and 2 (*C. reyssi*) distal setae, respectively.

HAMOND's most instructive table results in the clear demarcation of three species groups (no taxonomical units): a group displaying no dimorphic P3 endopodite in the male and having a female 0-0.1.1 setal formula in the P3 (type A); a group with a single distal seta on the third endopodal segment of the dimorphic male P3 and a female P3 setal formula as 0-0/1.1.0 (type B); and a group with two distal setae on the male dimorphic P3 but with a P3 female chaetotaxy as 0-0/1.2.1 (type C).

Adding the characteristics of the male of *C. millerorum* HAMOND and of the more recently described *Cletodes* species, Hamond's table 3B has to be updated as follows:

(1) to the type A group we add:

*C. dissimilis* WILLEY, 1935 (pers. obs.: specimens from the Gulf of Mexico);

*C. millerorum* HAMOND, 1973 (pers. obs.: specimens from southern California);

*C. dorae* POR, 1979 (original description);

(2) to the type B group we add:

*C. reductus* MOORE, 1977 (original description);

*C. endopodita* (SCHRIEVER, 1984) (original description);

*C. setosus* MARINOV & APOSTOLOV, 1985 (original description);

*C. tuberculatus* FIERS, 1991 (pers. obs.: type-series);

and (3) to the type C group we add:

*C. macrura* FIERS, 1991 (pers. obs.: type-series).

If the five species of the *buchholtzi*-group are included within Hamond's table, we see that 4 out of the five species can be enrolled in the type C group as they have a P3 complement with two terminal setae on the distal segment in the male in addition to an outer sub-distal spine in the female (the female of *E. vervoorti* FIERS, 1987 is unknown, but is assumed to have a complement as in *E. buchholtzi*). Only *E. curvirostre* (T. SCOTT) *sensu* SARS (1909) cannot be assigned to a particular group as this species displays type B dimorphism but possesses an outer sub-distal spine in the female P3 (type A and C). Their are, however, indi-

cations that the original description of this species is wrong. The correct setal formula of the legs has to be confirmed (J.M. Gee pers. commn).

From the updated table, and by virtue of the descriptions, we can immediately conclude that:

(1) P3 dimorphism in cletodid species of Type B and Type C is fundamentally identical with the dimorphism found in the *buchholtzi*-group and is to be referred to the type 3 dimorphic nature as defined by GEE (1994);

(2) that the dimorphic P3 endopodite in Type B and Type C lacks an outer element on the median segment;

(3) that in type C of which the females possess an outer subdistal spine in the adult P3, the outer spine is absent in the male endopodite.

From the description of the copepodid development of *C. macrura* (see fig. 10 in GEE 1994, and figs 14d and 15i in FIERS 1991), and from additional observations on the development of *C. dissimilis* and *C. millerorum* (pers. obs.), it is known that the outer sub-distal element appears for the first time in Cop III and evolves in Cop IV and V to a large element: of hyaline nature in *C. macrura*, but as a normal spiniform element in *C. dissimilis* and *C. millerorum*. In *C. macrura*, it disappears when the P3 endopodite undergoes its reorganisation during the moult to the adult stage. Thus, the absence of an outer apophysis in the adult *Cletodes* species with a type C setal formula, and *E. curvirostre*, results not from a heterochronous event, but is a terminal deletion (definition according to KLUGE & STRAUSS 1985), and presents the apomorphic character state of the endopodites and the synapomorphic character of the species of the genus *Cletodes* grouped as type B and C and those species assigned to the enhydrosomid *buchholtzi*-group.

The type B setal formula must be a result of either a suppression in early stages of the onset of the inner seta or from a (terminal) deletion during the reorganisation of the P3 in Cop V stage to adult. Unfortunately, the male P3 development of none of these species is known but we can deduce from the female P3 development of *C. tuberculatus* that neither the inner nor the outer seta appears in the juveniles (see FIERS, 1991). *C. pusillus* still has the original inner element in its legs, while in the other species of this group (*C. tenuipes*, *C. smirnovi*, and the above listed species) the seta is absent in the adults. The advanced setal formulae of the legs and the fifth leg found in this group give support to the assumption that the type B dimorphism represents the most advanced character state of the male P3 within the genus *Cletodes*.

Examination of the copepodid development of *C. dissimilis* and *C. millerorum* (per. obs.), both members of the type A species group, revealed that the P3 endopodite in male and female copepodids is identical throughout the entire development. Sexes can be identified only using the length/width ratio of the antennular segments (from Cop

III on) and the number of setae on the juvenile P5 (in Cop V).

That the groupings within *Cletodes* based on presence and shape of sexually dimorphic characteristics of the P3 should not be interpreted as taxonomical units is obvious. In each group we can recognize species displaying distinct features requiring separate generic definition. However, in my opinion, the presence and shape of the dimorphic features of the male P3 endopodite will figure as a red line when the phylogenetic relationships between the genera come to be analyzed.

Finally, we return to the problem raised at the beginning of this rubric, namely the origin and homology of P3 dimorphism in *Kollerua* and *Enhydrosoma baruchi* where the homology of the P3 outer spine in male and female has to be refuted. After reexamination of the copepodid development of the male P3 endopodite previously described by FIERS (1991) for *Cletodes macrura*, GEE (1994) concluded that: 'the evidence of the female CV (of *C. macrura*) lends weight to the theory that the apophysis in the type 3 sexual dimorphism found in *Cletodes* and the *buchholtzi*-group of species is formed from the chitinous ridge across the anterior surface of endopodite-2 in the male CV and therefore is not homologous with the outer spine of type 2 sexual dimorphism found in other species of *Enhydrosoma* but is a novel structure.'

Important here is the striking similarity of the P3 development in *Enhydrosoma* and *Cletodes* (type C and the *buchholtzi*-species group included). In both taxa the sub-distal outer element appears in the third copepodid stage, but whereas this element is rather minute in *C. macrura* it is present as a distinct hyaline conical structure in *E. lacunae* (Fig. 8J). The similarity of this element in both species is very clear in Cop IV and V, where both stages possess a large conical hyaline apophysis.

It has been demonstrated (FIERS 1991) that during the reorganisation of the Cop V endopodite to the adult shape in *C. macrura* the outer and inner sub-distal elements disappear and become replaced by an inner S-shaped apophysis on the median segment. In contrast, the reorganisation of the juvenile male P3 endopodite to adult ramus in *E. lacunae*, does not affect the outer sub-distal element. It reappears *quasi* unchanged in the adult. Thus, the adult morphology of the male P3 endopodite is a retained juvenile feature, and should thus be considered as the neotenic (apomorphic) character state of this element.

Furthermore, it is presumed here that the development of those *Enhydrosoma* species possessing a three-segmented type 2 male P3 endopodite (*E. baruchi*, *Enhydrosoma* sp. IVESTER & COULL), display a P3 developmental pattern similar to that known for *Cletodes macrura* i.e. 2-segmented throughout the development, but with a distinct anterior transversal chitinous ridge in the distal half of the second segment. The reorganisation



of the male P3 endopodite during the moult from copepodid V to adult stage results in a 3-segmented type 2 endopodite type.

Consequently, the statement that the three-segmented dimorphism is a secondary development from an originally two-segmented endopodite (GEE 1994:104) implies that the absence of a dimorphic P3 is plesiomorph, which in my opinion is contradictory to the facts for two reasons. Firstly, those cletodid species constituting HAMOND'S (1973) Type C group possess the most 'primitive' chaetotaxy (and also the most primitive armament on the buccal appendages) and display a distinctly three-segmented dimorphic P3 endopodite in the males. In other words, their development of the P3 (as shown for *C. macrura*) represents the most ancestral development constraint known for this appendage (in-group analysis).

Secondly, whatever harpacticoid out-group is chosen in the study of character state transformations and polarities of the cletodid taxa, a three-segmented P3 endopodite in the male is a general feature. In addition, personal observations on the development of this appendage in question in other taxa (out-groups) clearly revealed that the constituting elements of the P3 are homologous with those found in cletodids. As such we are forced to consider a three-segmented male P3 endopodite as the plesiomorphic character state of this ramus.

When in the previous sections the adult morphology and chaetotaxy of *Enhydrosoma* and *Enhydrosomella* was discussed in the light of heterochronic developmental changes, it is assumed here that the type 1 dimorphism in the genus *Enhydrosomella* is a secondary result from its extreme neotenic development scenario. It seems evident to presume that the type 1 sexual dimorphism in the type 1 *Enhydrosoma* species (taking in consideration that dimorphic nature may be easily overlooked), and those *Cletodes* species of group Type A (thus all taxa without a dimorphic male P3 endopodite), represents the ultimate adult morphological expression of a transformation series from distinctly sexual dimorph (i.e.: 3-segmented type 2) to definite absence of dimorphic characteristics in the male P3 endopodite (type 1).

**P3 dimorphism in *Stylicletodes*.** To conclude the present study, some amendments to the literature concerning P3 sexual dimorphism in *Stylicletodes* are presented since there seems to be much confusion about the exact morphology of this structure in the male. LANG (1965:439, 443) referring to the observations of PETKOVSKI (1955) on the male P3 of *S. numidicus* MONARD, 1926, confirmed the presence of dimorphism in the P3 of the other *Stylicletodes* species, and corrected his original view that the P3 endopodites were similar in both sexes (LANG 1948). His illustration of a male P3 endopodite (LANG 1965, fig. 238L) of a specimen from Gullmarsfjorden

(Sweden) is in my opinion not very accurate. GEE (1994:104), discussing the dimorphic features known in the cletodid genera, interpreted the outer structure on the median segment as a small hyaline seta/apophysis.

Several specimens of a *Stylicletodes* species, including males and juveniles, were found in samples recovered from the Santa Maria Basin (southern California). They will form part of a forthcoming paper, but in the light of the discussion here, the male endopodite P3 is illustrated in Fig. 5G. In accordance with the observations made by LANG (1965) and PETKOVSKI (1955), the endopodite is clearly 3-segmented, with a distinct process on the median segment. This apophysis is a robust structure, confluent with the supporting segment, and ornamented with minute spinules along both margins of the stem in its distal half. It clearly arises from the frontal distal margin of the segment, but shows a position more closer to the outer corner than to the inner one. The position of the apophysis is basically the same as that of the dimorphic process found in males of *Enhydrosoma* characterized by (3-segmented) type 2 dimorphism, and as such the male P3 dimorphism is considered to be homologous in the three genera *Enhydrosoma*, *Kollerua*, and *Stylicletodes*.

In the introduction to the present paper, *Cletodes stylicaudatus* WILLEY, 1935 reallocated to the genus *Enhydrosoma* by LANG (1936) shortly after its original description was removed from its current genus to *Stylicletodes*. The corrections concerning the position and morphology of the apophysis of the male P3 endopodite of *Stylicletodes* supplied here clearly show that *Cletodes stylicaudatus* cannot be maintained in *Enhydrosoma*, but resembles most the known species of the genus *Stylicletodes* (viz. the long and narrow endopodites; the long, nearly geniculated exopodal setae in P1; and the long bristles on the exopodal spines in P2 and P4). The single male specimen of *C. stylicaudatus* described by WILLEY (1935) is clearly distinguished from the other *Stylicletodes* males by the reduced chaetotaxy of the P3 exopodite (absence of inner seta on median segment, only one inner seta on distal segment) and the reduced complement of the P5 exopodite (with 4 setae instead of five).

Whether the genus *Stylicletodes* constitutes several distinct evolutionary lines, requiring distinct generic denotations, is beyond the scope of the present paper. This should result from a detailed revision of the known species currently assigned to the genus *Stylicletodes*.

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