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A revision of the *Brementia*-group of genera (Copepoda: Notodelphyidae), with descriptions of a new genus and four new species

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Abstract

A new genus of parasitic copepod, *Paranoplodelphys*, is established in the family Notodelphyidae to accommodate a new, highly reduced species, *P. simplex* n. gen. et n. sp., collected from a tunicate host, *Didemnum dicolla* in Djibouti. The new genus retains only four paired limbs: antennules, legs 1, 2 and 5. Two new species of *Anoplodelphys*, *A. afri-*

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cana and *A.laubieri*, are described from tunicate hosts of the genus *Didemnum* collected in the Gulf of Suez and off the Kwazulu-Natal coast, respectively. A new species of *Achelidelphys*, *A. papuensis*, is described from a *Didemnum* species host collected off Papua New Guinea. New records are also reported for *Anoplodelphys corneci* and *Achelidelphys steinitzi* also from tunicate hosts. After re-examination of type material of most species, a phylogenetic analysis of relationships between the genera of the *Brementia*-group was performed using PAUP. This identified four main clades: *Brementia*, *Anoplodelphys*, *Paranoplodelphys* and the *Achelidelphys*-clade. There was no support for the continued recognition of *Cephalodelphys* and *Syndelphys* as valid separate genera, and it is proposed to treat as them synonyms of *Achelidelphys*. Both genera were monotypic and upon transfer *Cephalodelphys stellata* Lafargue & Laubier, 1977 becomes *Achelidelphys stellata* (Lafargue and Laubier, 1977) n. comb. and *Syndelphys reducta* Lafargue and Laubier, 1977 becomes *Achelidelphys reducta* (Lafargue and Laubier, 1977) n. comb.

Key words: Taxonomy, parasite, copepod, tunicate host, new genus

Introduction

The family Notodelphyidae currently comprises 47 genera and an estimated 148 species (Boxshall & Halsey 2004; Boxshall & Marchenkov 2005), although there is considerable uncertainty surrounding the number of valid species since so many old descriptions are inadequate and best treated as species inquirenda (Illg 1958). Body morphology varies markedly within the family, ranging from typical cyclopiform shapes to highly modified forms, lacking any external segmentation and with extremely reduced or transformed limbs. Chatton and Brément (1915) proposed a new family, the Ophioseididae, to include three genera, *Ophioseides* Giard, 1873, *Brementia* Chatton and Brément, 1915 and *Ooneides* Chatton and Brément, 1915 showing extreme reduction of mouthparts. Illg (1958) pointed to the inadvisability in recognising such a grouping based on the loss of one or more of the mouthparts because of the difficulty in establishing whether the same mouthpart had been lost in different genera, and therefore, in establishing whether the series was monophyletic. However, the term "ophioseidimorph" has been widely utilised for the loose assemblage of modified genera lacking at least one pair of mouthparts (Bocquet & Stock 1961; Lafargue & Laubier 1977, 1978a,b; Laubier & Lafargue 1974). As explicitly stated by several of these authors (e.g. Lafargue & Laubier 1978a), this ophioseidimorph grouping is almost certainly polyphyletic and we see little merit in continuing to refer to it.

The discovery of new material of modified notodelphyids within the large collection of ascidicolous copepods made by Drs Claude and Françoise Monniot has allowed us to identify a likely monophyletic lineage amongst the modified notodelphyids. We refer to this lineage as the *Brementia*-group since *Brementia* is the oldest genus within the group. The apomorphic character states shared by genera of the *Brementia*-group include: 1, body fleshy and vermiform, lacking externally expressed segmentation; 2, body with internal brood pouch; 3, frontal margin of cephalosome with inflated rostrum; 4, labrum inflated; 5, antennule swollen, unsegmented; 6, legs 1 and 2 forming unsegmented, bilobate processes; 7, legs 3 and 4 also forming unsegmented bilobate or unilobate processes when present, sometimes lost; 8, caudal rami swollen, fused to urosome at base, 9, urosome indistinctly 2-segmented or unsegmented; and 10, body surface and surface of rostrum (when present), labrum, legs 1–4 (when present) and caudal rami densely ornamented with setules.

The current genera sharing these derived features are: *Brementia*, *Achelidelphys* Lafargue and Laubier, 1977, *Cephalodelphys* Lafargue and Laubier, 1977, *Syndelphys* Lafargue and Laubier, 1977 and *Anoplodelphys* Lafargue and Laubier, 1978. The genus *Pholeterides* Illg, 1958 exhibits all these characters with the exception of character 9. It retains a discrete, apparently 4-segmented urosome. However, it is an ideal outgroup for any phylogenetic analysis since it is probably the sister-taxon of the core members of the *Brementia*-group.

In their redescription of *Brementia balneolensis* Chatton and Brément, 1915, Laubier and Lafargue (1974) referred to the presence of four pairs of metasomal expansions. Their stated reason for using neutral terminology in preference to the term "péréiopodes" (= swimming legs), was that they considered these structures to

be "[in reality only expansions of the body wall, lacking any sclerotised structures, sternites and musculature (translated by authors)]". However, they did note that these structures were of the same form as in *Pholeterides*, where they were identified as legs 1–4 by Illg (1958). We follow Illg (1958) in considering these structures to be derived from swimming legs.

Materials and methods

The new material was part of the extensive collections of associated and parasitic copepods made by Drs Claude and Françoise Monniot during their research on ascidian systematics and ecology. These collections are housed in the Museum national d' Histoire naturelle in Paris (MNHN) and were kindly made available for study by Dr Danielle Defaye. Some of this material is now stored in the collections of The Natural History Museum, London (BMNH). In addition, type material of related existing taxa was obtained on loan from the Zoology Museum, University of Amsterdam (ZMA) and from the U.S. National Museum of Natural History, Smithsonian Institution, Washington (USNM).

Specimens were cleared in lactic acid and then mounted in lactophenol as temporary slide preparations. All drawings were made using a camera lucida on an Olympus BH-2 microscope equipped with differential interference contrast. Material for SEM was washed in distilled water, dehydrated through graded acetone series, critical point dried using liquid carbon dioxide as the exchange medium, mounted on aluminium stubs and sputter coated with palladium. Coated material was examined on a Phillips XL30 Field Emission Scanning Electron microscope operating at 5 KV. Morphological terminology follows Huys and Boxshall (1991).

TABLE 1. Character matrix for phylogenetic analysis.

Taxon / Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Pholeterides furtiva	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Achelidelphys drachi	1	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	1	1	1
Achelidelphys chengae	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1
Achelidelphys ampla	1	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0	1
Achelidelphys nigra	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1
Achelidelphys steinitzi	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
Achelidelphys stellata	1	1	0	0	1	0	0	3	1	0	0	1	0	0	0	0	1	1	1
Achelidelphys reducta	1	1	0	0	1	0	0	3	0	0	0	1	0	0	0	0	1	1	1
Anoplodelphys africana	0	0	0	0	0	1	1	2	0	1	1	0	0	0	1	-	2	0	1
Anoplodelphys corneci	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1
Anoplodelphys incerta	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1
Anoplodelphys laubieri	0	0	0	0	0	1	1	2	1	1	1	0	0	0	1	-	2	0	1
Paranoplodelphys simplex	0	0	0	0	0	0	0	3	0	1	0	1	0	0	1	-	2	0	1
Brementia balneolensis	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1
Brementia illgi	0	0	1	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1

The phylogenetic analysis was conducted using PAUP version 4.0b10 (Swofford, 2001) on a matrix comprising 19 characters and 15 taxa (Table 1). The analysis was conducted to assess the relationships between the species of the genera *Brementia*, *Achelidelphys*, *Cephalodelphys*, *Syndelphys* and *Anoplodelphys*, in order to be able to assign the new material to the correct genera. The monotypic genus *Pholeterides* was used as the outgroup. In the matrix *Anoplodelphys incertae* Lafargue and Laubier, 1978 represents three taxa, *A. incertae*, *A. galli* Lafargue and Laubier, 1978 and *A.* cf. *galli*, which have identical scores for the characters used in the

analysis. Similarly, the new species *Achelidelphys papuensis* has identical scores to *Achelidelphys chengae* Lafargue and Laubier, 1978 and was therefore not included as a separate taxon in the analysis. Characters were scored 0, 1, or "–" for missing characters. A heuristic search was performed and all characters were treated as unordered. The results of the analysis are used below to support the establishment of a new genus and the relegation of two genera to synonymy, generating new combinations for the transferred species. The new names are used in Table 1 and in the figures, in order to avoid confusion.

Order Cyclopoida Burmeister, 1834
Family Notodelphyidae Dana, 1853

Genus *Anoplodelphys* Lafargue and Laubier, 1978

The two new species described below were all collected from didemnid ascidian hosts from around the coast of the African continent. Both are strongly modified, exhibiting numerous limb losses. Placing such secondarily simplified parasites in a genus can sometimes be problematic since independent reductions and losses in different lineages can result in convergence on highly reduced morphologies. The new species are placed in the genus *Anoplodelphys*, which was erected by Lafargue and Laubier (1978a) to accommodate three species of highly transformed notodelphyid copepods found in colonial ascidian hosts belonging to the genus *Didemnum*. This placement is supported by the phylogenetic analysis given below (following the descriptions).

Anoplodelphys africana n. sp.

Type material: Holotype female in alcohol, and 1 complete, plus 1 incomplete (posterior half only) paratype females. Registration nos: MNHN-Cp2323 (holotype), MNHN-Cp2313 (dissected paratype mounted on 1 slide), MNHN-Cp2314 (incomplete paratype in alcohol).

Type Locality: Gulf of Suez (Collector—Dollfus; 22.12.1928).

Host: *Didemnum* sp. [MNHN reg. no. A2 DID C 322]

Locality in host: within the common tunic between the zooids (F. Monniot, pers. comm.)

Etymology: the new species is the first *Anoplodelphys* to be described from the African continent.

Description: Adult female body (Fig. 1A–B) highly transformed, vermiform and lacking expressed external segmentation: divided into 3 regions, cephalosome, metasome and urosome, by shallow superficial furrows. Entire body surface densely ornamented with relatively short setules (Fig. 1D). Body length of holotype female 2.17 mm. Cephalosome slightly dorsoventrally flattened, tapering anteriorly; bearing paired antennules, antennae, and 2 pairs of lobes which probably represent reduced and modified oral appendages. Lateral margins of head expanded ventrally to form ridge-like swelling produced into thumb-like process at posterior extremity (Fig. 2A). Rostrum well developed (Fig. 1C), distinctly bilobed, located in midline on frontal margin of cephalosome. Metasome more or less cylindrical, slightly narrowing anteriorly, comprising 4 somites with boundaries marked by superficial integumental folds; first 2 somites only pedigerous, each bearing pair of modified, biramous thoracic legs. Urosome (Figs 1A–B, 2D–E) reduced and largely invaginated into pocket in posterior margin of metasome (Fig. 2D–E). Urosome lacking expressed segmentation; incorporating caudal rami (Fig. 2E). Surface of urosome and incorporated caudal rami ornamented with surface setules, cuticular folds and numerous small pores; lacking trace of caudal setae.

Antennules (Figs 1C, 2A) inserted just lateral to rostrum; divided into swollen basal part bearing 3 rounded processes, orientated anteriorly, laterally and posteroventrally, and conical, tapering distal part armed with 5 setal elements, 4 apical and 1 subapical (Fig. 1E). Surface of antennule ornamented with scattered setules, most dense on basal processes.

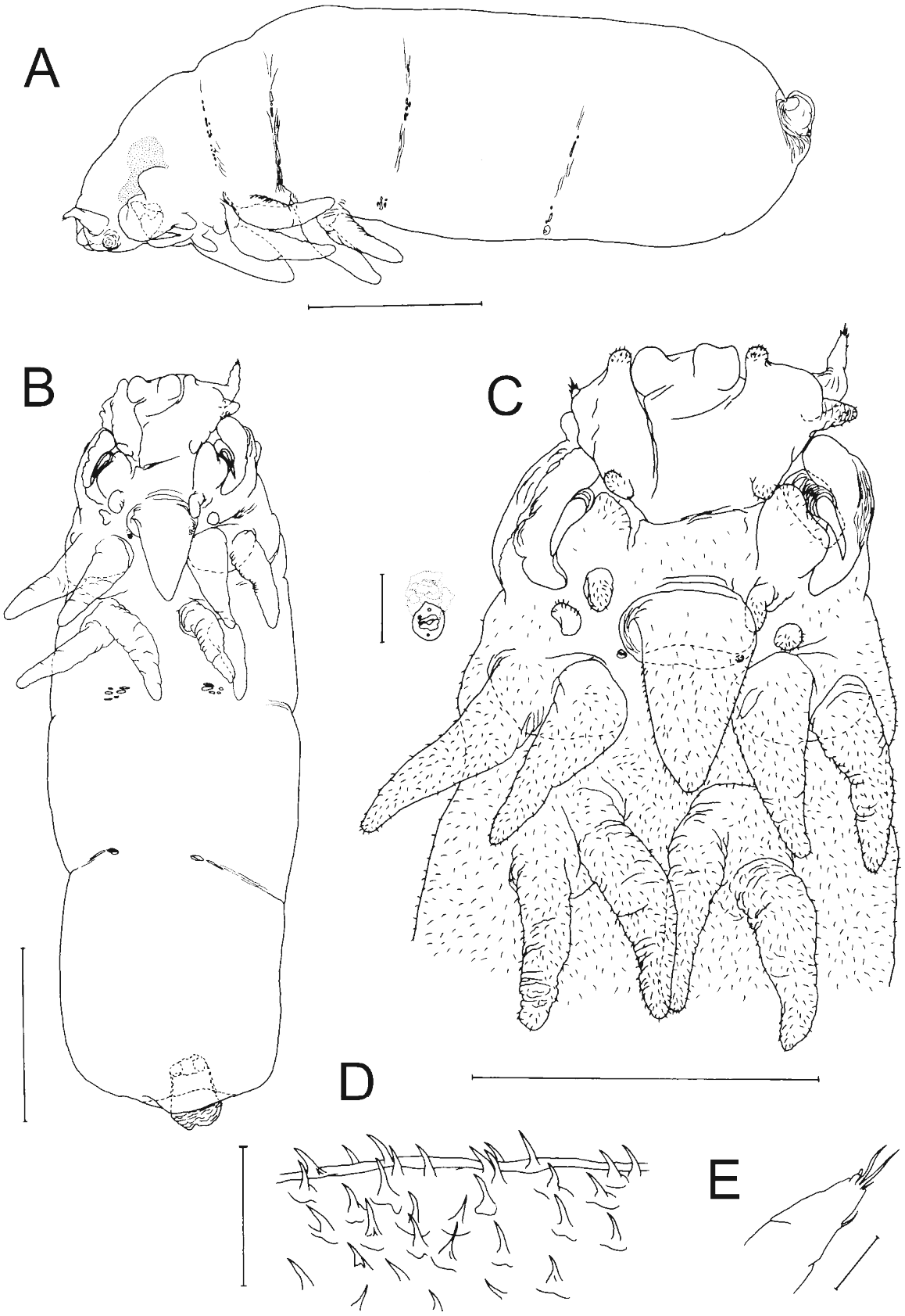

FIGURE 1. *Anoplodelphys africana* n. sp. holotype female (MNHN-Cp2323). A, Habitus, lateral; B, Habitus, ventral; C, Cephalosome and first pedigerous somite, ventral, with inset showing detail of post-labral pore (?maxillary gland opening); D, Surface ornamentation from lateral surface of third metasomal somite; E, Tip of antennule, showing vestiges of antennulary setae. Scale bars: A–C = 500 μm, D = 50 μm, E = 25 μm.

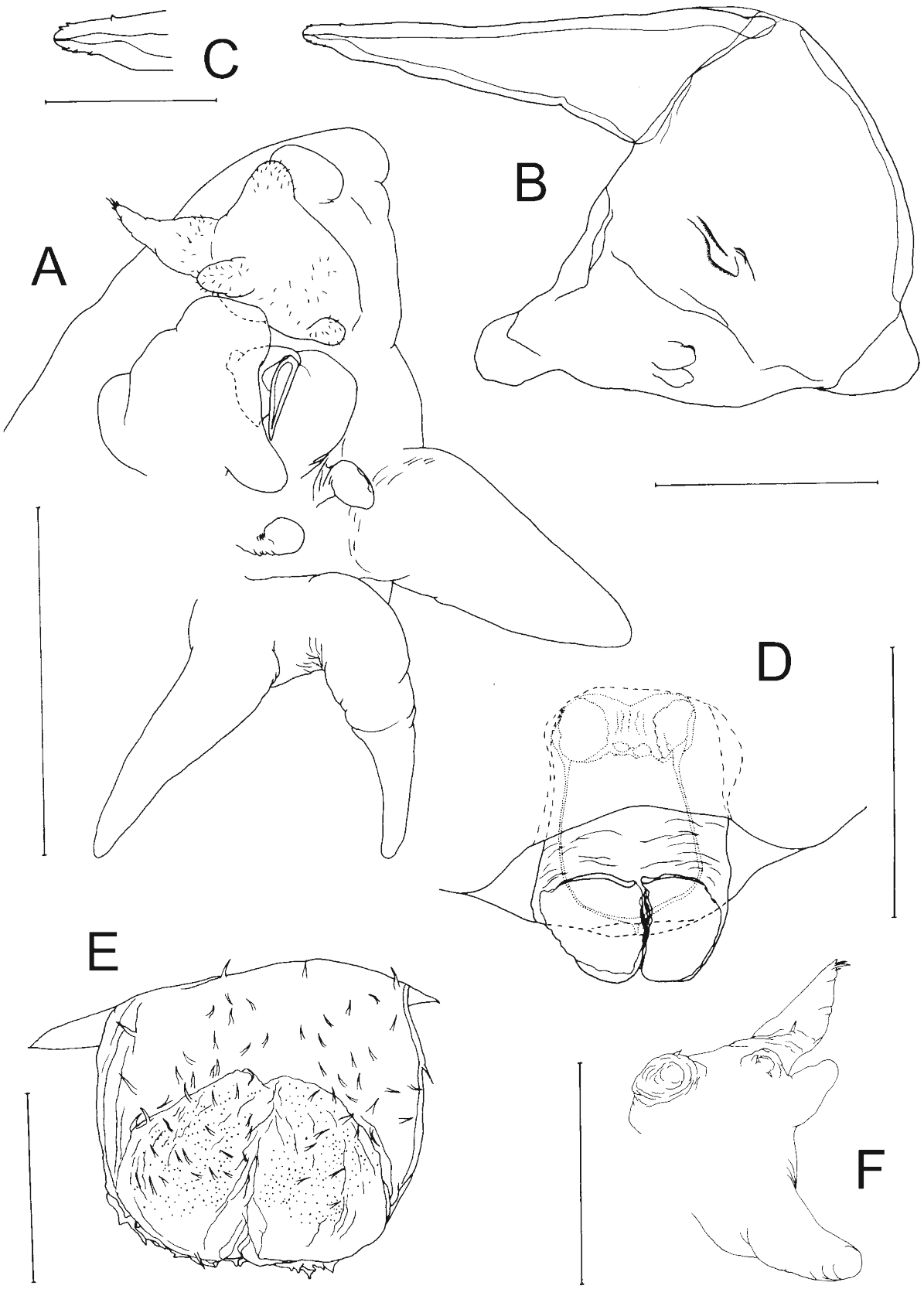

FIGURE 2. *Anoplodelphys africana* n. sp. paratype female (MNHN-Cp2313). A, Cephalosome and first pedigerous somite, lateral; B, Antenna, postero-lateral view; C, Tip of antennal claw; D, Urosome, dorsal view lacking surface ornamentation, with sperm ducts and seminal receptacles shown with dotted line; E, Urosome of second paratype (MNHN-Cp2314), showing surface ornamentation. *Anoplodelphys laubieri* n. sp. holotype female (MNHN-Cp2315). F, Antennule. Scale bars: A = 400 μm, B = 50 μm, C = 25 μm, D, F = 200 μm, E = 100 μm.

Antenna (Fig. 2B) 2-segmented: proximal segment, robust, triangular in shape and largely concealed between lateral cephalosomic process and prominent antennomedial lobe located just posterior to base of antenna on ventral surface of cephalosome (Figs 1C, 2A): distal segment forming strongly sclerotised subchela, ornamented with few small marginal denticles near tip (Fig. 2C).

Labrum (Fig. 1C) fleshy, forming massive tapering cone, with rounded tip reaching back to anterior border of second legs. Surface of labrum densely ornamented with setules.

Oral appendages (Figs 1C, 2A) reduced. Two pairs of small rounded processes present; 1 pair (?mandibles) lying just anterior to frontal margin of labrum, second pair (?maxillules) located lateral and posterior to first pair. Additional pair of sclerotised plates (see inset Fig. 1C) with transverse opening located immediately adjacent to base of labrum.

Legs 1 and 2 present (Fig. 1A–C), legs 3 and 4 absent. Leg 1 originating posterior and lateral to base of labrum; leg 2 originating slightly closer to midline. Each leg biramous, with unsegmented, lobate rami forming elongate conical processes, lacking recognisable setal armature but densely ornamented with surface setules. Exopodal and endopodal lobes about equal in size, arising from common protopodal part, largely incorporated into somite.

Leg 5 not observed.

Male unknown.

Remarks: The new species differs from *Anoplodelphys corneci* Lafargue and Laubier, 1978, *A. galli* and *A. incerta* in the presence of only the first two pairs of swimming legs rather than four pairs. It also differs in the bilobate condition of the rostrum and in having a swollen basal part to the antennule which is produced into three distinct processes.

The paired lobes in the oral region are here interpreted as representing reduced and modified mouthparts. The anterior pair, from its similar position to the mandibles present in *Brementia balneolensis*, is probably the mandibles, with each reduced to palp remnants. The posterior pair is interpreted as possible maxillules. The paired sclerotised plates may represent a vestige of the maxillae, since the transverse, slit-like opening may belong to the maxillary glands.

***Anoplodelphys laubieri* n. sp.**

Type material: Holotype female in alcohol, reg. no. MNHN-Cp2315 with antenna removed from one side and mounted on slide (MNHN-Cp2316).

Type locality: Sodwana Bay, Kwazulu-Natal, Republic of South Africa. Depth 0–22 m.

Host: *Didemnum rodriguesi* Rocha and Monniot, 1993 [MNHN reg. no. A2 DID C 361]

Locality in host: within the common tunic between the zooids (F. Monniot, pers. comm.)

Etymology: this species is named for Dr Lucien Laubier in honour of his contributions to knowledge of parasitic copepods.

Description: Adult female body (Fig. 3A–B) highly transformed, vermiform and lacking external segmentation: indistinctly divided into 3 regions, cephalosome, metasome and urosome, by shallow superficial furrows. Entire body surface densely ornamented with relatively short setules. Body length of holotype female 3.10 mm. Cephalosome slightly dorsoventrally flattened, tapering anteriorly; bearing paired antennules, antennae, and 1 pair of lobes which probably represent reduced and modified oral appendages. Lateral margins of head expanded ventrally to form ridge-like swelling produced into thumb-like process at posterior extremity (Figs 3C, 4A). Rostrum well developed on frontal margin of cephalosome (Fig. 3C), forming 2 broad, hemispherical lobes and with small, median ventral lobe. Metasome more or less cylindrical, comprising 4 somites but lacking surface expression; first 2 somites only pedigerous, each bearing pair of modified, biramous thoracic legs. Urosome (Figs 3A, 4B) indistinctly 2-segmented, inserted on posterior margin of

metasome and directed somewhat dorsally. Caudal rami (Fig. 4B) largely incorporated into urosome but each armed with 2 caudal setae terminally. Surface of urosome sparsely ornamented with setules.

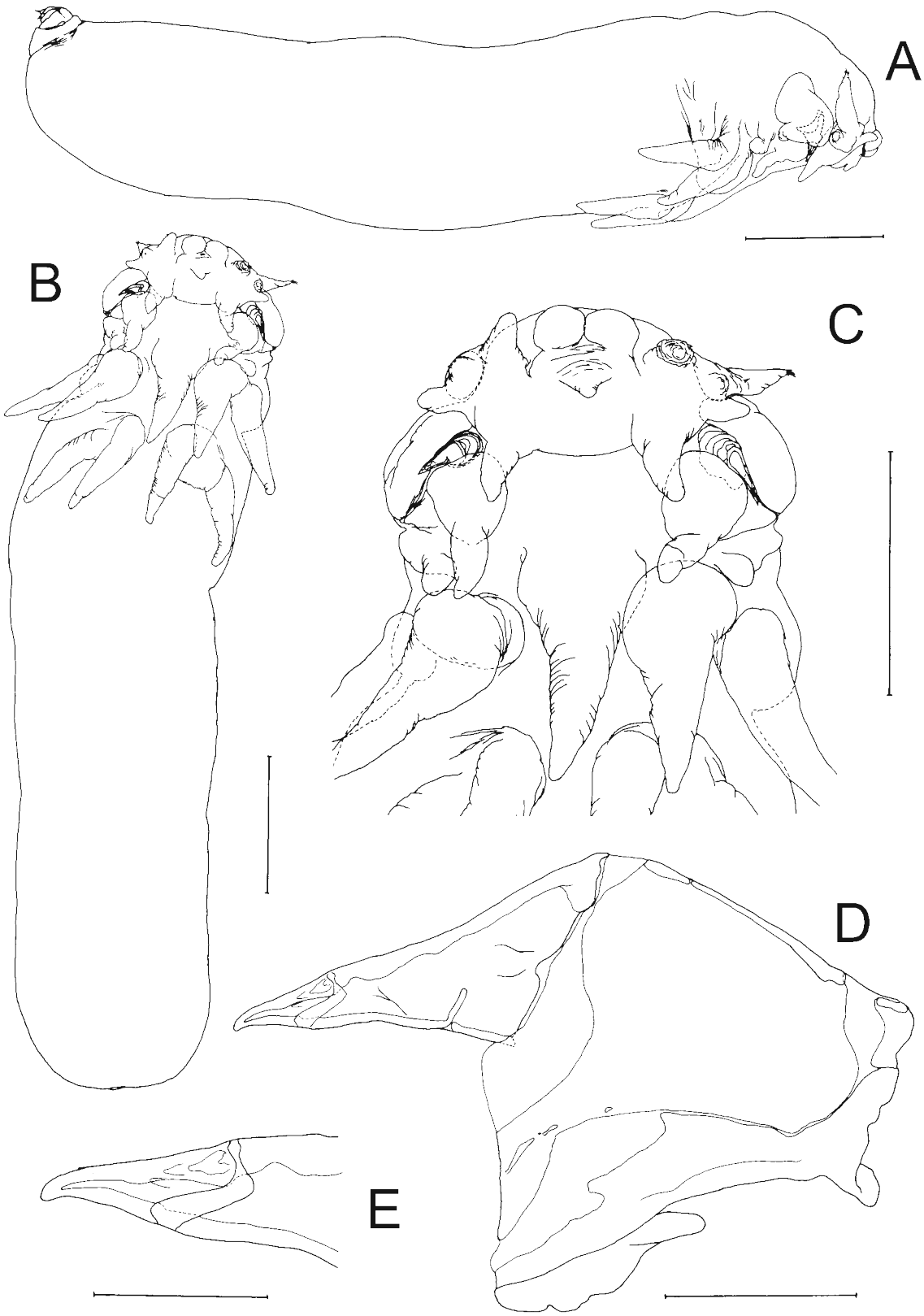

FIGURE 3. *Anoplodelphys laubieri* n. sp. holotype female (MNHN-Cp2315). A, Habitus, lateral; B, Habitus, ventral; C, Cephalosome and first pedigerous somite, ventral; D, Antenna, postero-lateral view; E, Tip of antennal claw. Scale bars: A–B = 500 μm, C = 400 μm, D = 50 μm, E = 25 μm.

Antennules (Figs 2F, 4A) inserted just lateral to rostrum; divided into swollen basal part bearing 4 rounded processes, orientated anteriorly, anterolaterally, laterally and posteroventrally, and conical, tapering distal part armed with 5 setal elements, 4 apical and 1 subapical (Fig. 4A). Surface of basal part of antennule ornamented with isolated spinules (Fig. 2F) on anterior and anterolateral processes.

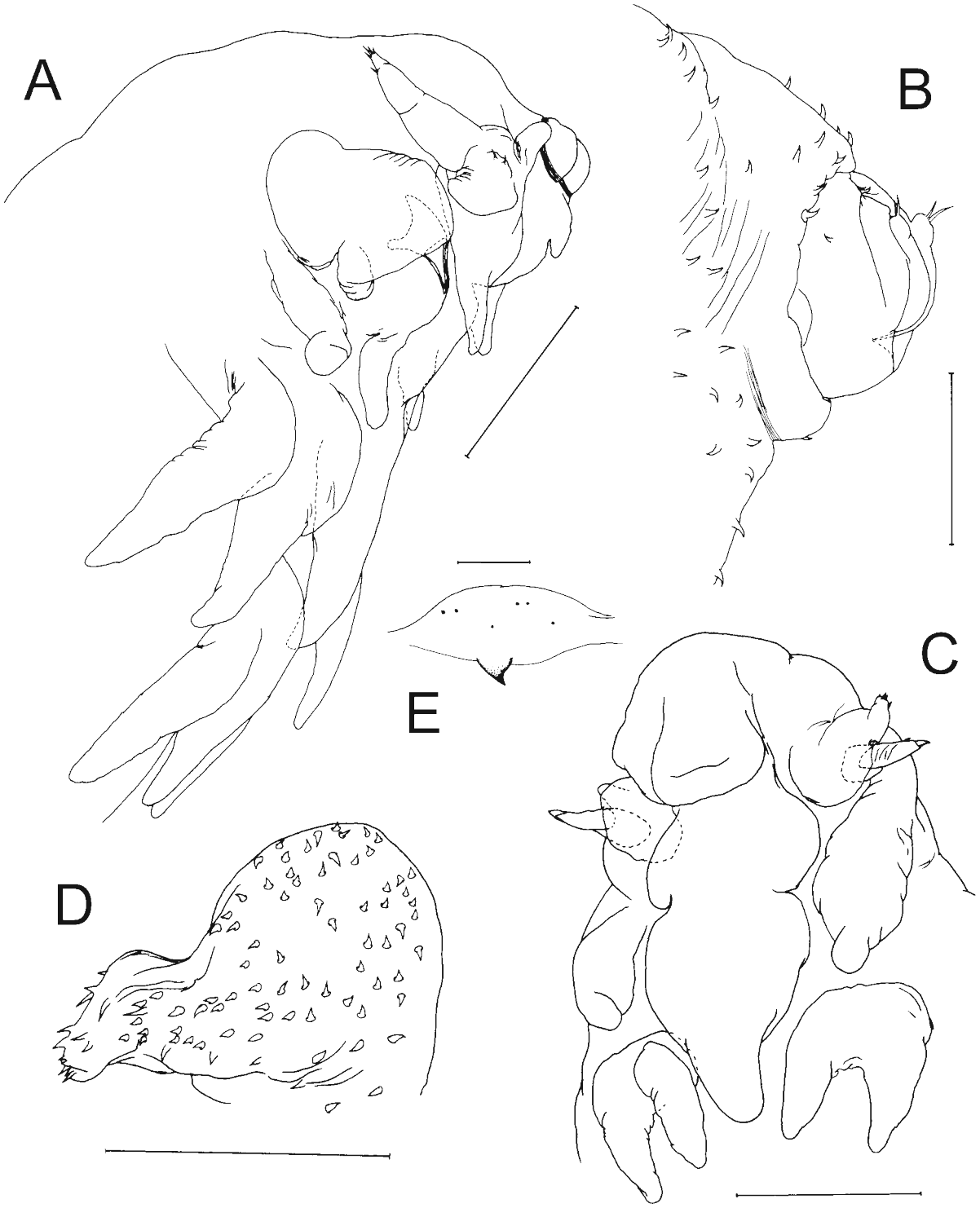

FIGURE 4. *Anoplodelphys laubieri* n. sp. holotype female (MNHN-Cp2315). A, Cephalosome and first pedigerous somite, lateral; B, urosome, lateral. *Anoplodelphys incerta* Lafargue & Laubier, 1977, holotype female (ZMA CO.106.602). C, Cephalosome and first pedigerous somite, ventral, D, Antennule showing surface ornamentation; E, Leg 5. Scale bars: A = 500 μm, B = 50 μm, C–D = 200 μm, E = 25 μm.

Antenna (Fig. 3D–E) 2-segmented: proximal segment, robust, triangular in shape and largely concealed between lateral cephalosomic process and antennomedial lobe located just posterior to base of antenna on ventral surface of cephalosome (Figs 3C, 4A): distal segment forming strongly sclerotised subchela. Subchela with defined apical section (terminal claw) retaining traces of 3 weakly sclerotised spines (Fig. 3E). Adjacent antennomedial lobe comprising inflated basal part and long, posteromedial process extending posteriorly as far as anterior border of leg 1.

Labrum (Fig. 3C) elongate, conical lobe, reaching to mid-level of leg 2; surface ornamented with setules.

One pair of oral appendages (?mandibles) present, reduced to unarmed lobes located about at mid level of labrum (Fig. 3C).

Legs 1 and 2 only present (Figs 3B, 4A); legs 3 and 4 absent. Leg 1 originating posterior and lateral to base of labrum; leg 2 originating close to leg 1, but slightly nearer midline. Each leg biramous, with unsegmented, lobate rami forming elongate conical processes, lacking setal armature but densely ornamented with surface setules. Exopodal lobe slightly longer than endopodal lobe, arising from common protopodal part, largely incorporated into somite.

Leg 5 absent.

Male unknown.

Remarks: As for the preceding species, *Anoplodelphys africana* n. sp., this new species differs from *A. corneci, A. galli* and *A. incerta* by the presence of only two leg pairs rather than four, and in details of shape of the rostrum and structure of the antennule. This species is closely related to *A. africana* n. sp., sharing the bipartite antennule and the bilobed rostrum. It can be distinguished from *A. africana* by the presence of two caudal setae, a small median post-rostral process, a fourth process (located anterolaterally) on the inflated basal part of the antennule, and a well developed posterior process on the large ventral lobe located immediately medial to the antenna.

The single pair of lobes in the oral region is here interpreted as probably representing vestigial mandibular palps, from their position just anterolateral to the base of the labrum.

Anoplodelphys corneci Lafargue and Laubier, 1978

Material examined: Holotype female, reg. no. ZMA CO.102.603. Two females in Monniot collection, from *Didemnum maculosum* (Milne Edwards, 1841) collected at Dinard, France; reg. no. MNHN-Cp2319.

Differential diagnosis: Body vermiform with indistinct segmentation. Cephalosome with narrow frontal margin bearing rostrum ventrally. Rostrum inflated, forming simple lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum inflated, forming elongate tapering lobe. Lateral margin of cephalosome expanded ventrally to form ridge-like swelling produced into process at posterior end. Adjacent antennomedial lobe drawn out into long posterior process. Metasome elongate with about 20% of length extending posterior to origin of leg 4: metasomal somites bearing legs ventrally near lateral margins. No mid-ventral processes present between legs. Urosome vestigial; located terminally, with median anal incision; bearing partly incorporated caudal rami armed with setae distally.

Antennule unsegmented with setose apex. Antenna reduced, 2-segmented, with triangular basal segment and distal subchela incorporating sclerotised distal claw, armed with 2 vestigial setal elements. Mandible to maxilliped lacking. Legs 1–4 biramous; each comprising short basal part (derived from protopod), largely incorporated into somite, carrying unsegmented, lobate rami. Leg 5 not observed.

Body length of female 0.85–3.90 mm. Male unknown.

Remarks: Examination of the holotype of *A. corneci* (ZMA CO.102.603) confirmed the original description in every respect. The new material comes from the same host species, *Didemnum maculosum*, collected in the same region. This species is readily characterised by the small size and simple structure of the rostrum (about the same width as the base of the labrum) and by the distribution of legs 1–4 along the metasome.

Anoplodelphys incerta Lafargue and Laubier, 1978

Material examined: Holotype female, reg. no. ZMA CO.102.602.

Differential Diagnosis: Body elongate, with indistinct segmentation. Cephalosome with narrow frontal margin bearing rostrum. Rostrum inflated, forming large ventrally-directed lobe (Fig. 4C). Post-rostral median lobe present. Labrum strongly inflated at base, tending distally into tapering lobe (Fig. 4C). Lateral margin of cephalosome expanded ventrally to form ridge-like swelling produced into process. Antennomedial lobe lacking. Metasome elongate with about 25% of length extending posterior to level of origin of leg 4: metasomal somites bearing small legs ventrally near lateral margins. No mid-ventral processes present between legs. Urosome small, unsegmented; located terminally; with median anal incision, bearing minute paired caudal rami armed with setae distally. Surface of body, rostrum, labrum, cephalosomic processes, and legs densely ornamented with surface setules.

Antennule unsegmented, tapering lobe (Fig. 4D). Antenna 2-segmented, with triangular basal segment and distal subchela incorporating sclerotised distal claw, armed with 3 vestigial setal elements. Mandible to maxilliped all lacking. Legs 1–4 biramous; each with protopodal part almost completely incorporated into somite so small lobate rami appearing to originate from somite surface. Ratios of gaps between legs along metasome as in Table 2. Leg 5 represented by tiny sclerotised points (Fig. 4E).

Body length of female 2.40–3.65 mm. Male unknown.

Remarks: In their paper on *Anoplodelphys*, Lafargue and Laubier (1978a) comment upon the very wide intraspecific variability between specimens of *Anoplodelphys incerta* collected from different host species. They recognised a so-called "typical" form of *A. incerta* from *Didemnum commune* (Della Valle, 1877) and an "atypical" form from *Didemnum fulgens* (Milne Edwards, 1841)*, D. protectum* (Daumézon, 1908)*, D. peyrefittense* (Brément, 1913) and *D. maculosum* (Milne Edwards, 1841). According to Lafargue and Laubier (1978a), the main distinguishing characters between "typical" and "atypical" forms were: the form and organisation of the elements of surface ornamentation, the general body shape, and the degree of development and position along the body of legs 1–4. Lafargue and Laubier (1978a) selected a specimen of the typical form collected from *D. commune* as the holotype (ZMA Co. 102.602) thereby fixing the name. Re-examination of this holotype of *A. incerta* leads us to conclude that the typical and atypical forms are not conspecific.

We propose to restrict the concept of *A. incerta* to the typical form (found on *D. commune*) characterised by the elongate body, the reduced size of legs 1 to 4, and the relatively wide spacing of legs 1 and 2 (18%) along the longitudinal axis of the body (Table 2). We here treat the atypical form as *Anoplodelphys* cf. *galli*, since the only differences from *A. galli* relate to the arrangement of the spinular ornamentation, a character that is difficult to assess with our current state of knowledge.

Anoplodelphys galli Lafargue and Laubier, 1978

Material examined: none.

Differential Diagnosis: Body with indistinct segmentation. Cephalosome with narrow frontal margin bearing rostrum. Rostrum forming simple, inflated lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum inflated, forming elongate tapering lobe. Lateral margin of cephalosome expanded ventrally to form ridge-like swelling produced into process at posterior end. Antennomedial lobe lacking. Metasome elongate with about 20% of length extending posterior to level of origin of leg 4: metasomal somites bearing legs ventrally near lateral margins. No mid-ventral processes present between legs. Urosome small, unsegmented, located terminally, with median anal incision; bearing partly incorporated caudal rami armed with setae distally. Surface of body, rostrum, labrum, cephalosomic processes and legs densely ornamented with surface setules arranged in triads (with long central setule and short setules either side).

Antennule unsegmented. Antenna 2-segmented, with triangular basal segment and distal subchela incorporating sclerotised distal claw, armed with 2 vestigial setal elements. Mandible to maxilliped lacking. Legs 1–4 biramous; each comprising short basal part (derived from protopod), largely incorporated into somite, with unsegmented, lobate rami. Ratios of gaps between legs along metasome as in Table 2. Leg 5 not observed.

Body length of female 0.70–2.85 mm. Male unknown.

Remarks: Lafargue and Laubier (1978a) concluded that *A. galli* and *A. incerta* (both forms) could be separated only by the details of their cuticular ornamentation. They showed that a triad-setule arrangement (a large central setule with 1 shorter setule on each side) was characteristic for *A. galli*. Their decision to base species-level discrimination on cuticular ornamentation patterns has not been tested subsequently, although their initial conclusions were based on the study of over 40 specimens (30 specimens of *A. galli* and 13 specimens of *A. incerta* (both forms) from across the four *Didemnum* host species).

We regard the spacing of the legs along the metasome as an important character for species discrimination. *Anoplodelphys galli* and *Anoplodelphys* cf. *galli* from *Didemnum peyrefittense*, *D. maculosum*, *D. fulgens* and *D. protectum* all share a similar pattern of leg distribution, with legs 1 and 2 separated by only 9–10% of the overall metasomal length, as compared to 18% in *A. incerta* (Table 2). This character is used here to restrict the definition of *A. incerta* and to distinguish it from *A. galli*.

Anoplodelphys cf. *galli*

Material examined: none.

Remarks: We are uncertain of the status of the specimens collected from *D. fulgens, D. protectum, D. peyrefittense* and *D. maculosum* originally described as the "atypical" form of *A. incerta* by Lafargue and Laubier (1978a: Figs 3H–J, 4A–E, 5A–B). These specimens share with *A. galli* characters such as body form, and the size and disposition of legs 1–4 along the body (Table 2). However, they differ in the fine-scale arrangement of setules comprising the cuticular ornamentation on the body surface: the setules are isolated and irregularly arranged, or grouped in twos and threes, but have never been observed in the particular triad arrangement found in *A. galli*. In addition, the sclerotised apical claw of the antenna has coarser marginal teeth compared to the fine teeth present near the tip only in *A. galli*.

TABLE 2. Distribution of legs along the metasome in *Anoplodelphys* species (calculated as distance between front edge of leg bases expressed as a percentage of total length of metasome).

Copepod species	Host ascidian	Leg 1–leg 2	Leg 2–leg 3	Leg 3–leg 4	Leg 4–end
Anoplodelphys incerta	*Didemnum commune*	18%	30%	26%	26%
Anoplodelphys galli	*Didemnum coccineum*	9%	28%	34%	29%
Anoplodelphys cf. *galli*	*Didemnum peyrefittense*	10%	24%	32%	34%
Anoplodelphys cf. *galli*	*Didemnum maculosum*	9%	32%	31%	28%

Paranoplodelphys n. gen.

Diagnosis: Body highly transformed; lacking external expression of body segmentation. Cephalosome with broad, strongly-convex frontal margin bearing paired antennule vestiges ventrolaterally. Rostrum lacking. Labrum forming elongate, posteriorly-directed lobe. Metasome extending posteriorly beyond end of dorsally located urosome. Urosome incorporating caudal rami, presented by caudal setae. Surface of body, labrum and legs densely ornamented with surface setules.

Antennules present as pair of wrinkled lobes originating close to labrum on ventral side of cephalosome. Antenna absent. Oral region lacking any vestiges of mouthparts. Leg 1 biramous; rami represented by unsegmented, rounded lobes; exopodal lobe reduced, laterally-directed; endopodal lobe large. Leg 2 uniramous, a simple lobe. Legs 3 and 4 absent. Leg 5 lobe bearing 2 setae.

Type species: *Paranoplodelphys simplex* n. gen. et n. sp. (by original designation)

Etymology: The genus name refers to the similarity between the new genus and *Anoplodelphys*.

Remarks: The phylogenetic analysis presented below (Fig. 14) places this new species as the sister-taxon to a lineage comprising *Achelidelphys*, *Cephalodelphys* and *Syndelphys*. It does not cluster with *Anoplodelphys* species but it lacks the stellate body form (defined by the apomorphic states of characters 1 and 2) of the *Achelidelphys–Cephalodelphys–Syndelphys* lineage. A new genus is established to accommodate this new species which represents the most extreme reduction known within the lineage. It retains only the antennules on the cephalosome and all other cephalosomic limbs are lost. The legs are also reduced: leg 1 is the only biramous leg, leg 2 is uniramous and legs 3 and 4 are lost. Combined with all these reductions is the retention of a well-defined leg 5, which is apparently lost in many of the less reduced relatives.

***Paranoplodelphys simplex* n. sp.**

Type material: Holotype female, 2 paratype females. Registration nos: MNHN-Cp2317 (Holotype in alcohol), MNHN-Cp2318 (paratype female in alcohol), BMNH 2006.1188. (1 paratype female in alcohol).

Type Locality: Mescha island, Djibouti: collected at depth of 0–20 m, in 1996

Host: *Didemnum dicolla* Monniot and Monniot, 1999 [MNHN reg. no. of host: A2 DID C 397-401]

Locality in host: within the common tunic between the zooids (F. Monniot, pers. comm.).

Etymology: the species name refers to the extreme reduction in limbs exhibited by this species.

Description: Adult female body (Fig. 5A–D) highly transformed, vermiform and lacking external segmentation: indistinctly divided into 3 regions, cephalosome, metasome and urosome, by shallow furrows. Body length of holotype female 1.63 mm (ranging from 1.63–1.70 mm for 3 studied specimens). Cephalosome with broad, rounded frontal margin; bearing single pair of appendages (antennules) ventrolaterally, and strongly developed labrum. Rostrum absent. Metasome more or less cylindrical, but tapering posteriorly; bearing 2 pairs of legs (legs 1 and 2). Developing eggs in uterus visible through body wall (Fig. 5C). Metasome lacking expressed segmentation but with visible cuticular folds indicating division into 4 somites; fourth somite bearing urosome inserted dorsally. Urosome (Fig. 5E) reduced, unsegmented, incorporating caudal rami represented by cluster of caudal setae (Fig. 5E). Entire body surface densely ornamented with relatively short setules, similar to those of *A. africana* (cf. Fig. 1D).

Antennules (Fig. 5A–B, D) extremely reduced, represented by pair of small conical protrusions located near anterolateral corners of labrum. No other cephalosomal appendages observed.

Labrum (Fig. 5A–B, D) massive, conical, with rounded posterior tip reaching anterior border of base of leg 2. Surface of labrum ornamented with setules.

Legs 1 and 2 only present (Fig. 5A–B, D); legs 3 and 4 absent. Legs 1 and 2 originating close to each other, just behind cephalosome. Leg 1 biramous, with common protopodal base bearing unsegmented, conical rami; endopodal lobe elongate, massive, exopodal lobe very reduced. Leg 2 uniramous, unsegmented, present as conical process half as long as endopodal lobe of leg 1.

Leg 5 (Fig. 5E–F) well developed as simple lobes armed with 2 setae located near anterior margin of urosome: 1 seta apical, other subapical.

Male unknown.

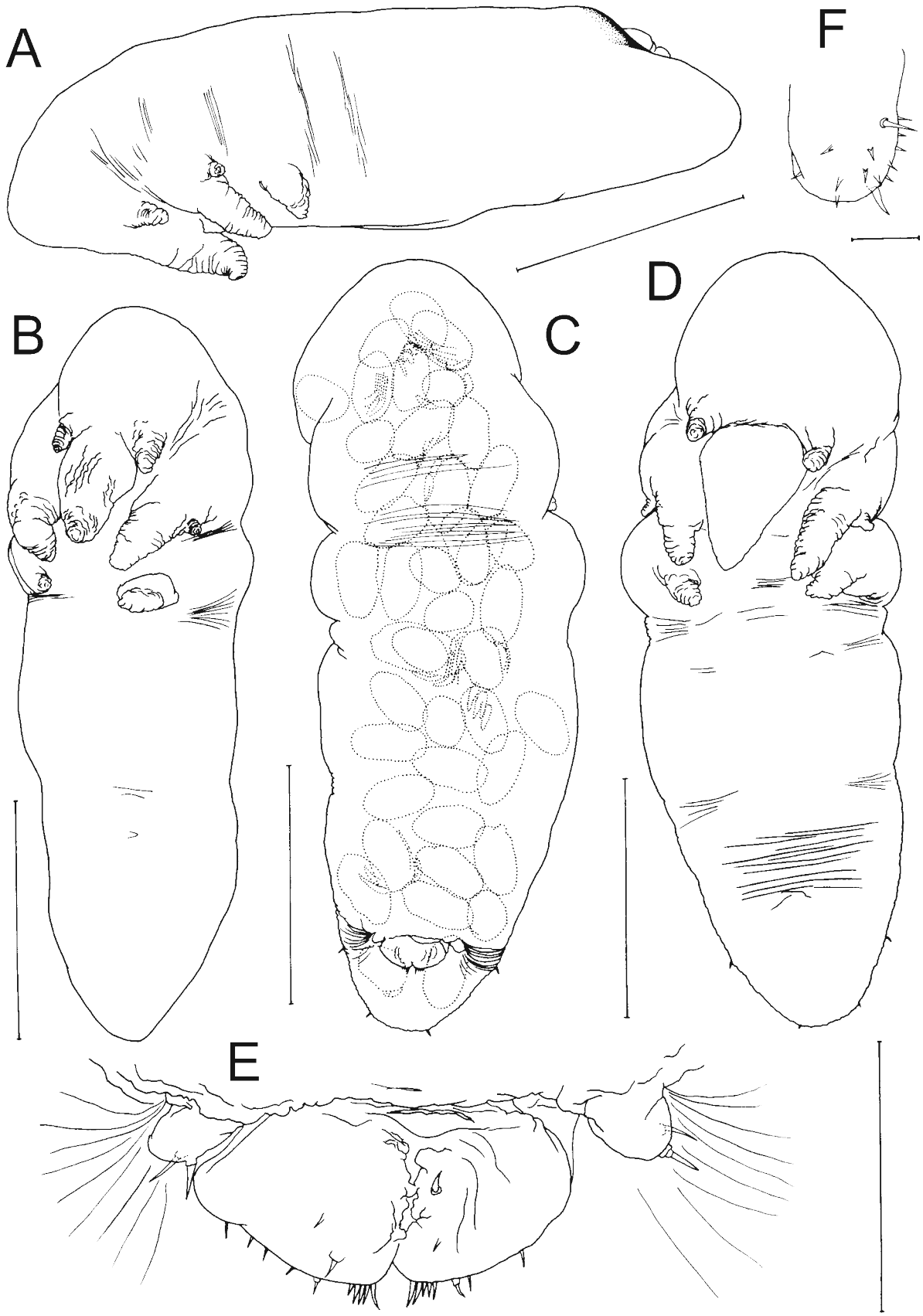

FIGURE 5. *Paranoplodelphys simplex* n. gen. et n. sp. A, Habitus of holotype female (MNHN-Cp2317) lateral; B, Habitus, ventral; C, Habitus of paratype (BMNH 2006.118), dorsal view showing developing eggs within uterus; D, Habitus, ventral; E, Urosome of holotype female (MNHN-Cp2317) *in situ* on metasome, ventral view showing surface ornamentation and clusters of caudal setae representing fully incorporated caudal rami; F, Fifth leg. Scale bars: A–D = 500 μm, E = 100 μm, F = 25 μm.

Remarks: The new species can be distinguished from all other species attributed to the *Brementia*-group of genera by extreme reduction: in particular by the absence of a rostrum, the loss of the antenna and all oral appendages, by the decrease in size of the exopodal lobe of leg I, and by the possession of a uniramous leg 2. Without access to developmental stages it is not possible to identify the homology of the remaining ramus on leg 2.

Genus *Brementia* Chatton and Harant, 1915
Brementia balneolensis Chatton and Brément, 1915

Material examined: none.

Differential Diagnosis: Body eruciform, with indistinct segmentation. Cephalosome with narrow frontal margin bearing anteroventrally-directed rostrum. Rostrum forming simple lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum a hemispherical lobe. Lateral margin of cephalosome expanded ventrally to produce ridge-like swelling. Metasome with about 30% of length extending posterior to origin of leg 4. Metasomal somites bearing ventrally-directed legs near lateral margins, lacking mid-ventral processes between legs. Urosome small, narrow and carrying partly-incorporated caudal rami. Caudal rami lobate, armed with setal remnants distally. Surface of body, rostrum, labrum, cephalosomic processes and legs densely ornamented with surface setules.

Antennule tapering with traces of segmentation, with apical segment setose. Antenna indistinctly 3-segmented, with distal segment incorporating reduced distal claw, and bearing 2 vestigial setal elements. Mandible forming large cylindrical lobe with vestigial gnathobase proximally bearing reduced setal elements; mandibular palp with bilobed apex. Maxillule represented by cylindrical lobe, bifid at apex. Maxilla indistinctly segmented, syncoxal part forming triangular lobe bearing vestiges of enditic armature along medial margin; basis bearing reduced claw and vestige of endopod. Maxilliped reduced to tiny conical lobe.

Legs 1 to 3 biramous, ventrally-directed; each comprising long basal part (derived from protopod), carrying short, unsegmented rami distally. Leg 4 reduced, largely incorporated into body somite, weakly bilobed distally, with lobes representing rami. Leg 5 not observed.

Body length of female approximately 2.35 mm. Male unknown.

Remarks: This is a strongly transformed copepod from the colonial ascidian *Didemnum commune* on the Mediterranean coast of France. It was redescribed to modern standards by Laubier and Lafargue (1974), based on new material collected from *Polysyncraton canetense* (Brément, 1913) in the same area. Despite the transformed body and swimming legs, this copepod retains a full set of mouthparts, although all are reduced in comparison with basal notodelphyids (Boxshall & Halsey 2004).

Brementia illgi Laubier and Lafargue, 1974

Material examined: none.

Differential Diagnosis: Body with indistinct segmentation. Cephalosome with narrow frontal margin bearing ventrally-directed rostrum. Rostrum forming simple lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum a small lobe, partly concealed beneath rostrum. Lateral margin of cephalosome expanded ventrally to produce ridge-like swelling. Metasome with about 30% of length extending posterior to origin of leg 4: metasomal somites bearing legs near lateral margins. Mid-ventral processes present between legs 2, 3 and 4. Urosome vestigial, largely incorporated into metasomal trunk. Caudal rami lobate, fused to urosome at base, armed with setal remnants distally. Surface of body, rostrum, labrum, cephalosomic processes, and legs densely ornamented with surface setules.

Antennule unsegmented, lobate with broad base, tapering to setose apex. Antenna modified, with traces of segmentation; distal segment reflexed, bearing vestiges of sclerotised distal claw and other setal elements. Mandible represented by tapering lobate palp, lacking gnathobase. Tiny paired lobes located posterior to mandibles possibly representing maxillules. Maxillae and maxillipeds lacking. Legs 1–3 biramous, ventrolaterally-directed; each comprising elongate basal part (derived from protopod), carrying elongate, unsegmented but superficially annulate rami distally. Legs 1–3 each bearing small outgrowths ventrally on protopodal part. Leg 4 reduced, largely incorporated into body somite, weakly bilobed distally, with reduced lobes representing rami. Leg 5 not observed.

Body length of female approximately 2.60 mm. Male unknown.

Remarks: This species was described from *Polysyncraton canetense* by Laubier and Lafargue (1974), who commented on the numerous differences between this species and *B. balneolensis*, the type species of the genus. They refrained from establishing a new genus of accommodate this species because of the poor state of knowledge of the phylogeny of the "ophioseidimorph" Notodelphyidae. The phylogenetic analysis performed here (Fig. 14) supports a monophyletic *Brementia* comprising both *B. balneolensis* and *B. illgi*.

Genus *Achelidelphys* Lafargue and Laubier, 1977
Achelidelphys steinitzi Lafargue and Laubier, 1977

Material examined: Holotype, reg. no. ZMA CO. 102.628. Four females from Monniot collection, from *Didemnum* sp. collected intertidally on shore at Mont Dore, New Caledonia. Three females in alcohol reg. nos MNHN-Cp2320. One female in alcohol, reg. no. BMNH 2006.1189.

Differential Diagnosis: Body highly transformed, stellate (Figs 6A–D, 7A–B); segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with frontal margin merging into tapering, laterally-directed antennulary lobes. Rostrum anteroventrally-directed; elongate lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum forming rounded hemispherical lobe. Lateral margin of cephalosome not produced into ridge-like swellings. Antenno-medial processes absent. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1–4 transformed, originating laterally, each occupying entire margin of somite; produced laterally giving body a stellate appearance. Mid-ventral metasomal processes present between legs 2 and 3 (Figs 6A, C; 7B). Urosome vestigial, located terminally; bearing partly incorporated caudal rami. Surface of body, rostrum, labrum, cephalosomic processes, and legs densely ornamented with surface setules.

Antennules forming tapering lobe on either side of frontal margin of cephalosome. Antenna to maxilliped lacking. Legs 1–3 biramous; rami represented by unsegmented, tapering lobes; exopodal lobe laterally-directed, with broad base, carrying smaller endopodal lobe ventrally. Leg 4 uniramous, comprising short, posterolaterally-directed lobe representing exopod. Exopodal lobes of legs 2 and 3 each housing internal expansion of uterus, containing eggs visible through body wall (Fig. 7A). Leg 5 absent.

Body length of female 1.40–2.50 mm. Male unknown.

Remarks: The three available, undamaged females of *A. steinitzi* from New Caledonia were compared in an attempt to assess the variability of different characters and their relative merit for species discrimination. These three specimens share with the holotype the number and arrangement of body processes, in particular they all possess median ventral processes between legs 2 and 3, the tapering conical rostrum, the hemispherical labrum, and the surface ornamentation of long setules. The new material also falls within the range of body lengths given for the type material (Lafargue & Laubier 1977). One of the new females contains eggs in the uterus, lobes of which extend into the exopodal lobes of legs 2 and 3, as in the holotype. There are differences in the degree of development of the cephalosomal, metasomal and leg processes but given the variability in specimens collected from the same host individual (cf. Figs 6A, C and 7B), we do not regard them as

sufficient to justify the establishment of a new species. All specimens also display some asymmetry in the development of processes, but this asymmetry varies individually and may possibly be due to the position within the host.

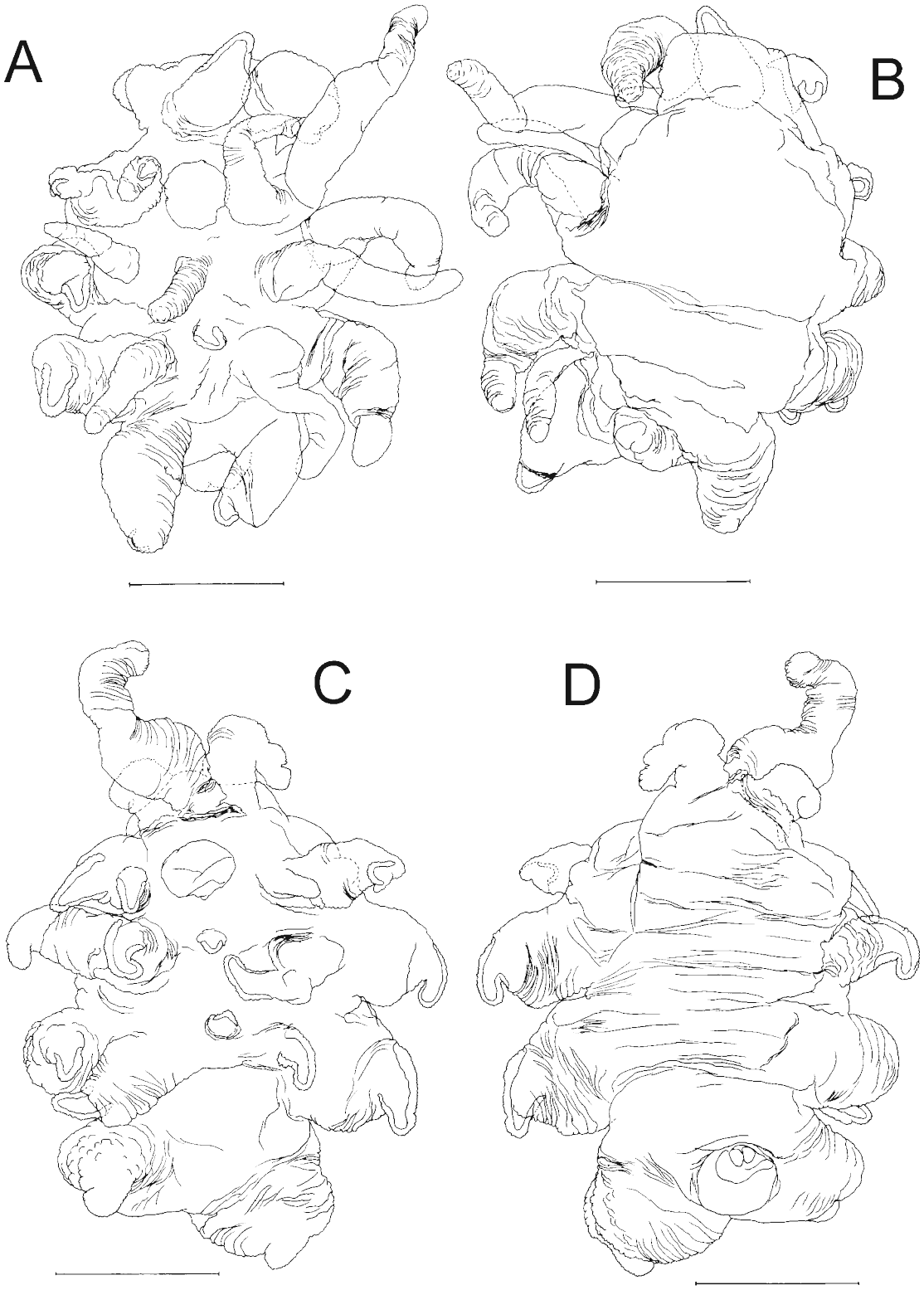

FIGURE 6. *Achelidelphys steinitzi* adult female. A, Habitus of specimen 1 (MNHN-Cp2320) from New Caledonia, ventral; B, Same, dorsal; C, Habitus of specimen 2 (BMNH 2006.1189) from New Caledonia, ventral; D, Same, dorsal. All scale bars = 500 μm.

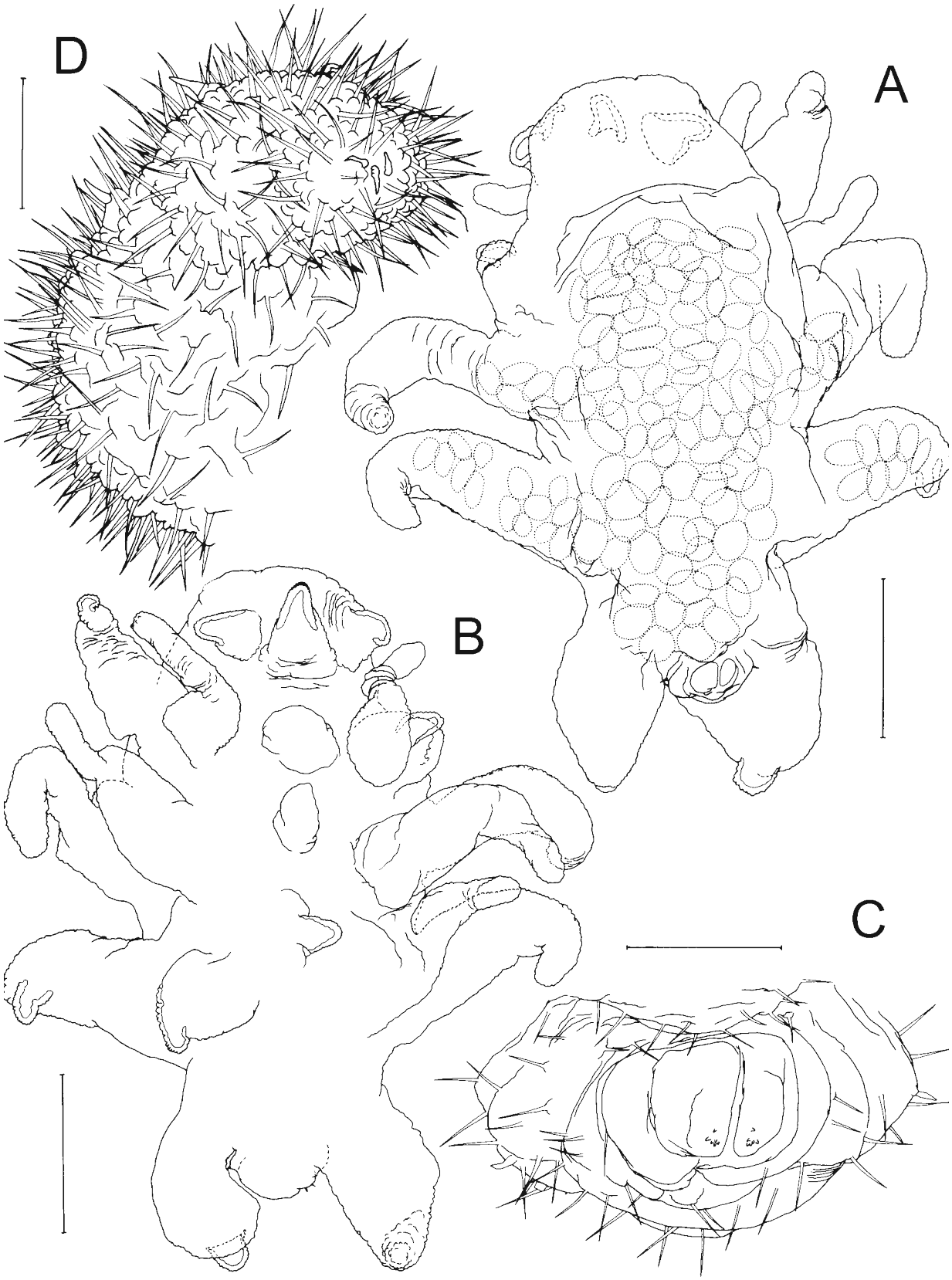

FIGURE 7. *Achelidelphys steinitzi* female. A, Habitus of specimen 3 (MNHN-Cp2320) from New Caledonia, dorsal; B, Same, ventral; C, Urosome, dorsal view showing vestiges of caudal rami; D, Antennule showing surface ornamentation. Scale bars: A–B = 500 μm, C = 100 μm, D = 50 μm.

Achelidelphys drachi Lafargue and Laubier, 1978

Material examined: Holotype female, reg. no. ZMA CO. 106.637.

Differential Diagnosis: Body highly transformed, stellate (Fig. 8A–B); segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with frontal margin merging into elongate, tapering, anterolaterally-directed antennulary lobes. Rostrum elongate, anteroventrally-directed lobe (Fig. 8B), without accessory median lobe. Post-rostral median lobe absent. Labrum inflated, forming rounded, slightly-elongate lobe. Lateral margin of cephalosome not produced into ridge-like swellings. Paired antenno-medial processes present on ventral surface of cephalosome, anterior and lateral to labrum. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1–4 transformed, originating laterally, each occupying entire margin of somite and produced laterally, giving body stellate appearance. Mid-ventral metasomal process present between second legs. Urosome vestigial, located terminally; bearing partly incorporated caudal rami (Fig. 8C). Surface of body, rostrum, labrum, cephalosomic processes and legs densely ornamented with surface setules.

Antennules forming elongate, tapering lobe directed antero-laterally on either side of frontal margin of cephalosome. Antenna to maxilliped lacking. Legs 1–3 biramous; rami represented by unsegmented, elongate lobes: exopodal lobes laterally-directed, with broad base, carrying elongate endopod ventrally. Leg 4 uniramous, comprising tapering, posterolaterally-directed lobe representing exopod. Exopodal lobes of legs 2–4 each housing internal expansion of uterus, containing eggs visible through body wall. Leg 5 absent.

Body length of female 2.50 mm. Male unknown.

Remarks: This species carries an additional tiny unpaired process on the ventral midline about at the level of the first pair of legs. The homology of this process is uncertain (i.e. whether it is a serial homologue of the processes present between legs 2–4 in *A. steinitzi*, for example). This species can be distinguished from its congeners by the extreme length of the tapering lobes derived from the antennules, rostrum and leg rami. The paired antenno-medial processes are shared only with *A. ampla* among the members of *Achelidelphys*.

Achelidelphys ampla Lafargue and Laubier, 1977

Material examined: Holotype female, reg. no. ZMA CO. 102.629.

Differential Diagnosis: Body highly transformed, stellate; segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with frontal margin merging into tapering laterally-directed antennulary lobes. Rostrum anteroventrally-directed, simple short lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum inflated, forming elongate, posteriorly-directed lobe. Lateral margin of cephalosome not produced into ridge-like swellings. Paired antennomedial processes present on ventral surface of cephalosome, anterior and lateral to labrum. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1–4 transformed, originating laterally, each occupying entire margin of somite; produced laterally giving body a stellate appearance. Mid-ventral metasomal processes between legs absent. Urosome vestigial, located terminally; bearing partly incorporated caudal rami armed with vestigial setae (Fig. 9A). Surface of body, rostrum, labrum, cephalosomic processes, and legs densely ornamented with surface setules.

Antennules forming short, tapering lobe on either side of frontal margin of cephalosome; surface ornamented with short spinules and vestiges of apical setae present (Fig. 9B). Antenna to maxilliped lacking. Legs 1–3 biramous; rami represented by unsegmented, tapering lobes: exopodal lobe laterally-directed, with broad base and unarmed tip (Fig. 9C), carrying smaller endopodal lobe ventrally. Leg 4 uniramous, comprising tapering, posterolaterally-directed lobe representing exopod. Uterus not expanded into exopods of legs. Leg 5 absent.

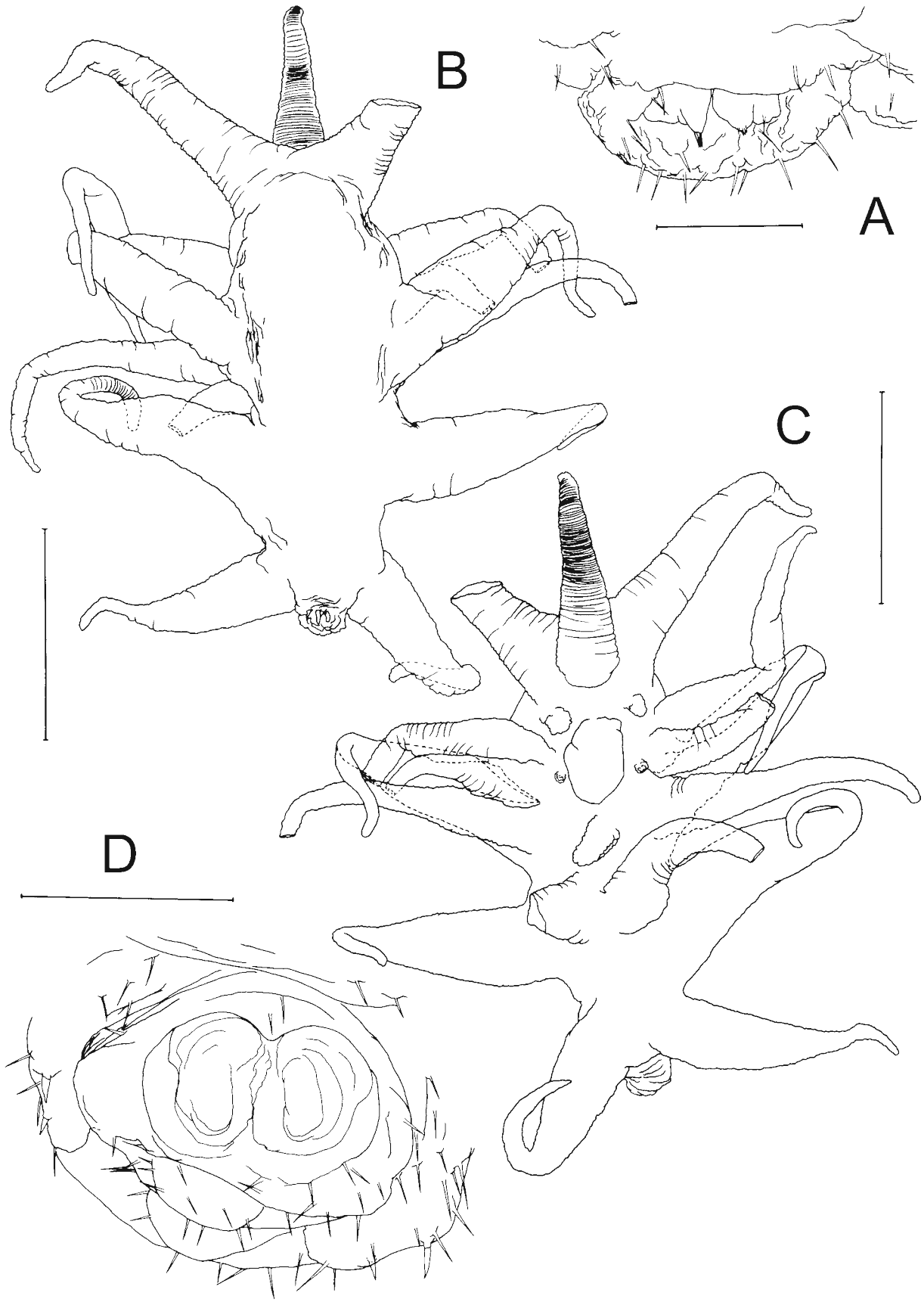

FIGURE 8. *Achelidelphys steinitzi* Lafargue and Laubier, 1977, holotype female (ZMA CO.106.628). A, Urosome, dorsal. *Achelidelphys drachi* Lafargue & Laubier, 1978, holotype female (ZMA CO.106.637). B, Habitus, dorsal; C, Habitus, ventral; D, Urosome, dorsal. Scale bars: A = 100 μm, B–C = 1 mm, D = 100 μm.

Body length of female 1.55–2.60 mm. Male unknown.

Remarks: *Achelidelphys ampla* has a compact uterus which does not extend into the exopodal lobes of the legs when full of stored eggs. This character, in combination with the lack of any median ventral processes on the metasome, serves to distinguish *A. ampla* from all other species. In *A. ampla* there is a pair of ventral process on the cephalosome originating anterior and lateral to the labrum. The origin of these antenno-medial processes is uncertain but we tentatively interpret them as homologous with the antenno-medial processes present in most *Anoplodelphys* species. A similar pair of antenno-medial processes is present in *A. drachi* but is absent in all other *Achelidelphys* species.

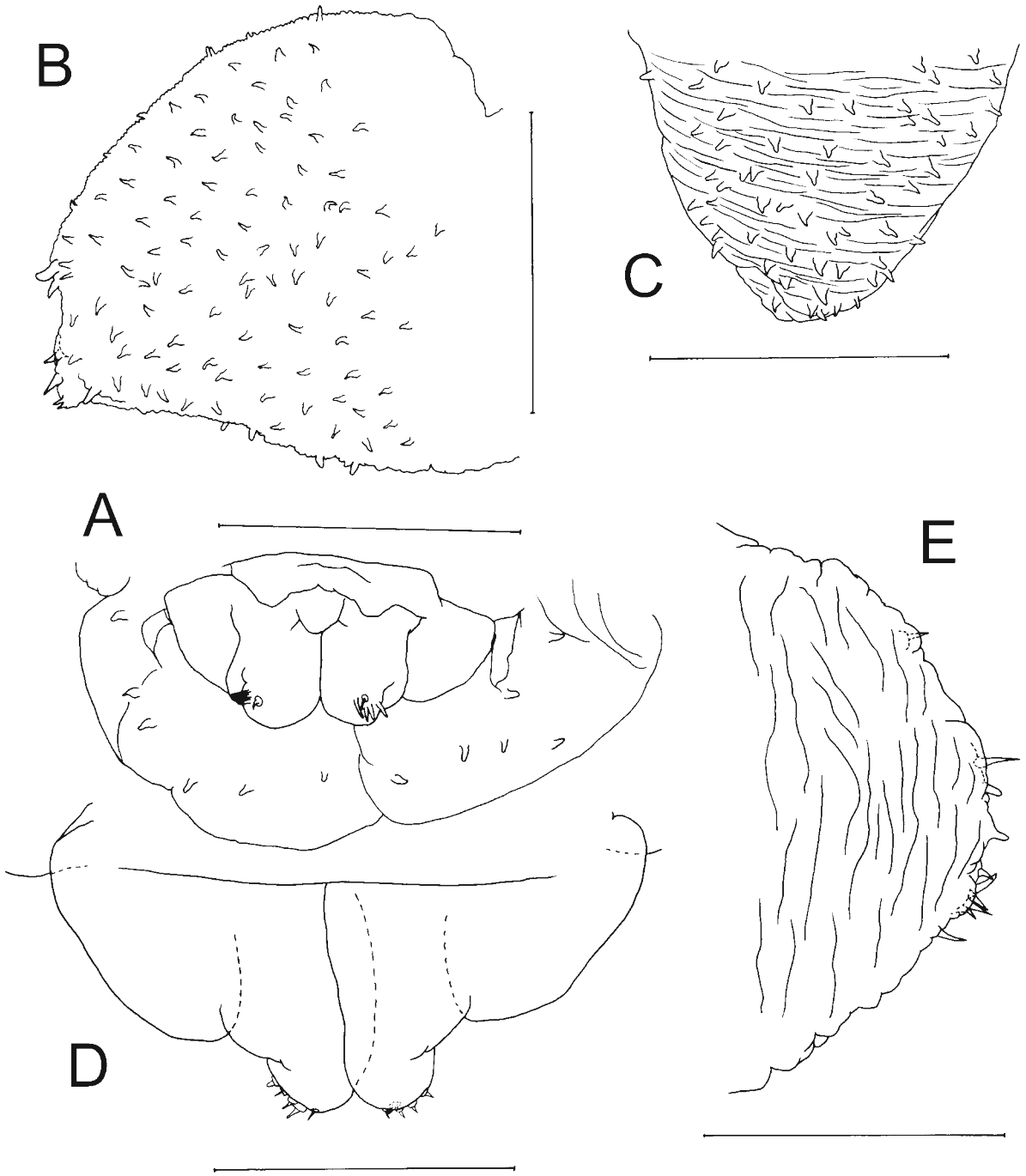

FIGURE 9. *Achelidelphys ampla* Lafargue and Laubier, 1978, holotype female (ZMA CO.106.629). A, Urosome, dorsal; B, Antennule, showing ornamentation and vestigial apical setae; C, Tip of leg 1, showing ornamentation. *Achelidelphys chengae* Lafargue & Laubier, 1978, holotype female (ZMA CO.106.638). D, Urosome, dorsal; E, Tip of antennule, showing vestigial apical setae. All scale bars = 100 μm.

Achelidelphys chengae Lafargue and Laubier, 1978

Material examined: Holotype female, reg. no. ZMA CO. 106.638.

Differential Diagnosis: Body highly transformed, stellate; segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with frontal margin merging into tapering anterolaterally-directed antennulary lobes. Rostrum simple, frontally-directed lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum forming tapering, posteriorly-directed lobe. Lateral margin of cephalosome not produced into ridge-like swellings. Antenno-medial processes absent. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1–4 transformed, originating laterally, each occupying entire margin of somite and produced laterally, giving body stellate appearance. Mid-ventral metasomal processes absent. Urosome vestigial, located terminally; bearing partly incorporated caudal rami with short caudal setae (Fig. 9D). Surface of body, rostrum, labrum, cephalosomic processes, and legs sparsely ornamented with minute surface setules.

Antennules forming bluntly-rounded lobe on either side of frontal margin of cephalosome, with vestigial apical setae (Fig. 9E). Antenna to maxilliped lacking. Legs 1–3 biramous; rami represented by unsegmented, tapering lobes; exopodal lobe laterally-directed, with broad base, carrying smaller endopodal lobe ventrally. Leg 4 uniramous comprising short, posterolaterally-directed lobe representing exopod. Exopodal lobes of legs 2–4 each housing internal expansion of uterus, containing eggs visible through body wall. Leg 5 absent.

Body length of female 1.35–1.90 mm. Male unknown.

Remarks: *Achelidelphys chengae* also lacks any median ventral processes on the metasome as does *A. ampla*, but in the adult female the uterus extends into the exopodal lobes of legs 2–4 when full of stored eggs. It also differs from *A. ampla* in the lack of antennomedial processes.

Achelidelphys nigra Lafargue and Laubier, 1977

Material examined: none.

Differential Diagnosis: Body highly transformed, stellate; segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with frontal margin merging into tapering laterally-directed antennulary lobes. Rostrum anteroventrally-directed; inflated, simple elongate lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum forming rounded, hemispherical lobe. Lateral margin of cephalosome not produced into ridge-like swellings. Antennomedial processes absent. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1–4 transformed, originating laterally, each occupying entire margin of somite; produced laterally giving body a stellate appearance. Mid-ventral metasomal process present between leg 2 only. Urosome vestigial, located terminally; bearing partly incorporated caudal rami. Surface of body, rostrum, labrum, cephalosomic processes, and legs densely ornamented with surface setules.

Antennules forming tapering lobe on either side of frontal margin of cephalosome. Antenna to maxilliped lacking. Legs 1–3 biramous; rami represented by unsegmented, tapering lobes; exopodal lobe laterally-directed, with broad base, carrying smaller endopod ventrally. Leg 4 uniramous comprising short, posterolaterally-directed lobe representing exopod. Oviducts tubular, containing eggs visible through body wall. Leg 5 absent.

Body length of female about 2.25 mm. Male unknown.

Remarks: The main character distinguishing *A. nigra* from *A. steinitzi* is the presence of only a single median ventral lobe, located between the second pair of legs in the former compared to two lobes, located between legs 2 and 3, in the latter. The oviducts are tubular and form loops within the body cavity in *A. nigra* but they do not form an expanded sac-like uterus as in *A. ampla*, or a multi-lobate uterus, as in all other *Achelidelphys* species.

***Achelidelphys papuensis* n. sp.**

Type material: Holotype female, 6 paratype females. Registration nos MNHN-Cp2411 (holotype in alcohol), MNHN-Cp2412 (3 paratype females in alcohol), BMNH 2007.1 (1 paratype female in alcohol), BMNH 2007.2–3 (2 paratype females mounted on SEM stubs).

Type Locality: 02°39.49'S 150°25.56'E off Papua New Guinea, 18 m depth; 2 July 2003.

Host: *Didemnum* sp.

Locality in host: within the common tunic between the zooids (F. Monniot, pers. comm.).

Etymology: the species name refers to the type locality.

Description: Body highly transformed, stellate (Figs 10, 11A); segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with frontal margin merging into tapering anterolaterally-directed antennulary lobes. Rostrum simple, elongate, frontally-directed lobe, without accessory median lobe. Post-rostral median lobe absent. Labrum forming short, tapering, posteriorly-directed lobe (Fig. 11B). Lateral margin of cephalosome not produced into ridge-like swellings. Antennomedial processes absent. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1 to 4 transformed, originating laterally, each occupying entire margin of somite and produced laterally, giving body stellate appearance. Mid-ventral metasomal processes absent. Urosome vestigial, located terminally and typically directed dorsally (Fig. 11C); bearing partly incorporated caudal rami. Surface of body, rostrum, labrum, cephalosomic processes, and legs densely ornamented with surface setules: surface of rostrum, antennules and legs 1 to 4 densely folded, with deep folds orientated around circumference of process (Fig. 11D).

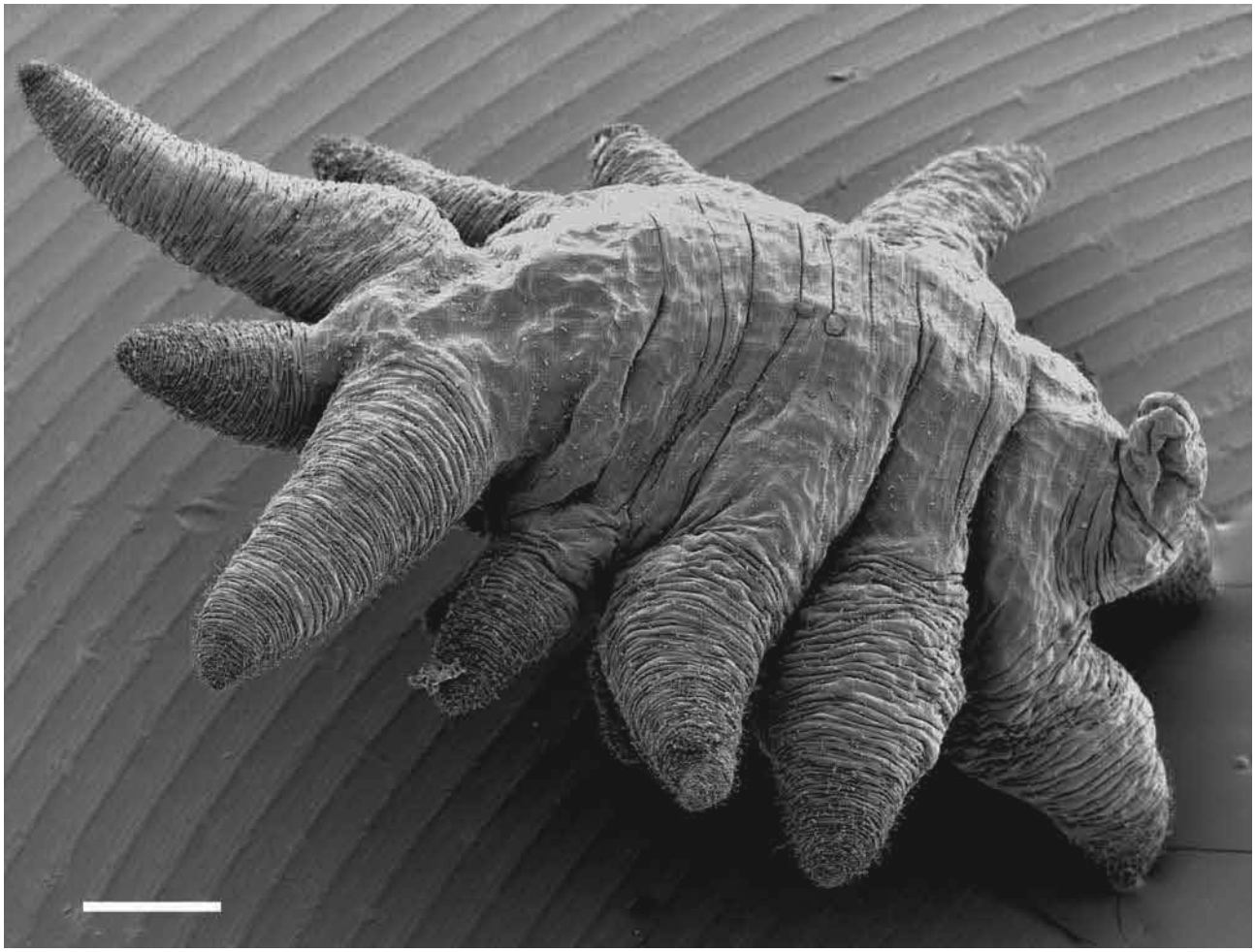

FIGURE 10. *Achelidelphys papuensis* n. sp. paratype female (BMNH 2007.2). SEM micrograph, dorso-lateral view showing highly folded cuticle of rostrum and appendages. Scale bar = 200 μm.

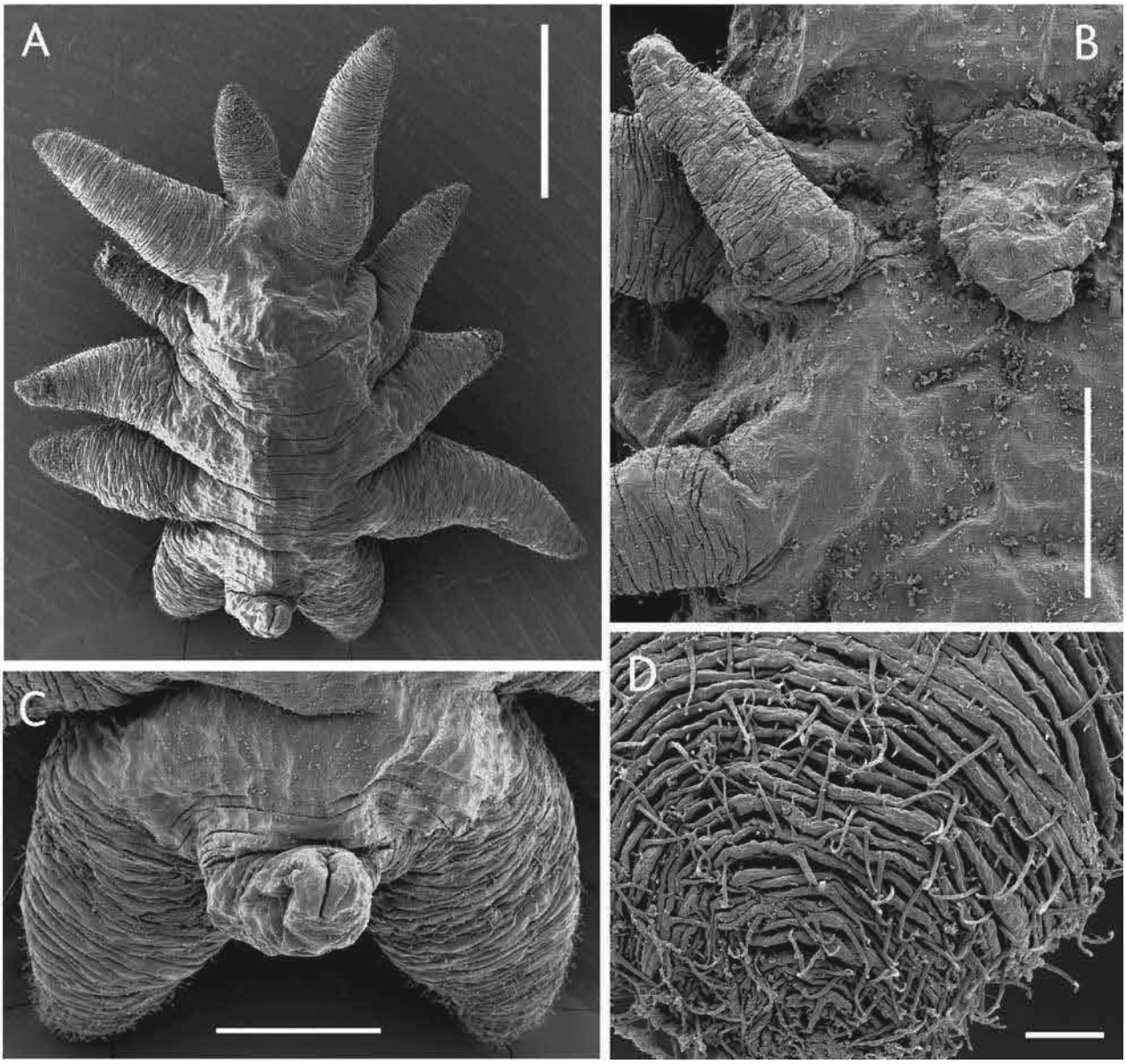

FIGURE 11. *Achelidelphys papuensis* n. sp. paratype females (BMNH 2007.2-3). SEM micrographs. A, Habitus, dorsal; B, labrum and endopod of leg 1, ventral; C, posterior extremity of body, with fourth legs and dorsally reflexed urosome, dorsal; D, tip of antennule, showing surface folding and setular ornamentation. Scale bars: A = 500 μm, B–C = 200 μm, D = 20 μm.

Antennules forming bluntly-rounded lobe on either side of frontal margin of cephalosome, with vestigial apical setae (Figs 10, 11A). Antenna to maxilliped entirely lacking. Legs 1 to 3 biramous; rami represented by unsegmented, tapering lobes; exopodal lobes laterally-directed, with broad base, carrying smaller endopodal lobes ventrally (Figs 10, 11B). Leg 4 uniramous comprising short, posterolaterally-directed lobe representing exopod; lobe strongly tapering, conical in shape, ranging from 0.90–1.38 times longer than width at base. Exopodal lobes of legs 2–4 each housing internal expansion of multilobate uterus, containing eggs visible through body wall. Leg 5 absent.

Body length of female 1.36–1.93 mm, measured from base of rostrum to posterior extremity of urosome (based on 6 specimens). Male unknown.

Remarks: The new species lacks any median ventral processes on the metasome between the legs. The lack of such processes serves to distinguish it from *A. steinitzi* which has two processes, one located between each of the second and third leg pairs, and from *A. drachi* and *A. nigra* which have a single process located

between the second legs. It differs from *A. stellata* and *A. reducta*, both of which have a strongly convex frontal margin to the head which merges laterally into the incorporated antennulary lobes. It differs from *A. ampla* in the shape of the uterus, which is compact and does not extend into the exopodal lobes of the legs in *A. ampla* but is multilobate and extends into the exopodal lobes in the new species.

Achelidelphys papuensis n. sp. most closely resembles *A. chengae* and these two species are also similar in body size, but they can be distinguished by the relative length of the paired lobes representing the fourth legs. In all specimens of the new species this lobe is short and conical, ranging from 0.9 to 1.4 times longer than the width at its base, whereas the lobes of *A. chengae* are elongate, about three times longer than the basal width. Although in these highly modified endoparasites overall shape appears to vary according to the degree of contraction or expansion of the limbs and rostrum, we believe that the difference in proportions of leg 4 exceeds the level that can be attributed to intraspecific variation. In addition, in their description of *A. chengae*, Lafargue and Laubier (1978b) state "L'ornementation cuticulaire est particulièrement réduite par rapport aux autres espèces du genre: elle se compose de minuscules spinules mesurant 1 à 2 microns de longeur." In contrast, the surface setules of the new species are an order of magnitude longer, often exceeding 20 microns in length. Finally, Lafargue and Laubier (1978b) describe the tip of the antennule of *A. chengae* as bearing some fine setae accompanied by very short conical-cylindrical setae, the presence of which we have confirmed (Fig. 9E), and they show these surrounded by very sparse surface setules. In the new species, the tip of the antennule lacks such short conical-cylindrical setae and the entire surface of the antennule is densely covered with long setules (Fig. 11D).

Achelidelphys stellata (Lafargue and Laubier, 1977) n. comb.

Syn: *Cephalodelphys stellata* Lafargue and Laubier, 1977

Material examined: Holotype female, reg. no. ZMA CO. 106.630.

Differential Diagnosis: Body highly transformed, stellate (Fig. 12A); segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with broad, strongly-convex frontal margin merging laterally into large, ventrally-directed antennulary lobes (Fig. 12B). Rostrum ventrally-directed; simple rounded lobe. Post-rostral median lobe present. Labrum forming elongate, posteriorly-directed lobe. Lateral margin of cephalosome not produced into ridge-like swellings. Antenno-medial swellings also absent. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1–4 transformed, originating laterally, each occupying entire margin of somite, produced laterally giving body a stellate appearance. Mid-ventral metasomal processes between legs lacking. Urosome reduced, located terminally; incorporating caudal rami. Surface of body, rostrum, labrum, cephalosomic processes, and legs densely ornamented with surface setules (Fig. 12C).

Antennules forming large, rounded lobe on either side of convex frontal margin of cephalosome (Fig. 12D). Oral region with 3 pairs of tiny lobes, arranged either side of labrum; positions of lobes suggesting possible homology with mouthparts (mandibles to maxillae?). Legs 1 to 3 biramous; rami represented by unsegmented, rounded lobes; exopodal lobe laterally-directed, with broad base, carrying smaller endopodal lobe ventrally. Leg 4 uniramous, comprising short, posterolaterally-directed lobe representing exopod. Exopodal lobes of legs 2–4 each housing internal expansion of uterus, containing eggs visible through body wall. Leg 5 absent.

Body length of female 0.87–2.30 mm. Male unknown.

Remarks: This species has a strongly convex frontal margin to the cephalosome, but retains a rostrum. The phylogenetic analysis places this species within the *Achelidelphys* group of species (Fig. 14) and does not support the retention of *Cephalodelphys* as a separate genus. Lafargue and Laubier (1977: Fig. 4A) figured a

small median ventral process (just posterior to the three pairs of oral lobes) concealed beneath the tip of the labrum but we were unable to confirm the presence of this structure in our re-examination of the holotype.

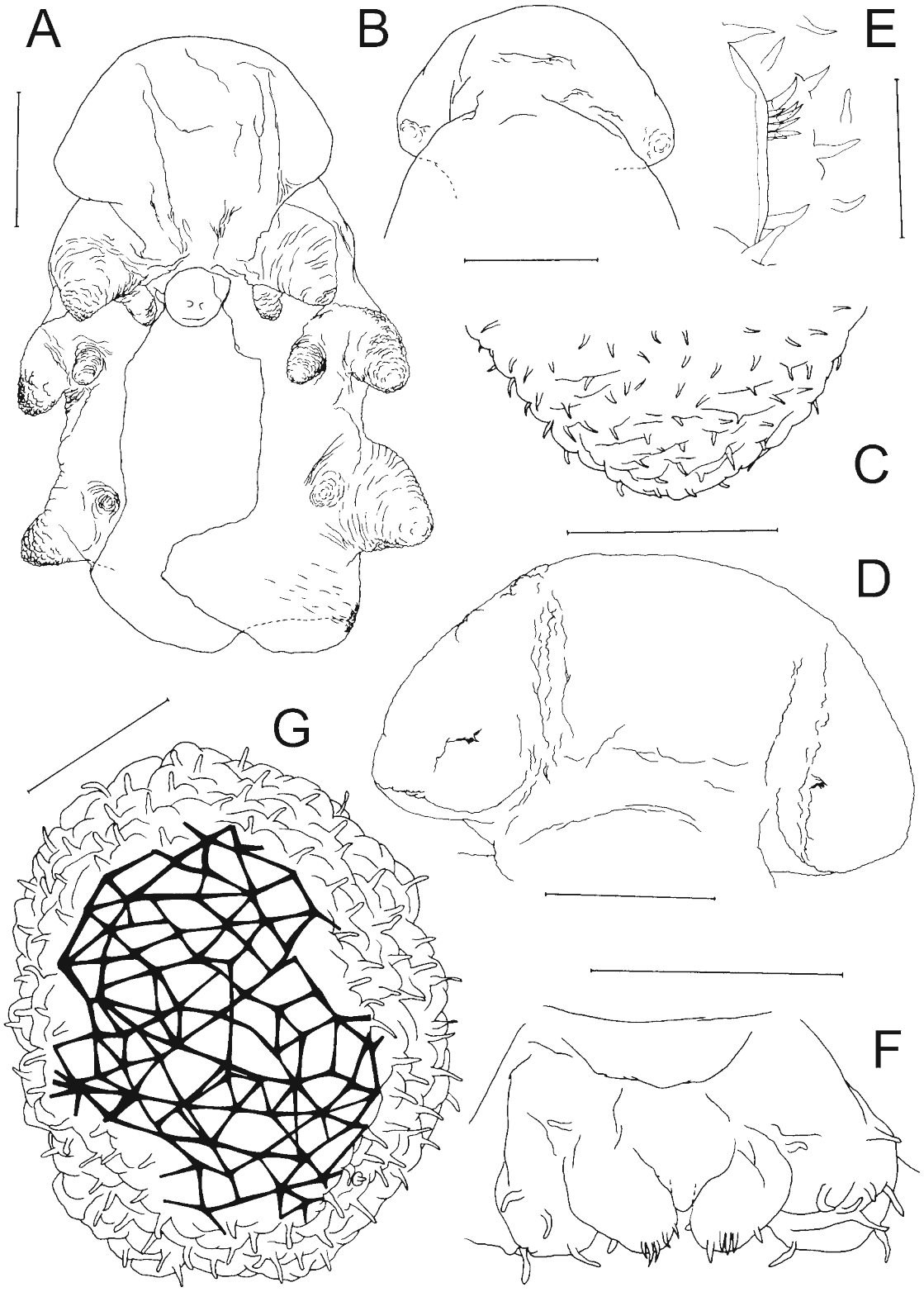

FIGURE 12. *Achelidelphys reducta* (Lafargue and Laubier, 1977) n. comb., holotype female (ZMA CO.106.632). A, Habitus, ventral; B, Cephalosome, dorsal; C, Tip of exopodal lobe of leg 1, showing surface ornamentation. *Achelidelphys stellata* (Lafargue and Laubier, 1977) n. comb., holotype female (ZMA CO.106.630). D, Cephalosome, dorsal; E, Tip of antennulary lobe, showing cluster of setae representing apex of limb; F, Urosome, dorsal; G, Post-rostral lobe, ventral view with surface removed showing internal support network of fibres. Scale bars: A–B = 500 μm, C = 100 μm, D = 200 μm, E–G = 100 μm.

***Achelidelphys reducta* (Lafargue and Laubier, 1977) n. comb.**

Syn: *Syndelphys reducta* Lafargue and Laubier, 1977

Material examined: Holotype female, reg. no. ZMA CO. 106.632.

Differential Diagnosis: Body highly transformed, stellate in appearance due to laterally-directed legs; segmentation indistinct with segmental boundaries marked by superficial folds. Cephalosome with broad convex frontal margin merging laterally into large antennulary lobes (Fig. 12E). Rostrum not defined. Post-rostral median lobe absent. Labrum forming rounded hemispherical lobe. Lateral margin of cephalosome not produced into ridge-like swellings. Antennomedial swellings also absent. Metasome truncated, with urosome hardly extending posterior to origin of leg 4. Legs 1–4 transformed, originating laterally, each occupying entire margin of somite; produced laterally. Mid-ventral metasomal processes between legs lacking. Urosome reduced but apparently 2-segmented, located terminally; incorporating caudal rami (Fig. 12F). Surface of body, labrum, cephalosomic processes, and legs densely ornamented with surface setules.

Antennules represented by large, rounded lobe on either side of strongly convex frontal margin of cephalosome. Oral region lacking any trace of mouthparts. Legs 1 and 2 biramous; rami represented by unsegmented, rounded lobes; exopodal lobe laterally-directed, with broad base, carrying smaller endopodal lobe ventrally. Legs 3 and 4 uniramous, each comprising short, posterolaterally-directed lobe representing exopod. Exopodal lobes of legs 3–4 each housing internally expansion of uterus, containing eggs visible through body wall. Leg 5 absent.

Body length of female approximately 3.05 mm. Male unknown.

Remarks: This species is characterised by the strongly convex frontal margin of the cephalosome lacking a rostrum, combined with the loss of the endopodal lobe of leg 3. The phylogenetic analysis also places this species within the *Achelidelphys*-group (Fig. 14) and does not support the retention of *Syndelphys* as a separate genus. *Achelidelphys reducta* (Lafargue and Laubier, 1977) n. comb. is placed as the sister species of *Achelidelphys stellata* (Lafargue and Laubier, 1977) n. comb. in the analysis primarily because they share the derived, convex form of the frontal margin of the cephalosome.

Genus *Pholeterides* Illg, 1958
***Pholeterides furtiva* Illg, 1958**

Material examined: Paratype females (USNM 92606 and 92606[a]).

Supplementary Description: Illg (1958) provided a full description of the body form and swimming legs of this species. Here we add some details concerning the cephalosomal appendages and caudal rami. Illg (1958: Figure 19a, d) illustrated a claw-like structure (Fig. 13A) with strongly sclerotised tip located on the side of the cephalosome but did not mention it in the text. We interpret this as representing the posterolateral angle of dorsal cephalic shield. The caudal rami (Fig. 13B) are well developed with each ramus bearing a strongly sclerotised claw which carries a small barb on the margin near the tip.

The antenna is 2-segmented. Illg (1958: Figure 19h) described the claw of the antenna as bearing "two reduced setae … inserted at about equal intervals on one of the margins". The paratype material (Fig. 13C) shows the sclerotised curved claw at the tip, with 2 sclerotised triangular plates located near the base of the claw. Adjacent to these are numerous surface elements. We consider it not possible to identify these elements as either true setae or enlarged surface setules from the ornamentation covering the surface of this species. We are unable to accept Illg's interpretation of some of these elements as setae.

The 3 pairs of reduced and transformed mouthparts correspond in general with Illg's description. The only differences are in details of ornamentation. The first limb (Fig. 13D) is represented by a simple tapering lobe, with a wide base armed with 2 setae terminally and 3 setae basally. This appendage is probably the mandible,

represented only by the palp. The second limb (Fig. 13E–F) is indistinctly 3-segmented and bilobed. The basal segment is unarmed. The second segment bears 1 inner seta, 1 outer seta and medial and lateral lobes: medial lobe elongate with 1 long and 1 short seta inserted terminally; lateral lobe smaller and armed with 3 terminal setae. This is probably the maxillule. The third limb (Fig. 13G–H) is indistinctly 4-segmented and ornamented with setules, so distinguishing between true setal elements and ornamentation is problematic. The first segment is large and probably armed with 2 setae near inner distal angle; second segment short with stout lateral seta; third segment armed with 1 elongate seta and 1–2 short elements; distal segment with 2 long and 1 short terminal setae. This is probably the maxilla.

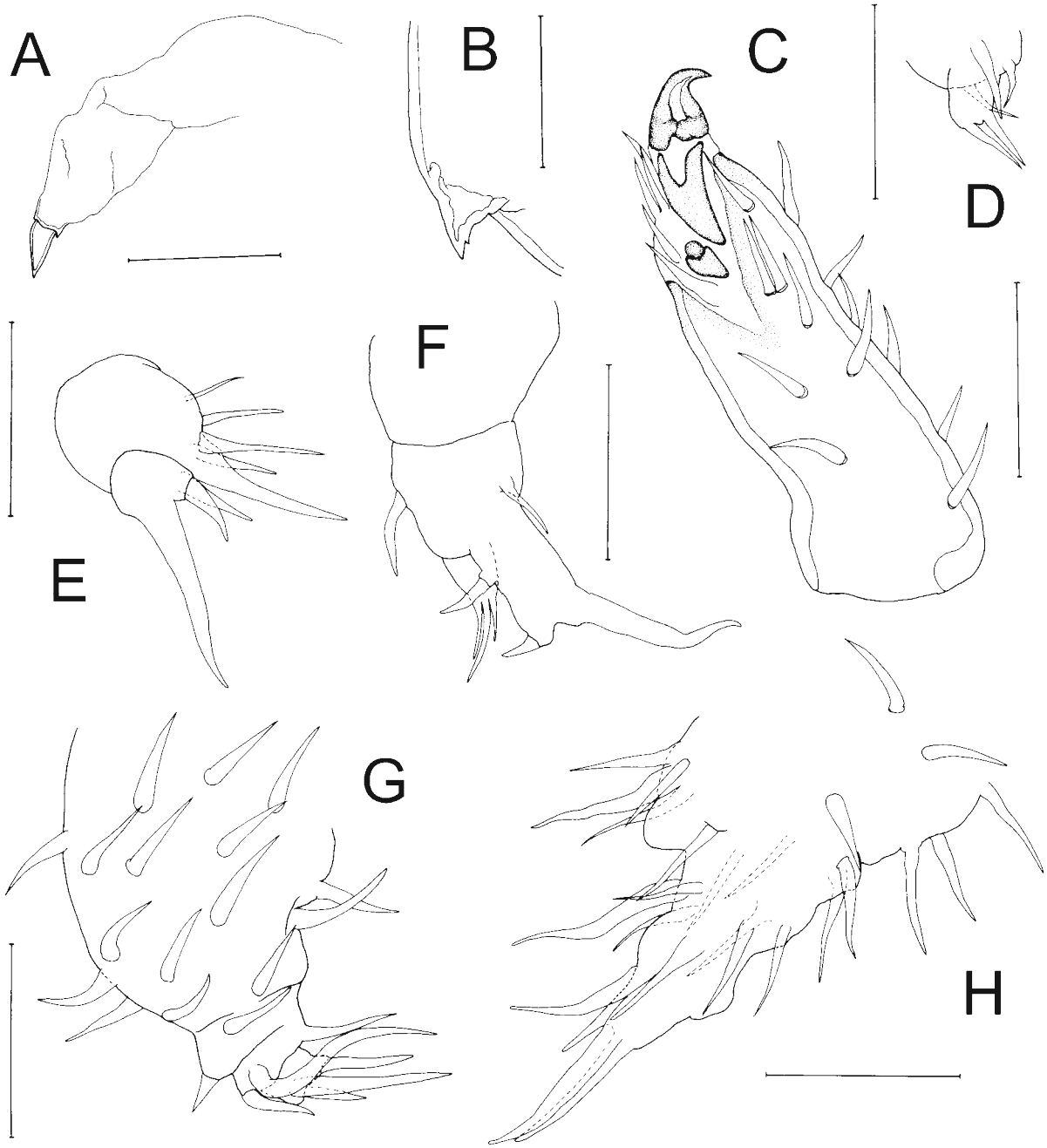

FIGURE 13. *Pholeterides furtiva* Illg, 1958 paratype female (USNM 92606 and 92606[a]). A, Sclerotised angular process representing posterolateral corner of dorsal cephalic shield; B, Caudal ramus; C, Distal part of antenna, with claw and adjacent sclerotised areas stippled; D, First oral appendage; E, Second oral appendage on left side; F, Second oral appendage on right side; G, Third oral appendage on left side; H, Third oral appendage on right side.
Scale bars: A–B = 50 μm, C–H = 25 μm.

Remarks: Illg (1958) was unable to determine the homology of the three pairs of retained mouthparts. We consider it likely that they represent the mandibles to maxillae, with the maxillipeds lacking, but confirmation of this must await the discovery of copepodid stages or males.

Characters for phylogenetic analysis

Body shape

The body comprises a head, metasomal trunk and urosome which is typically reduced and may be incorporated into the metasome. The body lacks expressed external segmentation but the pedigerous somites forming the metasome can be separated by furrows, especially in contracted specimens, that mark the former segmental boundaries.

Character 1. Legs 1–4 originating ventrally / Legs 1–4 originating laterally and laterally-directed, with broad based-exopodal lobes giving body stellate appearance.

Character 2. Metasomal trunk extending posterior to plane of origin of fourth legs by at least 20% of total body length / metasome not extending posteriorly beyond plane of insertion of fourth legs

Character 3. Median ventral process absent / present between second leg pair.

Character 4. Median ventral process absent / present between third leg pair.

Cephalosome

The shape of the head and the presence of paired processes, or unpaired median processes are significant characters, as is the shape and size of the lobate rostrum and the lobate labrum. Rarely the rostrum can apparently be lost, presumably by incorporation into the frontal part of the cephalosome.

Character 5. Frontal margin of head straight or rounded (but not merging into broad lateral antennulary lobes) / strongly convex and merging into anterolateral lobes derived from incorporated antennules.

Character 6. Lateral margin of head simple, without processes or ridges / Lateral margin of cephalosome expanded ventrally to form ridge-like swelling produced into process posteriorly.

Character 7. Cephalosome without swellings or processes medial to antenna / Antennomedial swellings present on ventral surface of cephalosome, with posterior extremity of swelling produced into process.

Character 8. Rostrum small and hemispherical / rostrum elongate / bifid / absent.

Character 9. Post-rostral lobe absent / present on ventral midline between rostrum and labrum.

Character 10. Labrum hemispherical / elongate and posteriorly-directed.

Antennule:

Character 11. Antennule a cylindrical or tapering lobe / bipartite with swollen, multilobed basal part and cylindrical distal part.

Antenna

Character 12. Antenna 2-segmented with sclerotised claw / absent.

Mandible to maxilliped

The possible characters based on the degree of reduction or (more usually) loss of the mouthparts are not included in the phylogenetic analysis due to the difficulty is determining the homology between the various lobes retained around the oral region in some species.

Leg 1:

Character 13. Leg 1 with short protopodal part / protopodal part elongate

Leg 2:

Character 14. Leg 2 with short protopodal part / protopodal part elongate

Leg 3:

Character 15. Leg 3 biramous / leg absent

Character 16. Leg 3 with short protopodal part / protopodal part elongate

Leg 4:

Character 17. Leg 4 biramous / uniramous (endopod lost) / leg absent

Egg Storage system

character 18. Eggs stored in tubular oviduct or expanded sac-like oviduct / eggs stored in multilobate uterus extending at least into exopod of some legs.

Urosome

Character 19. Urosome 4-segmented / urosome at most indistinctly 2-segmented.

Phylogenetic Relationships within *Brementia*-group of genera

The phylogenetic analysis generated ten equally parsimonious trees with a branch length of 34. The strict consensus and majority rule (Fig. 14) trees show four distinct clades which support the current generic classification with regard to *Brementia* and *Anoplodelphys*, but do not support the continued recognition of *Achelidelphys*, *Cephalodelphys* and *Syndelphys* as separate genera. Bootstrap values of 100 support all four of the main clades, with lower values found only within the *Achelidelphys* clade. The proportion of character reversals is low, only 14.7%. The five reversals relate to the shape of the labrum (character 8—two reversals), the shape of the rostrum (character 10) and the shape of the uterus (character 18—two reversals). All of these characters are relatively labile.

The first offshoot is *Brementia* which is a monophyletic taxon defined by the elongate protopodal part of legs 1–3 (derived states of characters 13, 14, and 16). The main lineage is characterised here by the elongate state of the labrum (character 10). The next branch to diverge is *Anoplodelphys*, which is also monophyletic and is defined by the expansion ventrally of the lateral margin of cephalosome, to form ridge-like swelling produced into a process posteriorly (derived state of character 6). *Paranoplodelphys* n. gen. and *Achelidelphys*-*Cephalodelphys*-*Syndelphys* all share the loss of the antenna and the loss of the endopodal lobe of leg 4 or the entire leg (derived states of characters 12 and 17). Members of the *Achelidelphys*-*Cephalodelphys*-*Syndelphys* group all share a stellate body and a truncate metasome (derived states of characters 1 and 2) and form a well defined group, distinct from *Paranoplodelphys*. However, within the group the separation of distinct genera is not supported since *Achelidelphys* would be paraphyletic if *Cephalodelphys* and *Syndelphys* were retained as valid genera (Fig. 14). It is proposed here to treat *Cephalodelphys* and *Syndelphys* as synonyms of *Achelidelphys*. Both these genera were monotypic and upon transfer *Cephalodelphys stellata* Lafargue and Laubier, 1977 becomes *Achelidelphys stellata* (Lafargue and Laubier, 1977) n. comb. and *Syndelphys reducta* Lafargue and Laubier, 1977 becomes *Achelidelphys reducta* (Lafargue and Laubier, 1977) n. comb.

Characters relating to the mouthparts (mandibles to maxillipeds) were not used in the analysis primarily because of the difficulty in determining the homology of the reduced lobate structures present in the oral region of the different taxa. Instead the analysis has been based primarily on the appearance of novel structures and the profound modification of other existing structures. It is interesting, however, to review the distribution of possible mouthpart vestiges across the four main clades recognised (Fig. 14). The *Brementia*-clade comprises *B. balneolensis* which retains vestiges of the entire set of mouthparts, according to Laubier & Lafargue (1974), and *B. illgi* which retains a vestige of the mandible and a pair of tiny lobes of indeterminate homology. There is, therefore, considerable loss of mouthparts within the *Brementia*-clade.

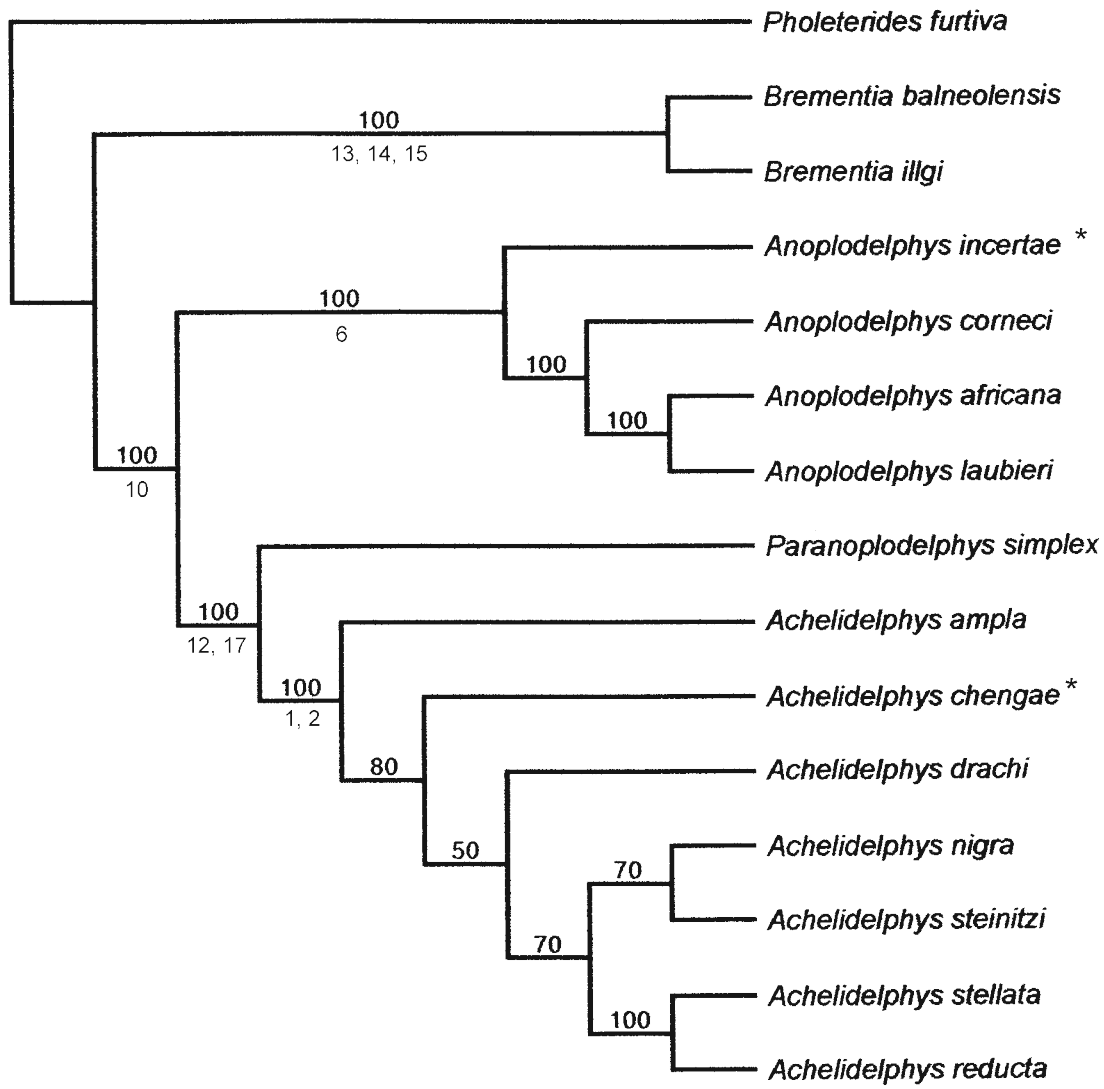

FIGURE 14. Majority rule consensus tree showing estimated relationships between genera of *Brementia*-group with the family Notodelphyidae. The tree is the consensus of 10 equally parsimonious trees (branch length = 34). Values given above line are bootstrap values. Numbers below the line indicate the characters supporting the main clades.
* *Anoplodelphys incertae* represents three taxa: *A. incertae*, *A. galli* and *A.* cf. *galli*, all of which have identical scores for the characters used in the analysis. Similarly, *Achelidelphys chengae* also represents *Achelidelphys papuensis* n. sp. which has identical scores for the characters used.

Within the *Anoplodelphys*-clade vestiges of two or possibly three pairs of oral appendages are retained in *A. africana* n. sp., a single pair of lobes is present in *A. laubieri* and none is present in *A. corneci*, *A. incerta* and *A. galli*. The new genus, *Paranoplodelphys*, is characterised by the most extreme loss of paired limbs, with only the antennules being retained on the entire cephalosome. Similarly, within the *Achelidelphys*-clade there are species, such as *A. stellata*, which retain tiny lobate vestiges apparently representing three pairs of oral appendages, but there are other species, such as *A. reducta*, with none.

All four clades show clear evidence of reduction in mouthparts. There is independent loss of mouthparts within the *Brementia*-clade, within the *Anoplodelphys*-clade, in *Paranoplodelphys*, and within the *Achelidelphys*-clade. Parasitic reduction is a widespread phenomenon and its impact in these endoparasitic notodelphyid genera appears to be reflected primarily in the feeding apparatus (i.e. the mouthparts). With such extensive convergent loss of mouthparts it seems unlikely that the use of mouthpart characters would improve the resolution of the phylogenetic analysis.

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